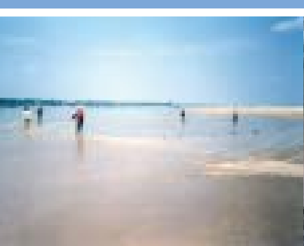
PROCEEDINGS OF THE SECOND INTERNATIONAL SYMPOSIUM ON THE MANAGEMENT OF LARGE RIVERS FOR FISHERIES

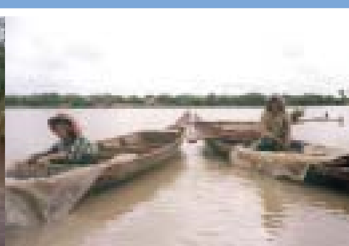
Sustaining Livelihoods and Biodiversity in the New Millennium

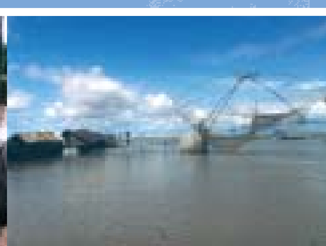
11th – 14th February 2003 in Phnom Penh, Kingdom of Cambodia

Edited by Robin L. Welcomme and T. Petr

Volume II







RAP Publication 2004/17

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VOLUME 2

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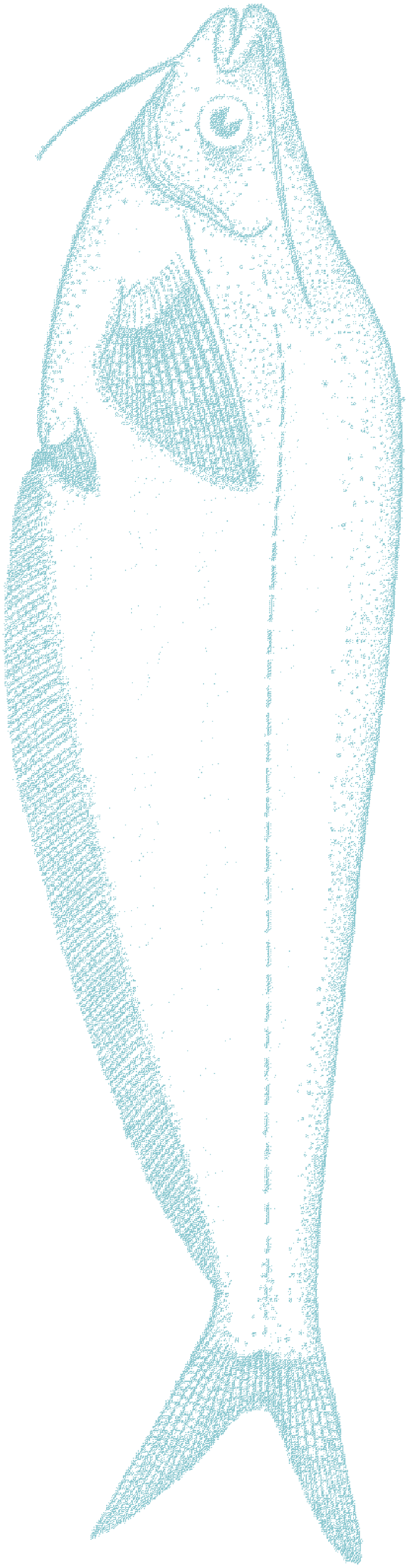
FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
& THE MEKONG RIVER COMMISSION, 2004



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ORIGINS of the SYMPOSIUM

The Second International Symposium on the Management of Large Rivers for Fisheries was held on 11 – 14 February 2003 in Phnom Penh, Kingdom of Cambodia. It had three primary objectives:

- to provide a forum to review and synthesize the latest information on large rivers;
- to raise the political, public and scientific awareness of the importance of river systems, the living aquatic resources they support and the people who depend on them; and
- to contribute to better management, conservation and restoration of the living aquatic resources of large rivers.

The Symposium was organised in six sessions:

Session 1 Status of rivers
Session 2 Value of river fisheries
Session 3 Fisheries ecology and conservation
Session 4 Management of river fisheries
Session 5 Statistics and information
Session 6 Synthesis

Over 220 river scientists and managers from around the world attended the Symposium.
Contributed papers represented 96 rivers from 61 river basins from all continents and climatic zones.

Selected papers submitted to the Symposium appear in these proceedings, which consist of:
Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries: Volume 1
Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries: Volume 2

Papers appearing in these proceedings have been subject to the regular academic refereeing process. Additional selected papers will appear in the journal Fisheries Management and Ecology.

CONTENTS VOLUME II

ECOREGION CONSERVATION FOR FRESHWATER SYSTEMS, WITH A FOCUS ON LARGE RIVERS

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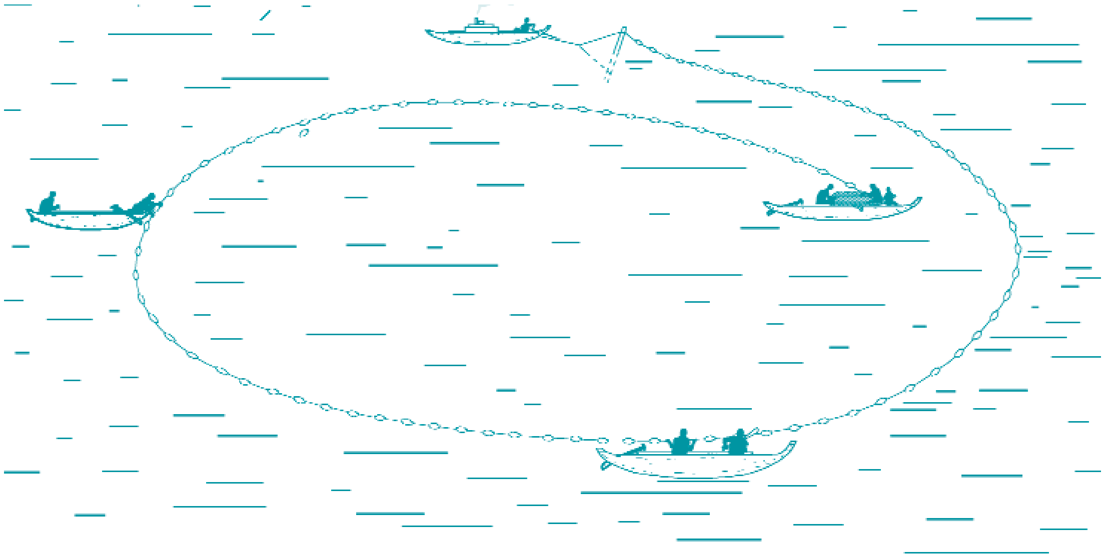


ABSTRACT

Conservation planning with the express purpose of protecting the aquatic biodiversity of large river systems is a relatively new endeavour. A conservation blueprint should be designed around the protection of sufficient habitat for the most wide-ranging and sensitive species and of the physical processes that create and maintain those habitats. WWF and several other organizations have adopted an approach to large-scale planning, referred to as ecoregion conservation (ERC). An ecoregion is a large unit of land or water containing a geographically distinct assemblage of species, natural communities and environmental conditions. The boundaries of an ecoregion encompass an area within which important ecological and evolutionary processes most strongly interact. Large river basins often fit this definition. Conservation strategies that are formulated at the ecoregion scale have the potential to address the fundamental goals of biodiversity conservation: 1) representation of all distinct natural communities within conservation landscapes and protected-area networks; 2)

maintenance of ecological and evolutionary processes that create and sustain biodiversity; 3) maintenance of viable populations of species; and 4) conservation of blocks of natural habitat that are large enough to be resilient to large-scale stochastic and deterministic disturbances as well as to long-term changes. Through ERC we generate a vision for what an ecoregion should look like in 50 years if its biodiversity targets are to be maintained. These targets fall into five main categories: distinct communities, habitats and species assemblages; large expanses of intact habitats and intact native biotas; keystone habitats, species and phenomena; large-scale ecological processes; and species of special concern. The nature of freshwater systems requires that we go beyond identifying discrete aquatic areas on a map. A vision for a freshwater system must take into account the importance of lateral, longitudinal and even vertical connectivity; examine threats originating upland, upstream and even downstream; incorporate strategies for protecting hydrologic processes operating over large scales; and consider the implementation of land-based conservation strategies in the larger catchment. WWF and partners, has undertaken ERC in a number of freshwater systems, including the Amazon, Congo, Niger and lower Mekong Rivers. The many lessons we have derived from our work include the critical need to integrate the expertise of hydrologists with that of biologists, the importance of starting with catchments rather than small "hotspots" and the value of integrating freshwater strategies with parallel efforts in adjacent terrestrial and marine systems. Next steps for our work involve improving the classification of aquatic habitats so that all types can be represented in a conservation blueprint; investigating the habitat requirements and metapopulation structures of select wide-ranging focal species; forecasting future threats like climate change and incorporating that information into our strategies; and conducting research to begin to identify thresholds in land use that translate into threats to aquatic biodiversity.

INTRODUCTION

Conservation planning with the express purpose of protecting the aquatic biodiversity of large river systems is a relatively new endeavour. From headwaters to mouth, these systems typically are characterized by high habitat heterogeneity with corresponding high species richness. Many also support large numbers of endemic species and may be distinguished by ecological phenomena (e.g. large-scale migrations of fish) and evolutionary phenomena (e.g. radiations of multiple species from a common ancestor).

Unfortunately, these systems' large size also hampers the development and implementation of effective conservation strategies. There is consensus within the conservation community that strategies must be scale-appropriate, tailored to the spatial and temporal scales over which ecological processes operate (Fausch *et al*. 2002). Freshwater managers have long recognized the need to take a whole-basin approach to planning, as evidenced by the large number of river and lake basin planning organizations and authorities around the world. However, protecting or restoring hydrological and ecological processes over millions of square kilometres is a daunting task, especially where river systems cross international boundaries. Additionally, freshwater systems are often highly degraded, particularly in their lower reaches, having been modified extensively for irrigation, waste disposal, hydropower, flood control, navigation and other uses. Restoration of these downstream reaches can require enormous expenditures for uncertain conservation returns, but these areas are essential components of a representative suite of conservation priorities (Frissell 1997).

Understanding the trade-offs associated with different conservation strategies is critical for any large-scale planning effort. This is certainly the case for large river or lake systems, where stakeholder dynamics are nearly as complex as ecological dynamics. One well-known, basin-wide approach that focuses on trade-offs is Integrated River Basin Management (IRBM). In past IRBM projects, the maintenance of a reliable and safe water supply for human use has generally taken precedence over the protection of biodiversity, or the goals have been vaguely defined (Hooper and Margerum 2000).

Ecoregion conservation (ERC), a large-scale planning approach adopted by World Wildlife Fund (WWF, known also as the World Wide Fund for Nature) and several other organizations, shares IRBM's whole-system perspective but puts biodiversity solidly first. An ecoregion is a large unit of land or water containing a geographically distinct assemblage of species, natural communities and environmental conditions (Dinerstein *et al.* 1995). The boundaries of an ecoregion encompass an area within which important ecological and evolutionary processes most strongly interact. For aquatic biodiversity, large river basins often fit this definition, though in some cases biogeographic barriers separate a basin into two or more ecoregions, or neighboring basins are biotically similar enough to be combined together (Abell *et al.* 2000; Thieme *et al.* unpublished data).

The first step in ERC is to develop a "biodiversity vision." The vision aims to outline those areas and processes that are essential for maintaining an ecoregion's biodiversity features for at least the next 50 to 100 years. We then build a conservation strategy around this vision, taking into account the range of trade-offs inherent in different options. Beginning with a vision that is firmly grounded in biodiversity targets is one of the characteristics that distinguish ERC from most past IRBM endeavours.

We build a vision around a subset of biodiversity features – targets – that distinguish the ecoregion and/or serve as umbrellas for other features. These targets fall into five main categories:

- Distinct communities, habitats and species assemblages (e.g. "hotspots" of richness or ende-mism);
- Large expanses of intact habitats and intact native biotas (e.g. un-impounded rivers, assemblages without exotics);
- Keystone habitats, species and processes (i.e. features that exert a powerful influence on the composition, structure and function of ecosystems and consequently on biodiversity, such as seasonal flooding);
- Large-scale ecological phenomena (e.g. long-distance migrations of fish);
- Species of special concern (e.g. sensitive species that can serve as focal species for planning).

ERC is applicable to terrestrial, freshwater and marine systems, but the approaches for each realm are somewhat different. A terrestrially focused vision normally identifies a suite of biologically distinct areas for protection (Dinerstein *et al.* 2000), but the nature of freshwater systems requires that we go beyond identifying discrete aquatic areas on a map. A vision for a freshwater system must take into account the importance of lateral, longitudinal and even vertical connectivity; examine threats originating upland, upstream and also downstream; incorporate strategies for protecting hydrologic processes operating over large scales; and consider the implementation of land-based conservation strategies in the larger drainage basin (Abell *et al.* 2002).

Conservation strategies that are formulated at the ecoregion scale have the potential to address the fundamental goals of biodiversity conservation (modified from Noss 1992):

- Representation of all distinct natural communities within conservation landscapes and protected-area networks;
- Maintenance of ecological and evolutionary processes that create and sustain biodiversity;
- Maintenance of viable populations of species; and
- Conservation of blocks of natural habitat large enough to be resilient to large-scale stochastic and deterministic disturbances as well as to long-term changes. These goals, developed for biodiversity conservation in general, are essential for the freshwater realm and for large river systems in particular.

WWF and its partners have undertaken ERC in a number of freshwater systems around the world. Here we review a general methodology that we have developed for applying ERC to freshwater systems and we discuss variations of this methodology as applied to the Congo, Lower Mekong, Amazon and Niger River systems.

GENERAL ERC METHODOLOGY

No two ERC projects have used identical methodologies, due to differences in each ecoregion's ecology and available biodiversity data. Nonetheless, all vision-building efforts share some basic components (Table 1). A more detailed flowchart of steps is given in Abell *et al*. (2002).

The foundation of a vision is a biological assessment:- a record of the distribution of species, communities and habitats in the ecoregion, of ecological processes sustaining this biodiversity and of current and future threats to its maintenance. WWF's approach to ERC focuses on historic, rather than current, distributions of biodiversity features, with the understanding that many of these features have disappeared or are impaired. We take this approach because the vision is intended to go beyond maintaining the status quo, incorporating restoration as a tool where necessary.

WWF has developed maps of freshwater ecoregions for North America and Africa (Abell *et al.* 2000; Thieme *et al.* unpublished data) and is in the process of

Table 1: Basic steps for developing a freshwater biodiversity vision through ERC

Representation groundwork
■ Develop representation decision rules
■ Refine ecoregion boundaries and define biogeographic sub-ecoregions
■ Identify habitat types for representation analysis or map habitats across ecoregion
Biological importance
■ Generate overall map of important areas
■ Identify and delineate areas (e.g. river reaches, wetlands) of biological importance
■ Assign levels of importance to areas based on their relative contribution to maintaining the ecoregion's biodiversity targets
■ Identify and delineate areas (including terrestrial) that are important for maintaining abiotic processes (e.g. hydrologically active areas)
Ecological integrity
■ Assign levels of ecological integrity to important areas
■ Map threats to aquatic biodiversity across the region of analysis (including terrestrial and/or marine areas)
■ Evaluate ecological integrity of important areas, based on habitat intactness and population/species viability
Prioritization
■ Prioritize among important areas based on the combination of biological importance and ecological integrity levels
Representation analysis
■ Conduct a representation analysis to ensure that all biogeographic sub-ecoregions and naturally occurring habitat types are sufficiently represented in the suite of priority areas; add to the priority areas to achieve representation, if necessary

Connectivity

- Evaluate connectivity of the priority areas based on the dispersal and migratory requirements of focal species; add corridors/linkage areas to achieve connectivity, if necessary

Future threats

- Evaluate future threats to the priority areas and across the ecoregion

Conservation interventions

- Develop specific recommendations for conservation interventions in the priority areas
- Develop recommendations for broad conservation interventions (e.g. aimed at all riparian zones across the ecoregion)

Biodiversity vision

- Evaluate if the recommendations, if implemented, would achieve protection of the ecoregion's biodiversity over the long term (50 years)
- Modify the recommendations, if necessary, to achieve a sufficiently ambitious biodiversity vision

finalizing a global ecoregion map (Abell *et al.* unpublished data). Ecoregion delineations are based on biogeography of freshwater taxa, with an emphasis on the distribution of freshwater fishes. These delineations are relatively coarse and a first step for an ERC project team is to revise the boundaries of its ecoregion based on more detailed information and regional expertise. For ecoregions that cover one or more sub-basins of a larger river or lake drainage basin, an ERC team may choose to extend the visioning effort to cover multiple ecoregions, in order to capture the entire area over which hydrological processes occur. Similarly, an ERC effort for a riverine ecoregion with diadromous species (e.g. salmon) might consider the adjoining marine environment in its region of analysis.

Most ecoregions are sufficiently large and biologically complex to justify dividing them further into biogeographic sub-ecoregions. We define sub-ecoregions for the purposes of achieving representation. If sub-ecoregions contain different species assemblages, then we should have examples from each sub-ecoregion in the vision's ultimate set of priorities.

A second, finer representation filter relates to habitats. In each sub-ecoregion, our goal is to capture examples of all naturally occurring habitats. This approach is based on the assumption that, as with sub-ecoregions, different habitat types typically support different species assemblages. Habitat types can be mapped and classified across the entire ecoregion using satellite imagery or other data layers (van Niewenhuizen and Day 2000; Higgins 1999). Alternately, experts can assign habitat type designations to areas, based on a pre-defined list.

Representation goals – the number of habitat occurrences that should be protected in each sub-ecoregion and the size or other minimum quality that the occurrences must achieve – are specific to each ecoregion. Goals are often set based on the habitat needs of focal species, which serve as umbrellas for other taxa. A variety of criteria can be used to select focal species (Table 2). Most often these species are either wide-ranging, sensitive, or both. We attempt to define the minimum characteristics that an area would need if it were to support a viable population of the focal species.

Table 2: Attributes of focal species

Biological characteristics
1. Climatic sensitivity
2. Sensitive to pollution
3. Low reproductive rate
4. Limited dispersal ability
5. Space-demanding/wide-ranging
6. Migratory, with specialized spawning sites
7. Large-bodied/largest member of feeding guild
8. Dependent upon rare, widely dispersed habitat
9. Narrow temperature or water chemistry requirements
10. Adapted to particular flow regime, water level, flood cycle
11. Specialized dietary, habitat requirements (particularly breeding, nursery sites)
12. Population seasonally/daily concentrated and/or aggregates during part of life cycle

Population status
1. Population small or declining
2. Meta-populations with unique genetic compositions

Human-impact factors
1. New and large markets for consumptive use
2. Habitat threatened by loss, conversion, degradation, or fragmentation
3. Population threatened by direct exploitation, harassment, or ecological interactions

Once this groundwork is complete, the assessment can proceed with the identification of biologically important areas. Biologially important areas are those places, such as certain river reaches, headwater drainages, wetlands, or waterfalls, that are known (or highly suspected) to support one or more identified targets. For example, a given river reach may be distinguished by high species richness or endemism in one or more taxonomic groups; it may provide habitat for an endemic genus or even family; it may support an unusually intact species assemblage; it may represent one of the last remaining large expanses of intact habitat; it may be one of few areas where ecological processes like flooding and associated migrations occur; it may serve as an important refuge or source pool for keystone species; it may contain a rare habitat type; or it may harbor one or more species of special concern.

Typically, experts from a variety of disciplines use published and unpublished data, combined with their own observations, to identify these important areas. A strong expert group is knowledgeable about a range of taxa representing the most important biotic components of the ecoregion (Table 3). Maps of important areas for different taxa (e.g. fish, molluscs, amphibians) are often produced separately and then combined with other maps (e.g. important floodplains) to create a single depiction of areas of biological importance.

In many of the world's river systems, however, there are scant species and assemblage data to inform

Table 3: Taxonomic groups to consider for a freshwater ERC assessment (modified from Abell *et al.* 2002)

Waterbirds
1. Aquatic plants
2. Freshwater fish
3. Aquatic mammals
4. Trichoptera (caddisflies)
5. Ephemeroptera (mayflies)
6. Aquatic and semi-aquatic reptiles
7. Amphibians with aquatic life stages
8. Odonata (dragonflies and damselflies)
9. Diptera (mosquitoes, black flies, midges)
10. Neuroptera (hellgrammites, dobsonflies, alderflies)
11. Crustaceans (crabs, lobsters, copepods, ostracods)
12. Aquatic and/or wetland molluscs (snails and mussels)
13. Coleoptera (diving beetles, riffle beetles, whirligig beetles)
14. Hemiptera (backswimmers, diving bugs, water striders, water scorpions)

this process of identifying important places. Where data are lacking, sub-ecoregions and habitat classifications can serve as proxies. In this situation, we recommend identifying areas of biological importance based on size, intactness, connectivity, or other attributes, making sure that the areas cover all habitat types occurring naturally in all sub-ecoregions.

Areas of high biological importance cannot be protected if hydrologic and other abiotic processes fail to function within their natural ranges of variation. Maintaining these processes requires looking upstream and upland from the biologically important areas. Methodologies for identifying such "abiotic" areas are crude but evolving and almost by necessity must rely on models for large river systems. For a given ecoregion, consultation with hydrologists, biogeochemists and other physical scientists is essential, both to identify the critical processes and interpret any model outputs.

Important areas for biological targets and abiotic processes are often collectively referred to as "candidate priority areas." These areas are usually each assigned a level of importance (highest, high, moderate) based on their relative contribution to maintaining the ecoregion's biodiversity features. This classification helps to differentiate among the areas during the later prioritisation process.

The other major input to prioritisation is an evaluation of the areas' ecological integrity. Habitat in the areas can range from virtually intact to critically degraded. Even intact areas, however, may be unable to support viable populations of species over the long term because of insufficiencies of size, connectivity, or other characteristics. An evaluation of ecological integrity, in the context of ERC, incorporates both habitat intactness and the likelihood that the species and communities in that area can endure over the long term, barring additional disturbances. We call this latter attribute "population/species persistence." Levels of ecological integrity (e.g. intact, altered/degraded/ highly degraded) are assigned to each important area based on assessments of habitat intactness and population/species persistence.

An evaluation of habitat intactness normally combines an analysis of geospatial data with expert assessment. A wide variety of geospatial information can be used (Table 4), though not all possible measures (Table 5) will be relevant to or available for a given ecoregion. Most, though not all, geospatial information and measures will relate to activities on the terrestrial landscape resulting in altered flow regimes and water quality. The analysis of habitat intactness, then, is typically conducted across each of the important areas' watersheds.

Table 4: Possible geospatial data layers to inform an evaluation of habitat intactness

Biotic	Abiotic
1. Indigenous areas	1. Roads
2. Vegetation/land cover	2. Canals
3. Areas of deforestation	3. Railroads
4. Aquaculture operations	4. Refineries
5. Cattle/livestock densities	5. Toxic sites
6. Human population density	6. Major ports
7. Species distributions (e.g. IBAs)	7. Industrial sites
8. Ranges of exotic species or areas of known introductions	8. Protected areas
	9. Fishing centres
	10. Towns and cities
	11. Areas of conflict
	12. Drainage projects

13. Water temperature
14. Runoff (by grid cell)
15. Pesticide application
16. Extent of floodplains
17. Power generation plants
18. Discharge (by river segment)
19. Water abstractions/Water use
20. Channelized or dyked streams
21. Erosion potential (by grid cell)
22. Pipelines (present and planned)
23. Sediment transfer (by grid cell)
24. Land uses (current and historic)
25. Mining activity and concessions
26. Logging activity and concessions
27. Irrigated and non-irrigated croplands
28. Fish passage devices (working and failing)
29. Inter-basin water transfers (present and planned)
30. River network (e.g. derived from Digital Elevation Model)
31. Impoundments and reservoirs (present and planned), plus additional barriers to passage

Table 5: Possible geospatial analyses for an assessment of habitat intactness. Additional examples are given in Abell *et al*. (2002)

1. Percentage of area grazed, by sub-basin
2. Average population density, by sub-basin
3. Length or area of floodplain habitat cut off from river
4. Urban expansion or population growth, by sub-basin
5. Sediment contribution or erosion potential, by sub-basin
6. Number of impoundments per stream length, by sub-basin
7. Road density or number of road-stream crossings, by sub-basin
8. Number of pipeline-stream crossings, or length of pipeline, by sub-basin
9. Average discharge, flow accumulation, or runoff of grid cells, by sub-basin
10. Length or percentage of streams with riparian vegetation cover, by sub-basin
11. Degree of protected area coverage (all areas, or only aquatic habitats), by sub-basin
12. Number or coverage of mining, logging, or other resource extraction operations, by sub-basin
13. Percentage of land-use classes within fixed-width buffer of streams or other water bodies, by sub-basin
14. Percentage of land-use classes, by sub-basin (e.g. 20 percent forest, 40 percent agriculture, 10 percent urban)
15. Percentage of headwaters (defined by elevation, gradient, stream order) with original land cover, by sub-basin
16. Number or length of free-flowing streams, divided by number or length of impounded streams, by sub-basin
17. Length of stream habitat lost as a result of channelization (requires historic and current stream morphology maps)
18. Length of stream flooded by impoundments, or length of stream above impoundments made inaccessible to migrating species, by sub-basin

Evaluating the population/species persistence of a given area is more of a challenge than evaluating its habitat intactness, because we generally have little or no information about species' life cycles, habitat requirements and metapopulation structures. Layering that information for all or a subset of species historically occurring in the area would allow evaluation of the overall population/species persistence of the area. For obvious reasons, detailed assessments like these are many years off. Where there is literally no information available to evaluate population/species persistence, the assessment of habitat intactness can be used alone to signify ecological integrity.

Biological importance and ecological integrity levels are typically the two main inputs used to prioritise among important areas. A matrix with levels of importance on one axis and levels of ecological integrity on the other provides a simple tool for assigning priority levels. ERC teams have often chosen to take a "triage" approach, assigning lower priority to those areas considered to be highly degraded and probably beyond repair (Table 6). An alternative approach might assign highest priority both to those degraded areas most urgently in need of protection to stem further habitat loss and to those intact areas representing rare opportunities for preservation. Once the matrix is designed, priorities are assigned to important areas to highlight those that should be given attention first.

Table 6: Example of an integration matrix for assigning priority levels to important areas

Ecological Integrity	Biological Importance		
	High	Medium	Low
Intact	I	II	III
Altered/degraded	I	II	III
Highly degraded	II	III	IV

This ERC effort focused only the subset of Amazonian rivers with associated flooded forests or grasslands.

Following the prioritisation, a representation analysis is undertaken to ensure that all sub-ecoregions and habitat types have been captured in the suite of priorities. Elevating the priority level of certain areas or adding new areas to the set fills gaps in representation.

Similarly, new areas may be added to address issues of connectivity. Important areas that are functionally isolated could theoretically be reconnected through the restoration of intervening areas or the removal of a structural barrier.

This process yields a set of areas – a combination of linear and polygonal features – that represent those parts of the ecoregion that are most important from a biodiversity conservation perspective. This collection of places does not necessarily constitute a vision. There remain the issues of impending threats, conservation interventions for the important areas and conservation strategies needed more broadly within the ecoregion and perhaps even outside of it.

Forecasting future threats – their form, direction, location and magnitude – is an inexact science, but developing a conservation plan without an eye to the future is surely shortsighted. Some future threats, such as structural developments and land concessions, are gazetted and thus have a degree of predictability. Others, such as population growth, may be forecasted based on current trends. Climate change models can yield predictions about future changes in water availability and water temperature over large scales, providing an idea of possible impacts and their extent; different models, however, often show inconsistencies in their results, which demand careful interpretation. We recommend combining quantitative information with expert assessment to identify those areas in need of urgent attention if impending threats are to be forestalled. A future threats assessment can also suggest actions to be implemented across the ecoregion.

With information on current and future threats, it is possible to recommend conservation interventions for each important area, for the ecoregion as a whole and for areas of intermediate size. These recommendations will likely relate to the type of protection required (e.g. creating buffer zones along a river, reducing water withdrawals), rather than to the exact approach (e.g. land purchases, regulations) for achieving it.

The biodiversity vision is the sum total of these outputs. An ERC team looks at the final set of recommendations and evaluates if these actions would, in its best judgement, result in protection of the ecoregion's biodiversity features over the long term. If not, then the vision is probably not ambitious enough and requires modification. Once the vision is complete, the next step is development of an actual implementation strategy, based on a host of biological and socio-economic considerations. A vision, though, should never be so final that new scientific and socio-economic information cannot be incorporated as it becomes available.

APPLICATION OF THE ERC APPROACH TO SPECIFIC LARGE RIVER SYSTEMS

The approach described above is based on a theoretical ecoregion. In the real world, especially for large river systems, data and expertise limitations prevent undertaking many of the steps. Here we briefly describe the variations that resulted from applying ERC to the Congo, Lower Mekong, Amazon and Niger River systems.

Our first major attempts to apply ERC to large rivers were for the Congo and Lower Mekong systems. These efforts were undertaken consecutively, in March 2000. In each of these situations, we relied solely on expert assessment workshops to develop visions, with few geospatial data sets available to inform the process. Each of the workshops lasted three days and the expert groups were comprised of about a dozen individuals each. Experts identified biologically important areas on maps, evaluated the areas' ecological integrity and developed recommendations for those areas and the ecoregion as a whole. Data insufficiencies required the experts to take coarse approaches and their frustration with the lack of information led them to focus their recommendations largely on how to fill data gaps.

Within the Amazon River system, with its vast size and almost complete lack of species data for all but a few locations, we took a different approach based almost entirely on geospatial data. Instead of identifying important areas for biodiversity, a team of scientists first divided the basin into sub-ecoregions, for the purposes of representation. They then divided the sub-ecoregions into major sub-basins, which were the units of analysis for the remainder of the assessment. Landsat TM imagery was used to map habitat types within the floodplains and associated rivers. Biological importance for each sub-basin was based on a combination of calculated habitat diversity (applying a Shannon-Weaver Index), the presence and extent of special habitats (lakes, secondary rivers, islands, cataracts) and the results of prior biodiversity assessments (i.e. PROBIO and ProVárzea/PPG7).

Ecological integrity of the Amazonian sub-basins was also assessed primarily as a function of geospatial indicators. These indicators were percent natural vegetation coverage within floodplain habitats; percent natural vegetation coverage within each sub-basin; size of population centres within each sub-basin; presence and assessed degree of impact of urban, petroleum, mining and farming within each sub-basin; and number and location of dams within each sub-basin. Population/species persistence was not explicitly addressed. The biological importance and ecological integrity values were used to identify a highest priority sub-basin in each sub-ecoregion, in order to achieve representation at a very coarse scale. Additional areas were added to achieve connectivity within the Amazon River main stem.

To identify major threats and opportunities for each priority sub-basin, experts again relied heavily on geospatial data and developed general recommendations for conservation interventions. The next step will be conducting more detailed assessments of the priority sub-basins to identify smaller priority areas. In effect, the ERC process will be repeated for these sub-basins, most of which are as large as entire ecoregions found elsewhere.

The Niger River Basin effort differed from the Congo, Mekong and Amazon efforts in two ways: it used a more balanced combination of expert assessment and geospatial data and it explicitly included hydrological considerations. The experts were provided with hardcopy maps displaying land cover (USGS 2001), protected areas (WWF data), roads (ESRI 1993), Important Bird Areas (BirdLife International data), dams (FAO 2001), agricultural suitability (FAO 2000) and population density (ORNL 2001). Data on runoff generation from a global hydrological model, provided by the University of Kassel, Germany (Döll, Kaspar and Lehner 2003), were used as a starting point for discussions about which sub-basins were most important for maintaining the flow regime.

Three taxonomic expert groups (for fish, birds and other vertebrates) and one for hydrological processes worked to delineate areas of importance across the Niger Basin. The experts selected 19 priority areas for conservation action. They assigned a level of threat to each area and developed a list of conservation actions that should be undertaken in the priority areas and at the level of the basin.

The visions for these four river systems are in various stages of completion (Baltzer, Nguyen Thi Dao and Shore 2001; WWF 2001; WWF 2002; Wetlands International unpublished data). Maps illustrating the results are available upon request from WWF.

DISCUSSION

Our experiences applying ERC to the four river systems of the Congo, Lower Mekong, Amazon and Niger have taught us a range of lessons. We have incorporated these lessons into each successive effort, but the nature of ERC is that all ecoregions present unique circumstances that require flexibility and innovation.

The most important and perhaps obvious, lesson is that terrestrial approaches to ERC translate imperfectly to freshwater systems. For instance, evaluating the ecological integrity of an aquatic area requires looking beyond it, since upland, upstream and downstream activities affect it and barriers to dispersal and migration can be impassable. Terrestrial areas are affected by activities outside their boundaries, but most often to a lesser extent.

A second lesson relates to the importance of expanding our analysis beyond pure biological information. Ever since we first applied ERC to freshwater systems, we have known that a robust vision must incorporate information on hydrologic processes. But, it was only with the Niger River Basin effort that quantitative hydrologic information was used and to relatively good effect. However, the global hydrologic dataset used for the modelling was coarse and the project would have benefited from the development of finer-scale data. The Niger experience has also taught us the value of explicitly linking the hydrological and biological parts of an assessment and in future efforts we intend to identify those places with the greatest hydrologic impact on biologically important areas.

In general, the inclusion of one or more hydrologists and perhaps biochemists as well, may be the most important way that an ERC team can improve upon a standard visioning process. Aquatic biologists and physical scientists rarely have opportunities to interact and many hydrologists have never been challenged to put their expertise to use in biodiversity conservation. Conserving aquatic biodiversity is as much about maintaining physical processes as it is about focusing on species.

All four ERC efforts have underscored the importance of entering an assessment effort with as much geospatial data on hand as possible. The most successful efforts have allowed experts to use and react to map-based information and to the results of geospatial analyses. In an ideal situation, a geographic information system (GIS) would be employed to divide an ecoregion into component sub-basins; the optimal scale of these sub-basins would vary by ecoregion according to the precision of digital elevation models and the scale of available geospatial data (e.g. there is no need to delineate very small sub-basins if land cover data are at a coarser scale). A variety of calculations related to the distribution of habitat types and threats could be undertaken for each sub-basin prior to an assessment, in order to inform it.

Geospatial data have weaknesses as well as strengths. They provide relatively standardized information about parts of ecoregions with which experts are unfamiliar and they allow for quantitative measures. On the other hand, geospatial data will always only be a proxy for direct measures of habitat intactness. They can also be outdated, inaccurate, or misleading (e.g. when a protected area is in fact no more than a paper park).

Expert assessment can complement and validate the results of a geospatial analysis, because experts make their assessments based on observations of actual aquatic habitats. But, because aquatic biologists may be unfamiliar with land-based threats occurring at a distance from their study sites, it is important to involve additional individuals with a detailed knowledge of activities occurring on the landscape. A usual challenge is finding experts who understand how specific land uses affect aquatic species and habitats (e.g. how plantation forest differs from native forest in terms of hydrologic and nutrient flows).

We have also learned the value of a pre-assessment habitat classification in enabling an automatic representation analysis once priority areas are delineated. A sophisticated classification would go beyond simply identifying different habitat types on a map and would assign classes based on similarities of geomorphology, ecological processes and environmental gradients (Higgins *et al*. 1999). Of course, the accuracy of these classifications must be ultimately checked on the ground, a task that can be daunting for remote, isolated areas of large river systems.

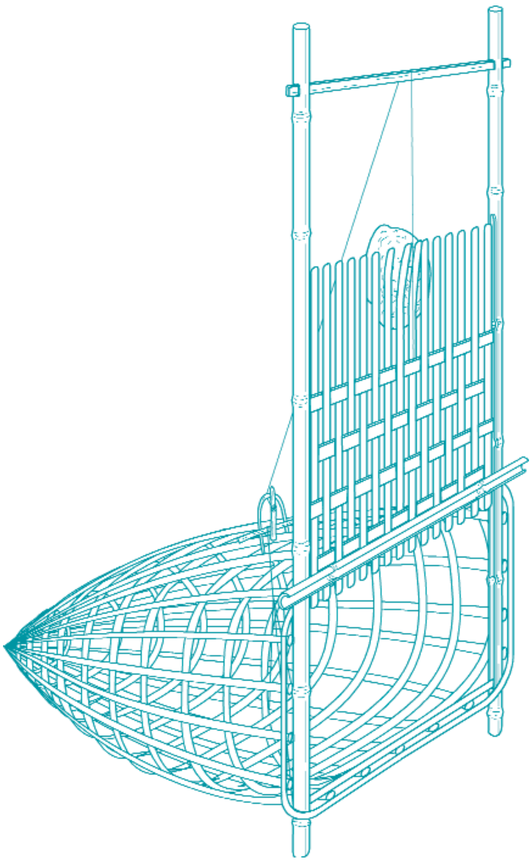
Habitat classifications and geospatial analyses cannot replace expert assessments entirely, but for ecoregions where biodiversity data are virtually nonexistent and experts are unfamiliar with large areas, the classifications and analyses can provide a preferred alternative to guesswork. Ecoregions that are the most data-poor in terms of biological information can be least suited to expert assessment, because the experts have a frustratingly small amount of information on which to base their decisions. In these cases, data surrogates and/or predictive models can provide a first cut at an assessment and experts can then review the results. On the other end of the spectrum, an ecoregion that is data-rich, with comprehensive information on species distributions, is a good candidate for the use of a systematic algorithm to assist priority-setting (Margules and Pressey 2000). In the middle are those ecoregions where some species and habitat distribution data exist, but data are not available for the entire region of analysis or they are largely unpublished. In this case, an expert workshop may be the most appropriate approach for conducting an assessment.

Our experiences in the Congo, Lower Mekong and Amazon have reinforced the value of integrating freshwater strategies with parallel efforts in adjacent terrestrial and marine systems. These realms are intimately connected, yet we tend to pursue independent planning efforts due to resource limitations, a lack of crossover expertise and a need to highlight the conservation of normally neglected aquatic biodiversity. Integrating separately derived results into a single vision is possible, but a true integration of planning for freshwater, marine and terrestrial biodiversity requires more than a simple overlay of priority areas. Incorporating hydrologic concerns into terrestrial and even marine planning may provide a good platform for a true integration.

Our methodology for conducting biological assessments and developing biodiversity visions in freshwater systems is still quite young and is evolving rapidly. We expect to improve our approach to classifying aquatic habitats by working with partners like The Nature Conservancy, which has developed a methodology for habitat classification in data-rich systems. We hope to catalyze investigations of the habitat requirements and metapopulation structures of select wide-ranging focal species, like the giant Mekong catfish (*Pangasianodon gigas* (Chevey), with the intention of exporting methodologies for species investigations in other similar systems. We are developing tools for forecasting future threats and incorporating that information into our strategies; climate change in particular is expected to have drastic consequences for aquatic biota in certain regions, yet we have failed to incorporate this information into the design of conservation plans. Finally, we hope to conduct research aimed at identifying thresholds in land use that translate into threats to aquatic biodiversity, so that we can begin to answer the critical question of ERC, "How much is enough?"

ACKNOWLEDGEMENTS

Presentation of this paper was made possible by the support of Jamie Pittock of WWF's Living Waters Programme and Marc Goichot of WWF's Mekong Programme. We would like to thank those individuals within WWF and its partner organizations who have led ecoregion conservation efforts in the Amazon, Lower Mekong, Congo and Niger River systems.



REFERENCES

Abell R.A., Olson D.M., Dinerstein E., Hurley P.T., Diggs J.T., Eichbaum W., Walters S., Wettengel W., Allnutt T., Loucks J.J. & Hedao P. 2000. *Freshwater Ecoregions of North America: A Conservation Assessment.* Washington, DC, Island Press.

Abell R., Thieme M. Dinerstein E., & Olson D. 2002. A Sourcebook for Conducting Biological Assessments and Developing Biodiversity Visions for Ecoregion Conservation. Volume II: Freshwater Ecoregions. Washington, DC, World Wildlife Fund. Available online at: www.wwfus.org/science/freshwater.cfml.

Baltzer M.C. Nguyen Thi Dao & Shore R.G. eds. 2001. Towards A Vision for Biodiversity Conservation in the Forests of the Lower Mekong Ecoregion Complex. WWF Indochina/WWF US, Hanoi and Washington.

Dinerstein E.G., Powell D., Olson E., Wikramanayake R., Abell C., Loucks E., Underwood, Allnutt T., Wettengel W., Ricketts T., Strand H., O'Connor S. & Burgess N. 2000. *A workbook for conducting biological assessments and developing biodiversity visions for ecoregion-based conservation. Volume I: Terrestrial Ecoregions.*Washington, DC, World Wildlife Fund.

Dinerstein E., Olson D.M., Graham D.J., Webster A.L., Primm S.A., Bookbinder M.P. & Ledec G. 1995. *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean.*Washington, DC, The World Bank.

Döll P., Kaspar F., & Lehner B. 2003. A global hydrological model for deriving water availability indicators: Model tuning and validation. *Journal of Hydrology*, 270: 105-134.

Environmental Systems Research Institute (ESRI) 1993. *Digital chart of the world*. Redlands, California, Environmental Systems Research Institute.

Fausch K.D., Torgensen C.E., Baxter C.V. & Li H.W. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience*, 52: 483-498.

Food and Agricultural Organization of the United Nations (FAO). 2000. Global Agro-Ecological Zones Global - AEZ. Rome, Italy and Laxenburg, Austria: FAO and International Institute for Applied Systems Analysis IIASA. (Available at: http://www.iiasa.ac.at/Research/LUC/GAEZ/index.htm.)

Food and Agricultural Organization of the United Nations (FAO). 2001. Atlas of Water Resources and Irrigation in Africa. Land and Water Digital Media Series CD 13. Rome, FAO. (Available at: http://www.fao.org/landandwater/lwdms.stm.)

Frissell C.A. 1997. Ecological principles. *In* J.E. Williams, C.A. Wood & M.P. Dombeck eds. *Watershed Restoration: Principles and Practices*. Bethesda, Maryland, American Fisheries Society: 96-115.

Higgins J. Lammert M. & Bryer M. 1999. Update No. 6: Including aquatic targets in ecoregional portfolios: Guidance for ecoregional planning teams. *In Designing a geographaphy of hope update: Reflections of current thinking and conversations*. Arlington, Virginia, The Nature Conservancy.

Hooper B.P. & Margerum R.D. 2000. Integrated watershed management for river conservation: Perspectives from experiences in Australia and the United States. *In* P.J. Boon, B.R. Davies & G.E. Petts eds. *Global Perspectives on River Conservation: Science, Policy and Practice*. New York, John Wiley & Sons. pp. 509-517.

Margules C.R. & Pressey R.L. 2000. Systematic conservation planning. *Nature*, 405:243-253.

Noss R.F. 1992. The Wildlands Project: Land conservation strategy. *Wild Earth Special Issue – The Wildlands Project* 10-25.

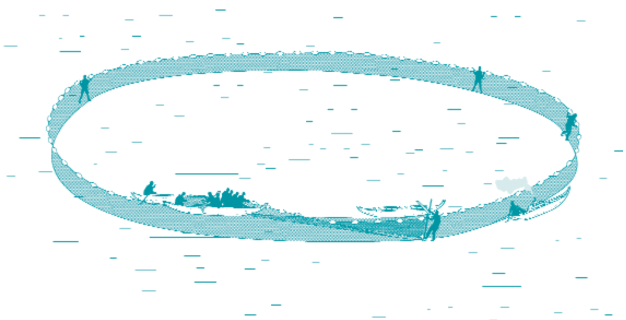
Oak Ridge National Laboratory ORNL 2001. Landscan 2001 Global Population Database. (Available at: http://www.ornl.gov/gist/landscan/index.html.)

United States Geological Survey USGS, IGBP 2001. Global Land Cover Characterization. (Available at: http://edcdaac.usgs.gov/glcc/glcc.html.)

Van Nieuwenhuizen G.D.P. & Day J.A. eds. 2000. Cape Action plan for the environment: The conservation of freshwater ecosystems in the Cape Floral Kingdom. Cape Town, SA, Freshwater Research Unit, University of Cape Town.

WWF 2001. *Biological Priorities for Conservation in the Guinean-Congolian Forest and Freshwater Region*.Washington, DC, WWF-US/CARPO.

WWF 2002. Biodiversity vision for the Amazon River and Floodplain Ecoregion. Technical report.Washington, DC, WWF-US. 86 pp.



THE COMMERCIAL FISHING SECTOR IN THE REGIONAL ECONOMY OF THE BRAZILIAN AMAZON

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ABSTRACT

The purpose of this study was to determine the magnitude of the fisheries sector along the Amazon River in Brazil. Total income and employment were estimated for the principal activities comprising the fisheries sector: fish processing plants, stores selling fishing material, gas stations, restaurants, ice factories and boatyards. Businesses were interviewed in 15 cities along the Amazon River. The number of fishing boats and total catch were estimated using data from the Brazilian Coast Guard (Capitania dos Portos) and fish landings data collected in 7 cities. Results show that the fisheries sector generates R$389 million yr^{-1} and 168 315 jobs. The major share of employment was generated by subsistence and commercial fishing activity, while most income was generated by the processing industry. It was also estimated that 7 531 fishing boats landed 83 847 tonnes in towns along the Amazon River.

INTRODUCTION

Fisheries have long played an important role in the Amazonian regional economy both for subsistence and trade. In recent decades, a modern commercial fishery has developed, as a result of technological changes and the growth of urban markets and exports. This is transforming Amazon fisheries. In the process total catch and direct and indirect employment and income have grown enormously. Today the fishery is one of the most important renewable resources of the basin and of fundamental importance to the population and economy along the Amazon-Solimões River.

Unlike other sectors of the economy, such as forestry or mining, the fisheries sector receives little or no attention from government policy makers or regional development programs. While generally excellent data on the biological aspects of Amazonian fisheries are now available, there are virtually no data of comparable scope and quality on the economic aspects of regional fisheries. What data are available are usually from questionable sources and grossly underestimate the magnitude and importance of the sector. As a result, Amazon commercial and subsistence fisheries have been the invisible sector, its size and importance to the regional economy largely unknown and grossly undervalued.

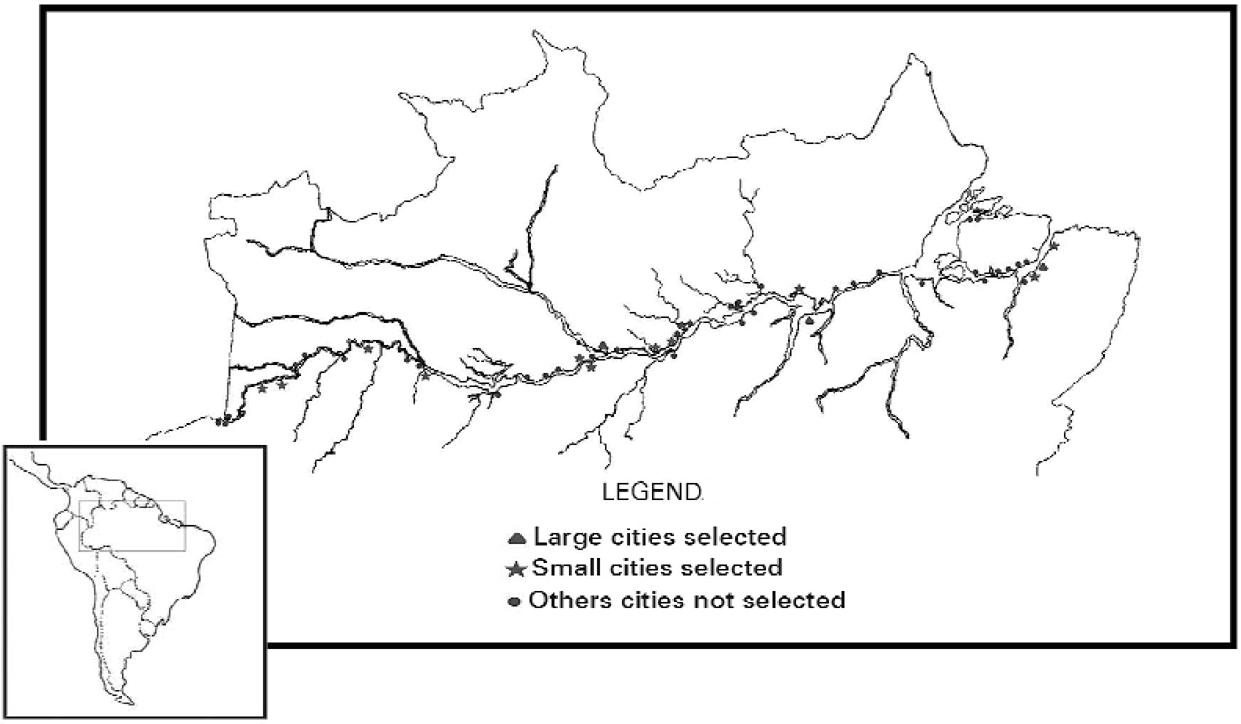
The purpose of this study is to determine the magnitude of the fisheries sector along the Amazon-Solimões River. Total income and employment are estimated for the main activities of the sector, including fish processing plants, stores selling fishing gear, gas stations, restaurants, ice factories and boatyards. The total number of fishers, boats and the total catch along the Amazon River are also estimated. Finally, the long-term benefits generated by the fisheries sector are compared to those generated by the forestry sector.

METHODOLOGY

DATA COLLECTION

The major activities comprising the sector were organized into four groups on the basis of their functional role within the sector, inputs (ice, boat building, fuel and fishing gear), fishing, processing and marketing (markets and fairs) and services (restaurants). To assess the importance of the fisheries sector, businesses, Coast Guard officers and Fisher Union officials were interviewed in 15 of a total of 52 cities along the Amazon-Solimões River corridor. Cities were chosen from a stratified sample. All three cities larger than 250 000 inhabitants were selected and a random sample of 12 cities was chosen from the remaining 49 (Figure 1). In each city we interviewed representatives of all fish processing plants, stores selling fishing material, gas stations, fish restaurants, ice factories and boatyards that were available and agreed to be interviewed, approximately 89 percent of the total number of businesses in the sampled cities (Table 1). Due to the large number of fish markets and individual vendors a sampling strategy was employed for this sector. In the two largest cities, Belém and Manaus, a random sample of markets was chosen and a sample of vendors was interviewed in each market. In the remaining sample cities all public fish markets were visited and a sample of individual vendors was interviewed. Overall, 17 percent (n=238) of the total number of vendors was interviewed in large and small cities. Businesses were identified based on interviews with key informants such as presidents of fisher's unions, government officials, researchers and businessmen. For activities such as boatyards and gas stations, owners were asked to estimate the proportion of their business that involved the fisheries sector.

A field team consisting of a researcher and assistant undertook interviews. The questionnaire was tested and adjusted in Santarém with one assistant and an extra field assistant was trained in a nearby sample city. Interviews in the remaining 13 cities were conducted from April to June 2001. Interviews were short and included questions on the number of employees, production or volume of product sold, selling prices of



■ **Figure 1.** Map of the Amazon-Solimoes Basin showing location of the sampled cities

products and seasonal variation in economic activity. The number of fishing boats in each city was obtained from the local Coast Guard office. A total of 436 interviews were conducted of which about half were with market vendors (Table 1).

Table 1: Total interviews per type of business, average income and total estimation of annual income (in R$1) in the Amazon/Solimões River, 2001. R$3 equivalent to US$1.

	Number of business (1)		Average annual income per city		Number business		Total Annual income All cities
	Interviewed	Existing	Large	Small	Large cities (3)	Small cities (49)	
Fish Markets	238	1 366	24 241	13 803	367.67	21.92	41 563 167
Business	48	51	80 786	19 761	10.33	1.67	4 118 183
Ship Yard	7	10	150 000	119 300	1.00	0.58	3 840 506
Ice factory	24	26	463 987	128 570	4.00	1.17	12 938 761
Fish processing plant (2)	12	14	10 896 806	8 462 500			193 593 060
Gas station	32	36	310 905	217 441	6.00	1.50	21 578 166
Restaurant	18	22	232 574	23 628	5.33	0.56	4 367 205
Total	379	1 525					281 999 048

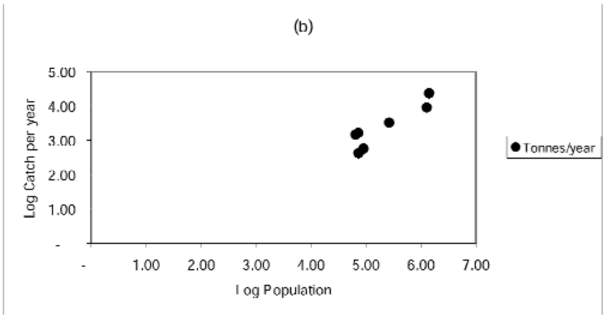
(1) Does not include interviews with unions, Coast Guard and fish markets managers.

(2) In the cities visited there were 14 fish industries from which 12 were interviewed. As we have the total number of fish processing plants for the two states (20) there is no need to estimate using the cities sampled.

ANALYSIS

Economic performance of the fishing sector was estimated in terms of employment and income. Gross income and employment were calculated in three steps: first, the average income and employment was calculated for each type of business for small and large cities separately. Then based on the total number of businesses in each city the total income and employment was calculated for a city. Finally this value was scaled up for the 49 small and 3 large cities along the Amazon-Solimões. For example, in the case of fish markets in small cities given an average of 22 vendors with a gross annual income of R$13 803 per vendor the total annual income for the fish market was of R$302 562. For all 49 small cities the total income was estimated at R$14 825 394 (Table 1). The same methodology was used to estimate number of boats. To avoid double counting fish in the marketing chain, the value of the fish sold by the commercial fleet to fish markets and processing plants was deducted from the total income of these two segments. Subsistence fishing is also valued using the price of fish sold in the community to highlight the economic importance of this segment in relation to others (Cowx 2003; Hanley, Shogren and While 1997).

The relationship between landings and urban population was used to estimate total landings. Data on fish landings in 7 cities were obtained from the literature and the relationship between urban population and landings was found to be linear. This relationship was used to estimate the catch of the cities that do not have landing data. A linear relation was used because of the tendency to overestimate results based on averages (Figure 2).



■ **Figure 2.** Number of tonnes landed in several cities in relation to county population (Source: Manaus, Itacoatiara, Manacapuru, Parintins based on Batista (1998); Santarém, Almeida *et al.* (2001); Tefé, Barthem (1999); Belém, Barthem (sd) Population data: IBGE several years). Does not include fish processing plant landings.

RESULTS

NUMBER OF BOATS AND FISHERS

Based on the number of fishing boats registered with the Coast Guard per city (Figure 2), we estimate that 7 531 fishing boats operate on the Amazon-Solimões river. Assuming there are 6.4 fishers per boat (Almeida, Lorenzen and McGrath 2003), we estimate that there are 48 198 fishers in the commercial fleet.

Data from the Santarém and Tefé regions were used to estimate the total number of rural families along the Amazon/Solimões River. In Santarém there are 198 communities with a total of 9 876 families (De Castro 1999) on 2 683 km^2 of floodplain resulting in a population density of 3 68 families km^{-2}. The floodplain area along the Amazon River in the State of Pará is estimated to be 21 720 km^2 (based on Bayley and Petrere 1989) for a total population of 79 930 families. Queiroz (1999) estimates the population of the Mamirauá Ecological Station on the Solimões River to be 672 families in an area of 2 420 km^2 for a population density of 0.28 families km^{-2} (Queiroz 1999). Multiplying by the area of várzea along the Amazon-Solimões River, we estimate that there are 18 166 rural families on the floodplain in the state of Amazonas. The total for the states of Pará and Amazonas is 98 096 families. Assuming 1.14 fishers per household (Ruffino, Mitlewski, Isaac *et al.* 1999), the number of fishers on the Amazon-Solimões floodplain is estimated to be 111 829.

Using a somewhat different methodology, Bayley and Petere (1989) arrive at a figure of 228 600 subsistence and commercial fishers in 1980 for the entire Amazon basin, equivalent to 102 870 (45 percent of the total), if only the Amazon-Solimões River is considered. Deducting our estimate of the number of commercial fishers (48 198) would leave a total of 54 672 subsistence fishers. This estimate is about half the one presented above. If one corrects for population growth over the last twenty years, Bayley and Petrere's estimate would increase to about 70 percent of that presented here. Since their extrapolation is based on an estimate of population density for a region in the

Peruvian Amazon, outside the present study area, we use here our estimate for the Brazilian Amazon.

Finally, based on landing data available for the regional markets of seven Amazon cities (Figure 2) the total volume of fish landed in urban centres along the Amazon-Solimões rivers is estimated at 46 269 tonnes (based on a log-log regression of catch and population of a = -1.72 and b = 0.959). The total commercial landings along the Amazon-Solimões River are estimated at 83 847 tonnes when the value of the catch landed at processing plants is included (37 578 tonnes; Cabral and Almeida 2003).

INCOME AND EMPLOYMENT GENERATED

Total income of the fisheries sector is estimated at R$389 million (Table 2). The activities generating this income include the commercial fishing fleet, fish processing plants, fish markets, boatyards, ice factories, commercial establishments, gas stations and fish restaurants. There are significant differences between activities in their contribution to total sector income and employment. Fish restaurants, businesses selling fishing equipment and boatyards specialized in building fishing boats each contribute 1 percent of the total income generated by the sector. Ice factories and gas stations specialized in selling to fishing boats contribute between 3 percent and 6 percent, respectively. The activities that contribute most to total sector income are fish processing plants (36 percent), subsistence fishing (33 percent) and the commercial fleet (16 percent) (Table 2).

The relative importance of fish processing plants, despite the small number operating in the Amazon, is due to their large size and high income per plant (averaging R$10 million in sales) (Table 2). Fish markets, in contrast, were not as important despite the large number of vendors and markets.

Fish processing plants account for a large part of the generated income. In 2001, for example, 20 fish

Table 2: Annual income and employment along the Amazon and Solimões riverbanks, Brazil, 2001.

	Annual Income (R$)		Annual Employment		
	Total for riverbank	Percent	Average per Business per year	Total for riverbank	Percent
Subsistence fishers (1)	127 485 060	33		111 829	66
Commercial fishing fleet (2)	62 000 460	16		48 198	29
Fish markets (3)	12 468 950	3	1.3	2 839	2
Commerce	4 120 027	1	2.8	324	0
Ship yard	3 859 594	1	4.63	124	0
Ice factory	12 918 190	3	9.61	397	0
Fish processing plant (4)	139 993 060	36	147.47	4 044	2
Gas station	21 578 166	6	4.29	301	0
Fish restaurant	4 364 332	1	6.93	259	0
Total	388 787 839	100		168 315	100

1) 111 829 families * 1 583 kg per family (based on Queiroz 1999; McGrath *et al*. 1998) multiplied by R$ 0.72 per kilo (Almeida and McGrath 2000).
2) Consider total landings in cities (46 269 tonnes, see text) multiplied by the average price of Santarém, Manaus and Belém (R$1.34; Ruffino 2002).
3) Consider 30 percent of the total income of fish market from Table 1.
4) Total income of fish processing plants estimated in Table 1 subtracted by the value paid to commercial fishers (40 000 tonnes times the price R$1.34; Ruffino 2002 and Almeida and Cabral 2003).

processing plants received approximately 38 thousand tons of fish (Cabral and Almeida 2003). Most of these plants are located in Belém, Manaus and Santarém (70 percent) and the main species processed included piramutaba (*Brachyplatystoma vaillantii)* and dourada (*Brachyplatystoma flavicans)*.

Subsistence (66 percent) and commercial fishing (29 percent) generated 95 percent of total employment in the sector. The remaining 5 percent was divided between fish processing plants (2 percent) and all other activities.

DISCUSSION

The results of this study show that the total income of R$389 million generated by the commercial fishery sector, is about four times greater than earlier estimates based on fish landings and subsistence catch (Mitlewski 1997). The study also found that subsistence and commercial fishing fleets are the major contributors to sector employment (95 percent). Other activities, such as fish markets, establishments selling fishing gear, gas stations, ice factories and restaurants, make a comparatively limited contribution to total sector income and employment, together generating only 15 percent of the total, or R$60 million annually. It is likely that because of the sampling methodology employed and because some types of businesses were not considered, such as supermarkets - an increasingly important outlet for fish in the three major cities, this figure underestimates the contribution of these activities. In addition, because we sampled only cities along the main river, employment and income generated by boatyards, many of which are located on tributaries with better access to wood, may also be underestimated.

This study also supports observations made in an earlier study; that the last twenty-five years of fisheries development have led to the growth, but only partial transformation of the sector. Employment has grown with the expansion of the commercial fisheries, but is still overwhelmingly concentrated in the capture of fish. The low level of capitalization of the fleet is reflected in the limited employment and income generated by activities that support the fishing fleet and by the muted presence of downstream activities. Every commercial fisher, for example, generates only 0.17 jobs in the rest of the sector. While processing activities are the second largest source of employment, they are still a small fraction of the total for the sector.

The importance of the subsistence fishery often goes unrecognized in terms of both its contribution to total catch, as well as, to the overall floodplain economy. The subsistence fishery accounts for 65 percent of the total catch in the Brazilian Amazon, twice the commercial catch. The subsistence fishery also accounts for a comparable proportion of employment (66 percent).

The subsistence fishery is a central element of the household economy that contributes directly and indirectly to total household income. Almeida, Lorenzen and McGrath (2003) found that 84 percent of floodplain households in the Santarém area fish for subsistence and occasional sale. The protein obtained from fishing is by far the most important source for floodplain populations (Murrieta 1998). Income from subsistence and commercial fishing represents 37 percent of total household income, providing food and cash that enable these households to generate at least the same income from other activities such as farming and ranching (Almeida *et al*. 2003). Furthermore, families with more diversified household economies tend to earn more as they take fuller advantage of the floodplain resource base. The subsistence fishery, then, is a strategic factor in the smallholder floodplain economy that policymakers should take into account in designing development policies for floodplain development (Allison and Ellis 2001; Cowx 2003; Hanley *et al*. 1997).

This study also reveals the deficiencies in official statistics for the fisheries sector. Table 3, for example, shows employment per activity in the primary sector. According to this table there are 1.2 million people employed in the primary sector in the states of Amazonas and Pará and only 17 742 employed in the fisheries sector. However, comparison of these government employment statistics with the number of fishers calculated in this study (160 027) shows that the official figure grossly underestimates employment in the sector. See also estimates by Bayley and Petrere (1989). The difference between official estimates and reality is actually even larger because the data in Table 3 cover two entire states while the estimate used here is only for the Amazon-Solimões River corridor.

processed by the fish processing industry, then the total area exploited would be 134 150 ha (half the area for half the catch). Based on present patterns of exploitation, this same area of forest would provide roundwood for 6 sawmills (134 150 ha/242 ha/90 year rotation cycle system (Almeida *at al.* 1995, Veríssimo *et al.* 1992) and generate an annual income of 4 million

Table 3: Number of people occupied in primary sector, Pará, Brazil, 1996.

	Amazonas State	Percent	Pará State	Percent	Total	Percent
Annual crops	203 842	58	371 794	42	575 636	47
Horticulture	8 458	2	7 323	1	15 781	1
Perennial crops	67 953	19	91 743	10	159 696	13
Ranching	30 858	9	175 900	20	206 758	17
Agriculture and ranching	7 762	2	95 465	11	103 227	8
Silviculture and forest exploitation	20 444	6	128 766	15	149 210	12
Fishing and aquaculture	10 525	3	7 217	1	17 742	1
Production of vegetable coal	597	0	5 717	1	6 314	1
Total	350 439		883 925		1 234 364	100

Source: IBGE (1997)

It is interesting to compare the relative contributions that the fisheries and forestry sectors make to the regional economy. This comparison hinges on the relative sustainability and long-term productivity of the two sectors in municipalities where a substantial part of their total area consists of floodplain and upland forest, as in the municipality of Santarém.

To compare the forestry sector with the fishing sector some assumptions have to be made. The total floodplain area of the municipality is estimated at 268 300 ha (Pro-Várzea, PPG7). Half of the commercial catch, of 3 500 tonnes is landed in local markets and the other half at fish processing plants. We consider the catch landed at local markets and consumed by the local population to be equivalent to roundwood production by the timber industry, as both are sold unprocessed. Likewise, the catch landed at the fish processing industry is equivalent to sawnwood production for the region. If we only consider the catch

dollars. By comparison, the main fish-processing factory in Santarém generates a gross annual income of R$10.5 million, almost twice that of the forestry sector for an equivalent area. While a more rigorous comparison would need to be refined to account for the importance in the annual catch of migratory species from outside the region, the basic point stands: when dealing with floodplain and upland areas of roughly equal size, floodplain fisheries generate more income and employment than forestry. Furthermore, unlike the forestry industry where most of the original forest area will not be available for a second cut, fisheries production can be maintained indefinitely. This example shows the enormous income generating potential of floodplain fisheries when properly managed; underscoring the strategic role they can play in the sustainable development of municipalities located along the Amazon floodplain.

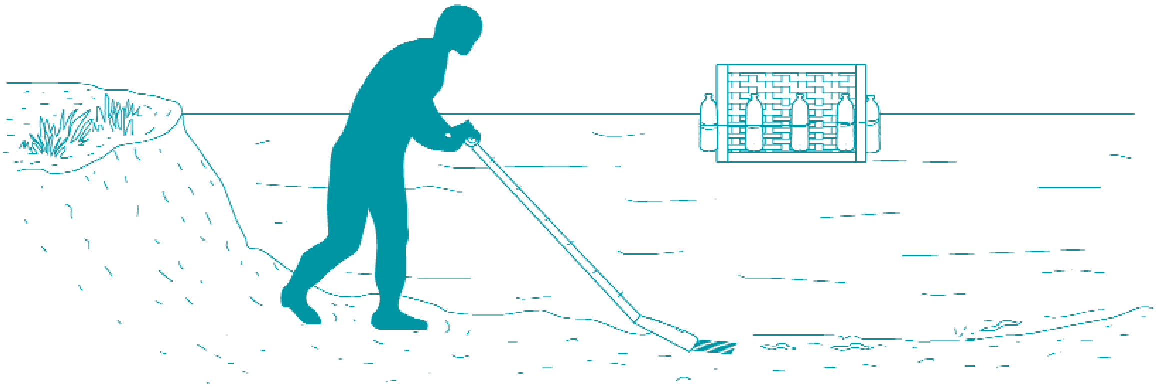
CONCLUSION

Earlier we referred to Amazon fisheries as the invisible sector whose contribution to the regional economy is grossly under-estimated and consequently under-appreciated by government policymakers. Here we present the results of a first attempt to estimate the actual magnitude of the sector in terms of employment and income generation for the Amazon-Solimões River corridor. Results of this analysis show that income generation by the sector is four times larger than previous estimates (Miltewski 1997, considering present dollar parity and only the Amazon-Solimões corridor), while direct employment is 8 times that in published government statistics. The study also reveals that the major contributors to sector employment are the subsistence and commercial fisheries. Fish processing plants are the major contributors to sector income. The contribution of other activities, both upstream and downstream, is just 15 percent of total income. As these results suggest, total job creation per commercial fishers is estimated very low, 0 17 and even lower if subsistence fishery is also included, underscoring the artisanal nature of the fishery. While the magnitude of the subsistence fishery is captured in this report, the sector's contribution to overall floodplain income and employment has not been adequately assessed, due to the absence of data on floodplain agriculture and ranching. However, data from the Santarém region indicate that it can be considerable. Finally, while at the basin level fisheries' income and employment are dwarfed by that of the forestry sector, for municipalities along the Amazon-Solimões River corridor the relative importance of local fisheries can be significantly greater than that of the forestry sector in the medium to long term, at least for the municipalities along the Amazon river.

In conclusion, we hope that this study helps to make the sector more visible, so that policymakers have a greater appreciation for the sector's contribution to regional income and employment and stimulates them to adopt policies that enhance the sector's contribution to regional livelihoods and development.

ACKNOWLEDGMENTS

This research was supported by the Darwin Initiative of the Department of the Environment of the United Kingdom, WWF and DFID. We would like to thank Lucilene Silva, Susan Siofi, Nadson Oliveira for collecting data and Nalinda Coutinho, Elisabeth Silva, Ivoneide Moreira for entering data to the computer and Horácio Almeida for helping with contacts in the cities in the Amazonas State. We would also like to thank the Agriculture Ministry and Gabriel Calvazara for the data on fish processing plant in Para and Amazonian State. We would like to thank John Viar for reading earlier drafts of this paper. Finally, we would like to thank all the businessmen, Fishers Union representatives and government employees in all these ports for taking their time and giving us these interviews.



REFERENCES

Allison E. & Ellis F. 2001. The livelihoods approach and management of small-scale fisheries. *Marine Policy*, 25: 377-388.

Almeida O., Lorenzen K. & McGrath D.G. 2003. Commercial fishing in the Brazilian Amazon: Regional differentiation on fleet characteristics and economic efficiency. *Fisheries Management and Ecology*, 10: 109-115.

Almeida O., Lorenzen K. & McGrath D. 2002. Impact of co-management regimes on the exploitation and productivity of the floodplain lake fisheries in the Lower Amazon. *In Proceedings of the International Association for the Study of Common Property*, Zimbabwe, 2002. 17-21 June 2002. 12 pp.

Almeida O., McGrath D. & Ruffino M.L. 2001. The commercial fisheries of the lower Amazon: An economic analysis. *Fisheries Management and Ecology*, 8. 253-269 pp.

Almeida O. & Uhl C. 1995. Planejamento de uso do solo de um município na Amazônia Oriental utilizando dados econômicos e ecológicos. *In* Almeida O. Org. *Evolução da fronteira Amazônica: oportunidades para o desenvolvimento sustentável*, Porto Alegre, Editora Caravelas. 139 pp.

Almeida O. & McGrath D.G. 2000. *Alternative of commercialisation for the artisanal fisherman in the Lower Amazon*. IPAM. Internal Report.

Batista V. 1998. *Distribuição, dinâmica da frota e dos recursos pesqueiros da Amazônia central*. Universidade do Amazonas & INPA. 291 pp. (Doctoral dissertation)

Barthem R. Ed. *Avaliação da exploração pesqueira no estuário e Baixo Amazonas 1993-1995. Final Project Report to Finep*.

Barthem R. 1999. A pesca Comercial no médio Solimões e sua interação com a Estação Ecológica do Mamirauá. *In* H. Queiroz & W. Crampton. *Estratégias para manejo de recursos pesqueiros em Mamirauá.* Brasilia: Sociedade Civil Mamiraua/CNPq. 72-107

Bayley P. & Petrere M. 1989. Amazon Fisheries: Assessment methods, current status and management options. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 385-398 pp.

Cabral W. & Almeida O. 2003. *O setor industrial pesqueiro da Amazônia*. Relatório Interno do Pro-Várzea. 49 pp.

Cowx I. 2003. Value of river fisheries. *In* R.L. Welcomme & T. Petr eds. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries: Volume 1. Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/16. pp. 1 - 20.

De Castro F. 1999. Fishing Accords: The political ecology of fishing intensification in the Amazon. University of Indiana. 206 pp. (Doctoral dissertation)

Hanley N., Shogren J. & While B. 1997. Environmental economics in theory and practice. London, McMillan Press. 464 pp.

IBGE Instituto de Brasileiro de Geografia e Estatísitca. 1997. *Contagem Populacional* 1996 – Resultados relativos a sexo da população e situação da unidade domiciliar. Rio de Janeiro, IBGE. Volume 1

IBGE Instituto de Brasileiro de Geografia e Estatística. 1997. *Censo Agropecuário 1996*. Rio de Janeiro, IBGE.

IBGE Instituto de Brasileiro de Geografia e Estatística. 1980. *Censo populacional* de 1980 e 1991 (Available at www.datasus.gov.br/cgideftoh tom.wxeibge/popam.def)

IBGE Instituto de Brasileiro de Geografia e Estatística. 1996. *Contagem da População 1996*. (Available at http://www.ibge.gov.br/ibge/estatistica/populacao/contagem/amcont96.shtm.)

McGrath D., Silva U. & Crossa M. 1998. The traditional floodplain fishery of the lower Amazon River, Brazil. *NAGA, The ICLARM Quarterly,* Jan-Mar: 4-11.

Mitlewski B. 1997. Strengthening dialogue and communication: Lessons from fisheries management in the Amazon. *Wald-und Viehwirstschaft, Fischerei, Naturschut*. 424: 149-164.

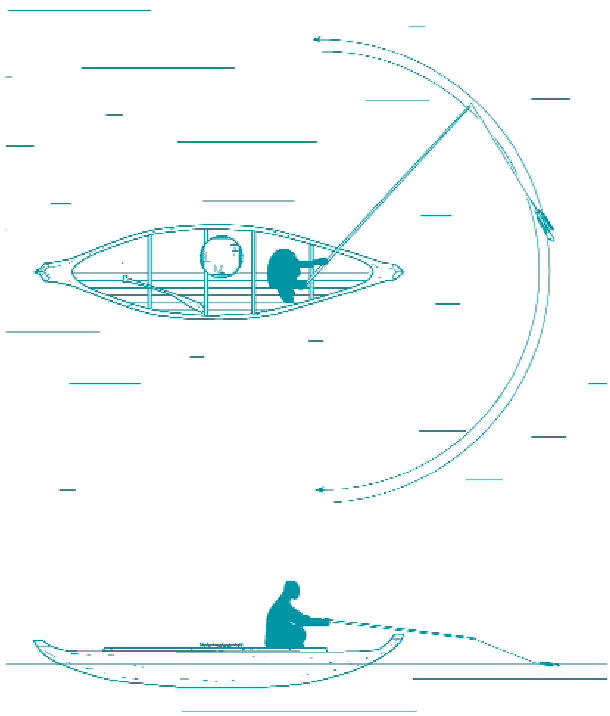
Murrieta R. 1998. O dilema do papa-chibé: consumo alimentar, nutrição e práticas de intervenção na Ilha do Ituqui, baixo Amazonas, Pará; *Revista de antropologia*, 41: 1.97-150.

Queiroz H. 1999. A pesca, as pescarias e os pescadores de Mamirauá. *In* H. Queiroz & W. Crampton eds. *Estratégias para manejo de recursos pesqueiros em Mamirauá*. Brasília, Sociedade Civil do Mamirauá-CNPq. pp. 37-71.

Ruffino M.L. 2002. *Estatística Pesqueira do Amazonas e Pará – 2001*. Manaus, IBAMA, Pro-Várzea, 2002. 73 pp.

Ruffino M., Mitlewski B., Isaac V. & Oliveira P. 1999. *Lago Grande de Monte Alegre: Uma analise de suas comunidades pesqueiras*. *In* IBAMA. Recursos Pesqueiros do Médio Amazonas. Abordagem Socioeconômica. pp. 31-75.

Veríssimo A., Barreto P., Mattos M., Tarifa R. & Uhl C. 1992. Logging impacts and prospects for sustainable forest management in an old Amazon frontier: The case of Paragominas. *Forest Ecology and Management*, 55: 169-199.



ORGANIZATION AND MAINTENANCE OF FISH DIVERSITY IN SHALLOW WATERS OF TROPICAL FLOODPLAIN RIVERS

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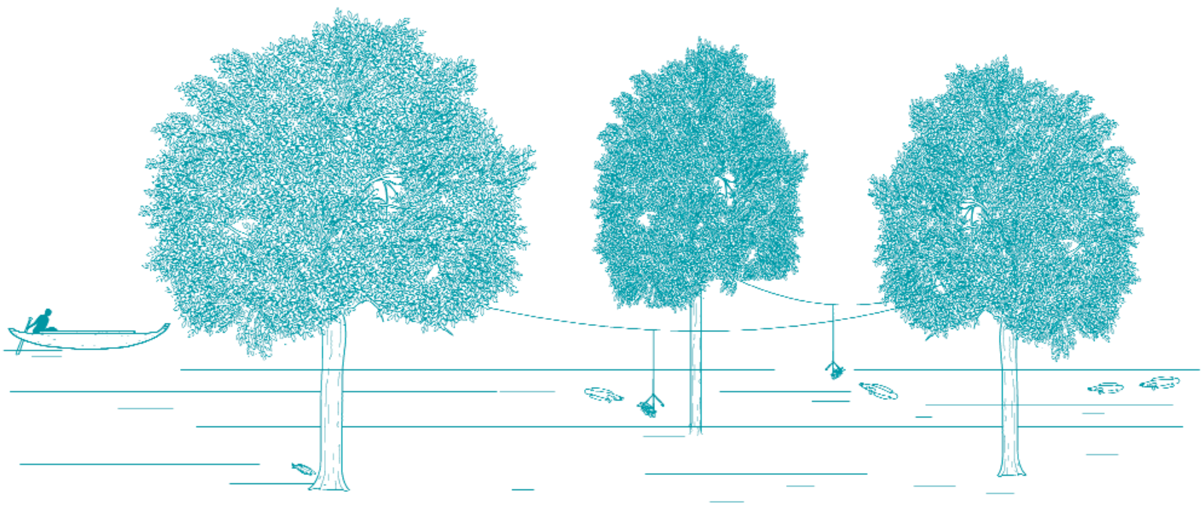


Key Words: beta diversity, colonization, community assembly, fishes, flood pulse, gamma diversity, spatiotemporal heterogeneity, Venezuela

ABSTRACT

Historical and zoogeographic factors appear to explain the origin of Neotropical freshwater fish diversity, but proximate factors maintaining such remarkable levels of regional diversity, particularly in large floodplain rivers, remains unknown. Floodplain rivers are characterized by high levels of landscape and temporal heterogeneity. The littoral zone is composed of a mosaic of habitat templets upon which local communities are assembled and represents a highly dynamic component of the landscape due to seasonal water level fluctuations associated with the annual flood pulse. Results presented indicate littoral species are forced to continually disperse across the landscape in association with a moving land-water interface

and lend support to an implicit theoretical trade off between colonization and competition ability among fishes of tropical floodplain rivers. The continual disassembly and reassembly (due to dispersal) of local communities across a spatially heterogeneous landscape should result in low extinction rates (i.e. at the regional level) and could theoretically maintain a nearly infinite regional species pool. Consequently, we suggest that the flood pulse paradigm should be expanded to include a potential mechanistic understanding of maintenance of high levels of beta and gamma diversity in floodplain rivers. Interactions among seasonal hydrology, variability in habitat structural complexity and landscape heterogeneity appear to maintain high aquatic species richness in these lowland rivers. It follows that alteration of seasonal water level fluctuation (e.g. damming) and habitat heterogeneity (e.g. channelization) should have substantial and negative consequences on the maintenance of regional biodiversity pools in floodplain rivers.

INTRODUCTION

Tropical floodplain rivers are home to the largest fraction of freshwater fish biodiversity (Dudgeon 2000; Lundberg 2001) and as such should be a focal point of global conservation efforts. Recently, conservationists have focused their efforts on species conservation through identification and conservation of hotspots (i.e. areas with high levels of endemism) (Meyers *et al.* 2000). Unfortunately, tropical rivers and associated fish faunas are absent from this conservation initiative (Meyers *et al.* 2000; Brooks *et al.* 2002). Not only have rivers been undervalued in conservation efforts, but also ecological understanding of community and assemblage dynamics in lowland rivers lags behind other fields of study (e.g. limnology in temperate lakes). We suggest that better conceptual understanding of these systems will lead to more effective conservation and restoration practices.

Recent studies have made great headway in understanding large-scale patterns of freshwater fish diversity. In an insightful review of the source of South American freshwater fish fauna richness, Lundberg (2001) identified area and latitudinal gradient as suitable explanations for large-scale maintenance of neotropical riverine freshwater fish diversity, but suggested that a historic-zoogeographic perspective is needed to understand the genesis of this diversity. Lundberg presented evidence that river basins were repeatedly transformed during periodic geological upheavals and changes in basin boundaries and interbasin connections resulted in sympatric speciation opportunities. Lundberg reasoned that low baseline extinction rates resulted in the present-day richness of neotropical freshwater fish species.

Although historical and zoogeographic factors may explain the origin of neotropical freshwater fish diversity, there is little understanding of proximate factors (*sensu* Resetarits and Bernardo 2001) maintaining this remarkable diversity across the landscape at regional and local scales, particularly in large floodplain rivers. Fish assemblages in European and North American temperate forested lakes are structured by a series of nested filters operating first at regional and subsequently at local scales (Tonn 1990; Tonn *et al.* 1990). Stream fish assemblages in the same two regions (Europe and North America) also exhibited hierarchical structure with regional zoogeography and local habitat templets structuring local fish assemblages (Matthews 1998; Lamouroux, Poff and Angermeier 2002). Characterization of the relationship between regional and local fauna richness has been identified as a useful metric to evaluate the degree that species interactions regulate local community dynamics (Cornell and Lawton 1992; Hugueny and Cornell 2000). Cornell and Lawton (1992) stated that unsaturated assemblages are ubiquitous in nature and as a consequence regional richness is free of local constraints, although this logic has been seriously challenged (Shurin *et al.* 2000). Cornell and Lawton (1992) speculated that the regional species pool regulates local richness, which should be a function of landscape heterogeneity and evolutionary diversification. Empirical data have revealed that contemporary energy availability and habitat heterogeneity successfully predict the current global distribution of riverine fish diversity (Guégan, Lek and Oberdorff 1998). Furthermore, fish assemblages in Africa, North

America and Western Europe may be either unsaturated i.e. non-interactive (Tonn *et al*. 1990; Hugueny and Paugy 1995; Griffiths 1997; Oberdorff *et al.* 1998) or saturated i.e. interactive (Tonn *et al*. 1990; Angermeier and Winston 1998). In their comparative study, Tonn *et al*. (1990) demonstrated that North American assemblages exhibited an asymptotic relationship between local and regional richness (i.e. interactive local assemblages), whereas European assemblages did not (i.e. non-interactive local assemblages). Similar to temperate lakes, North American stream fish assemblages (i.e. Virginia) also showed local community saturation (Angermeier and Winston 1998). The likelihood that neotropical fish assemblages are saturated seems high, because regional diversity in these settings is remarkably high (Jepsen 1997; Arrington and Winemiller 2003) yet alpha diversity is not substantially greater than similar North American samples (Matthews 1998), that have much lower regional diversity levels. Though a consensus on this subject has not been reached (Cornell and Lawton 1992; Shurin *et al.* 2000), the possibility exists that local community interactions may regulate regional species richness for fishes in neotropical rivers.

Much attention has focused on spatiotemporal dynamics in lotic environments as a mechanism for maintaining biodiversity (e.g. Schlosser 1987; Townsend 1989; Ward 1989, 1998; Poff and Allan 1995; Matthews 1998; Schlosser and Kallemeyn 2000; Oberdorf, Hugueny and Vigneron 2001). Recent work conducted on European floodplain rivers has characterized landscape attributes of floodplain rivers as shifting mosaics of habitat features with varying levels of among-habitat connectivity (Ward, Tockner, Arscot *et al.* 2002; Amoros and Bornette 2002). The combination of landscape heterogeneity and temporally variable among-patch connectivity are common features of floodplain rivers that result in observed patterns and levels of biodiversity (Ward 1998; Ward *et al.* 1999; Ward *et al.* 2001; Tockner *et al.* 1999; Amoros and Bornette 2002; Robinson *et al.* 2002). The general synopsis is that a dynamic landscape composed of a mosaic of habitat patches in various successional states maintains the high regional diversity levels observed in floodplain rivers. This should be the case whether or not local communities are saturated, because effects of landscape and temporal heterogeneity should overcome competitive exclusion (Levin and Paine 1974; Chesson and Huntley 1997; Hurtt and Pacala 1995).

In this limited review, we hope to address the following questions based on experience with fish assemblages in neotropical floodplain rivers. How are neotropical fishes organized across the river-floodplain landscape? What factors influence assemblage structure in these local communities? How are such large regional species pools maintained?

ORGANIZATION OF FISH DIVERSITY IN TROPICAL FLOODPLAIN RIVERS

Characterization of patterns of species occurrences and relative abundance is a major goal in community ecology (Hubbell 2001). A central debate among community ecologists has been the role of deterministic versus stochastic processes often inferred through examination of random or non-random patterns in assemblage data. Studies of fish assemblages in temperate streams have demonstrated both random (Grossman, Moyle and Whitaker 1982; Grossman *et al*. 1998) and non-random patterns (Meffe and Sheldon 1990; Jackson, Somers and Harvey 1992; Taylor 1996), with results often strongly dependent on the spatial, temporal and numerical scale of the study (Rahel 1990, Angermeier and Winston 1998). Tropical floodplain rivers have been studied less frequently and have yielded mixed results. Goulding, Carvalho and Ferreira (1988) concluded that fish assemblages of the Río Negro (Brazil) were random associations of species. More recent studies also support the random association hypothesis (Jepsen 1997; Saint-Paul *et al.* 2000).

A few studies in tropical river systems have concluded fish assemblages are structured in a non-random manner. Working in the same system as Jepsen (1997), Arrington (2002) documented non-random structure of fish and macroinvertebrate assemblages among major habitat types (e.g. sandbank, leaf litter, submerged wood) located in the moving littoral. Fish assemblages in these local habitats were maximally structured during the low-water period and less structured in rising- and falling-water periods. Consequently, juxtaposition of multiple habitat types and the resulting landscape heterogeneity resulted in high levels of observed beta diversity, which substantially influenced the estimate of the regional species pool. Similarly, fish assemblages on the floodplain of the Brazillian Amazon were found to be non-randomly structured among major habitat types (Petry, Bayley and Markle 2003), though habitats in this study were characterized by dominant macrophytes. Others have shown fish assemblage structure in tropical rivers is influenced by water type (Ibarra and Stewart 1989; Cox Fernandes 1999), sample depth (Lundberg *et al.* 1987; Stewart, Ibarra and Barriga-Salazar 2002; Hoeinghaus *et al.* 2003), seasonally falling water levels (Cox Fernandes 1999) and diel period sampled (Arrington and Winemiller 2003). Rodriguez and Lewis (1997) found structured assemblage patterns in Orinoco floodplain lakes that were correlated with water clarity. They inferred predation by alternative predators in clear or turbid lakes was driving assemblage structure. As Winemiller (1996) hypothesized, tropical floodplain river fish assemblages appear to be structured by both stochastic and deterministic processes and the magnitude of these processes varies seasonally (Arrington 2002).

MAINTENANCE OF FISH DIVERSITY IN TROPICAL FLOODPLAIN RIVERS

We suggest that the flood pulse paradigm be expanded to include a potential mechanistic understanding of maintenance of high levels of beta and gamma diversity in floodplain rivers. We hypothesize that the flood pulse (Junk, Bayley and Sparks 1989), i.e. the annual hydrologic pattern of predictable flooding of lateral floodplain habitats in large tropical rivers, regulates community assembly patterns and regional diversity levels. As conceived by Junk *et al.* (1989), the flood pulse concept linked riverine productivity to predictable annual patterns of flooding and characterized the main channel as a passageway for fish migrations. Although some fish species undoubtedly use the main channel for migration (Junk *et al.* 1989; Fernandes 1997; Wei *et al.* 1997; Duque, Taphorn and Winemiller 1998), many species either seasonally (low water) or consistently occupy main channel habitats (e.g. deep channel, shifting sandbanks, snag complexes). We shift our focus from the main channel / highway analogy (Junk *et al.* 1989) to the moving littoral as a dynamic habitat template. We define the moving littoral as the dynamic land-water ecotone occurring along main channel margins and extending onto the floodplain during high water. The moving littoral, thus, represents a highly dynamic component (i.e. shallow water) of the landscape composed of a mosaic of habitat templets upon which local communities are assembled (Southwood 1988; Townsend 1989; Bayley 1995; Arrington 2002; Petry *et al.* 2003). Furthermore, local habitat templates in the moving littoral may be thought of as being disturbed at some intermediate level (Connell 1978; Townsend, Scarsbrook and Dolédec 1997; Ward *et al.* 1999; Sheil and Burslem 2003) due to the seasonally predictable patterns of drying and wetting in lowland rivers (Junk *et al.* 1989; Arrington and Winemiller 2003).

As discussed above, there is considerable debate regarding the roles of deterministic and stochastic processes regulating local fish assemblages. A new hypothesis receiving considerable attention is Hubbell's (2001) "neutral theory", which assumes per capita equivalence of within-trophic-level community members. Community change is assumed to occur through stochastic ecological processes and random speciation. Application of the neutral theory has resulted in the generation of multiple testable predictions, which can serve as working null hypotheses in community studies. For example, local communities are expected to be sub-sets of the larger metacommunity, with species relative abundance equal between the two when migration rates into the local community are non-trivial (Hubbell 2001).

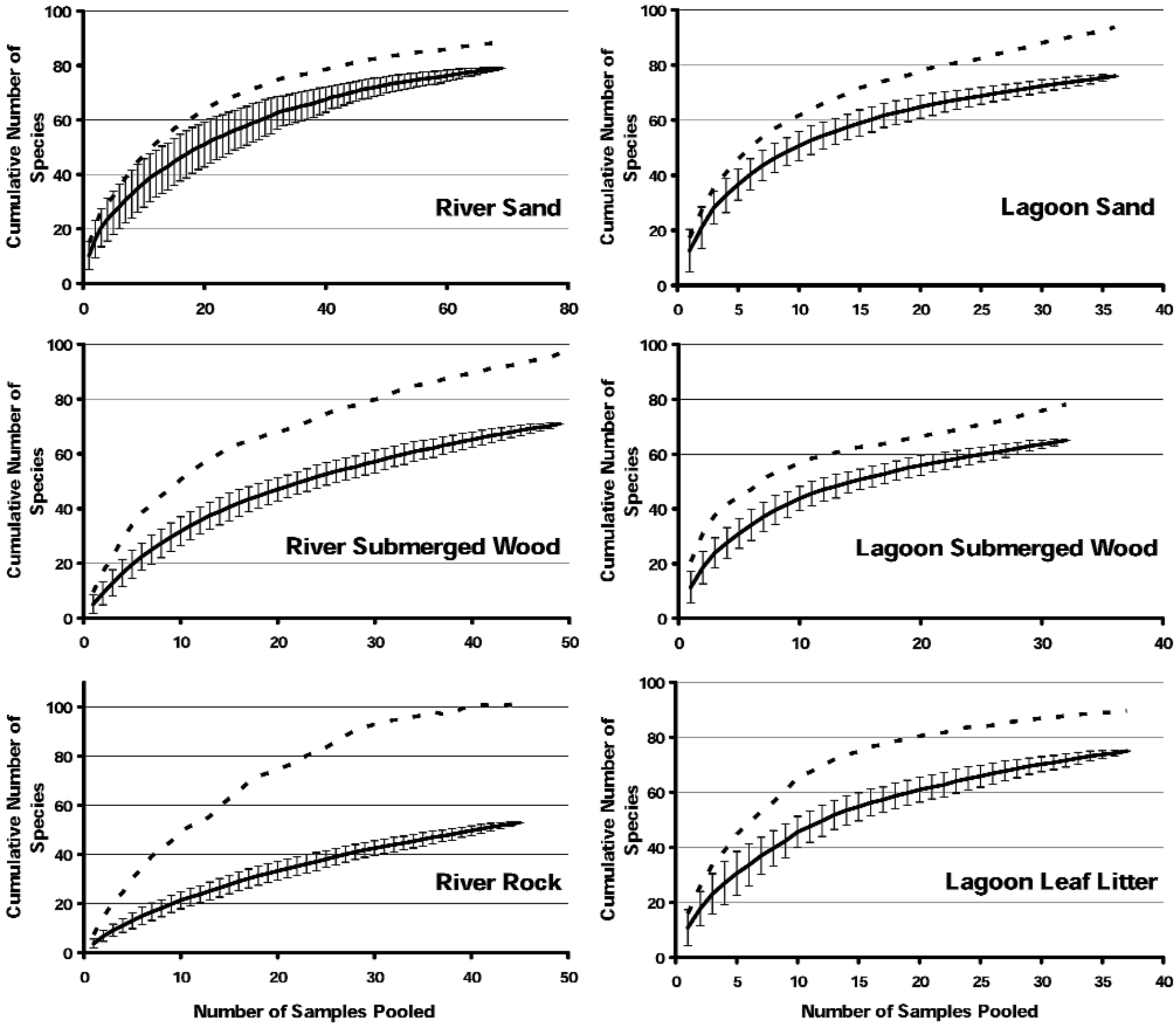
Previous studies have shown the importance of immigration rates on the structure (including richness) of local communities (MacArthur and Wilson 1967). Dispersal rates determine the importance of local community regulators in zooplankton assemblages

(Jenkins and Buikema 1998) and predominantly limit diversity in newly formed assemblages (Shurin *et al.* 2000). Temporal variation of fish assemblage structure in a Brazilian estuary has been linked to fish immigration and emigration dynamics (Garcia, Vieira and Winemiller 2001). For temperate streams, Schlosser (1987) offered a conceptual model indicating the generalized importance of immigration and extinction processes for the development of fish assemblage attributes. Using Schlosser's model as a starting point, Taylor and Warren (2001) showed stream fish immigration rates were positively related to stream size and negatively related to flow variability. They then documented patterns of nestedness in fish assemblage structure that were positively related to extinction rates and negatively related to immigration rates. They also observed that colonization and extinction dynamics of species appeared "more or less random" in habitats with high immigration rates, a result predicted by Townsend's (1989) patch dynamics concept.

Recent work by Arrington, Winemiller and Layman (in review) examined the influence of colonization rate and habitat complexity on the dynamics of local fish assemblages in the Cinaruco River, a floodplain river located in the Venezuelan *llanos*. Habitat patches of varying complexity and colonization rates were created within broad main-channel sandbanks and were colonized by fishes and macroinvertebrates for a period of 21 days. In accordance with island biogeography theory, Arrington *et al.* found a significant positive influence of colonization rate on the number of species in local habitat patches. Furthermore, they observed more complex habitats contained significantly more species. Results varied when treatment effects were evaluated separately for two distinct subsets of the fish assemblage. Richness of fish taxa with low vagility was positively related to colonization rate and habitat patch complexity, whereas richness of highly vagile fishes was positively related to patch complexity but not colonization rate. Presumably, increased colonization ability by vagile species swamped the influence of habitat patch isolation. These results suggest local community dynamics in this neotropical floodplain river are dominated by near continuous dispersal and colonization of habitat patches in the moving littoral (*sensu* "patch dynamics concept" Townsend 1989) by adult fishes (Arrington *et al.* in review). Furthermore, low concordance was observed between ranks of species from the meta-community and local habitat patches; thus falsifying one of Hubbell's (2001) hypotheses (see above). In a parallel experiment, Arrington *et al.* (in review) documented largely stochastic structure of local assemblages in newly formed habitat patches, but increasing levels of non-random organization were observed in patches as time progressed (> 24 days). Taken together, these data suggest dispersal is most important in structuring assemblages in newly formed patches, whereas the influence of local processes on assemblage structure increases as time progresses.

A considerable body of ecological theory has been developed that indicates tradeoffs in colonization and competitive abilities should preclude competitively dominant species from occupying all suitable habitats in a spatially heterogeneous landscape (i.e. the moving littoral of floodplain rivers) and as a consequence competitive subordinates should persist in the regional species pool (Levin and Paine 1974; Hurtt and Pacala 1995). The experiments by Arrington *et al.* lend support to an implicit theoretical trade off between colonization and competition ability in fishes of tropical floodplain rivers, where littoral species are forced to continually disperse across the landscape in association with a moving land-water interface. This continual disassembly and reassembly (due to dispersal) of local communities across a spatially heterogeneous landscape should result in low extinction rates (i.e. at the regional level) and could theoretically maintain a nearly infinite regional species pool (Hurtt and Pacala 1995).

Additional studies on the Cinaruco River appear to support such a mechanism in maintaining a very large regional species pool in a tropical floodplain river (Arrington 2002). Through most of 1999, six

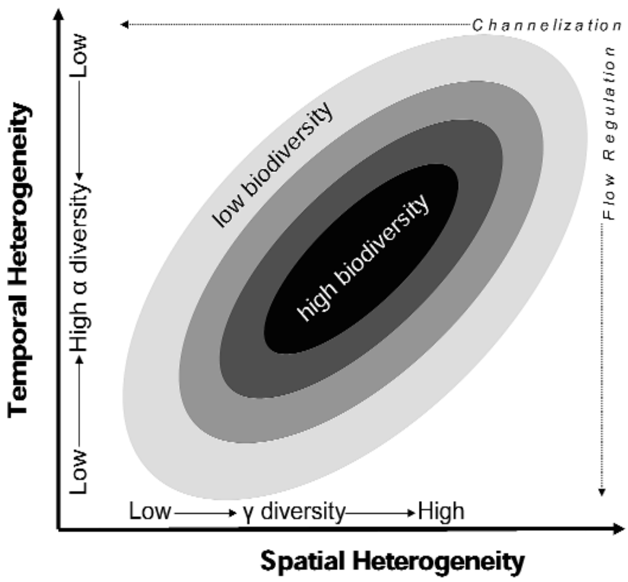


■ **Figure 1.** Species accumulation curves for standardized seine samples collected from six habitats located in the moving littoral zone of the Cinaruco River, Venezuela reveal the diversity of tropical floodplain fish assemblages. Samples were collected through most of 1999, excluding the peak-wet season (see Arrington 2002). Number of samples collected per habitat was: river rock 45, river sand 69, river snag 47, lagoon leaf 36, lagoon sand 36 and lagoon snag 31. Each point along the solid line represents an estimate of the total community richness (including taxa not sampled) for specific littoral zone habitats based on the relative abundances of the most rare species in our samples (see Colwell 1997).

habitats were sampled from the moving littoral zone in the Cinaruco River. These habitats function as habitat templets, upon which local communities are assembled (Arrington 2002) and their spatial distribution in the main channel and floodplain is a dominant component of spatial habitat heterogeneity. Each month seven replicate diurnal samples were collected using the same seine (see Arrington 2002 for a description of methods). We plotted fish species accumulation curves for each habitat independently (Figure 1). In each habitat, we observed a continual and positive slope of the accumulation curve, with observed total assemblage richness (γ diversity) reaching 50 to 80 fish species per habitat type. In addition to observed species richness values, we estimated γ diversity for specific littoral zone habitats using a non-parametric estimator based on observed relative abundance data. The technique, known as abundance-based coverage estimator, assumes information about un-sampled species is held in the rarest classes of species collected (Chao and Lee 1992; Colwell and Coddington 1994; Chazdon *et al.* 1998) and can be computed using freely-available software (Estimate S, Colwell 1997). In some habitats, such as river rock (Figure 1), the estimated size of the species pool far exceeds observed values. These local communities were consistently composed of relatively rare species. Thus, it appears that community assembly within isolated habitat patches, such as our river rock habitats, are more dependent upon stochastic colonization processes (i.e. colonization limitation). Furthermore, these patches often contained species characteristic of adjacent open sandbank habitats, which suggests leaky boundaries may lead to "mass effects" (Townsend 1989) in local patches that are not biologically saturated. Others have hypothesized that low dispersal or connectivity among patches should result in lowered α diversity, but promote β and γ diversity (Hubbell 1997), particularly in floodplain rivers that are characterized by high levels of spatiotemporal heterogeneity (Ward *et al.* 1999; Tockner *et al.* 1999; Amoros and Bornette 2002). In more contiguous (higher connectivity) patches, lower estimates of total richness may reflect reduced persistence of rare (Hubbell 2001) or competitively inferior (Hurt and Pacala 1995) species with higher colonization rates (higher α diversity but lower β diversity; Amoros and Bornette 2002). At present we are unable to identify the mechanism(s) driving the difference between observed and expected diversity (Figure 1). But, our experimental results indicate that a combination of colonization limitation (dispersal) and biotic interactions result in low α diversity but high β diversity (Arrington *et al.* in review). We submit that the annual flood pulse interacts with basin geomorphology and adds temporal heterogeneity to an already spatially heterogeneous landscape, both of which are critical in maintaining high levels of γ diversity observed in lowland tropical rivers (Figure 2).

THREATS TO FISH DIVERSITY IN TROPICAL FLOODPLAIN RIVERS

Rivers face a number of anthropogenic threats (Allan and Flecker 1993; Crisman *et al.* 2003) and dam building appears particularly damaging to tropical riverine biodiversity (Grossman, Dowd and Crawford 1990; Goulding, Smith and Mahar 1996; Pringle *et al.* 2000). Large floodplain rivers are characterized by a remarkable degree of spatiotemporal heterogeneity in their natural state (Ward *et al.* 1999, 2001, 2002) and this heterogeneity is maintained by fluvial dynamics acting on landscape features. In the Tagliamento River (Italy) corridor, for example, landscape features experienced up to 80 percent turnover in a 3-year period, but features maintained similar relative proportions across the landscape (Ward *et al.* 2001). Construction of dams for flood control or hydroelectric power generation constrains these fluvial dynamics and can result in dramatic loss of spatial heterogeneity (Toth *et al.* 1995; Schmidt *et al.* 1998). If the interaction between the natural rise and fall of flood waters and floodplain spatial heterogeneity (habitat templates for organisms) maintains regional diversity levels in tropical floodplain rivers (Figure 2), then loss of the flood pulse not only will impact biological production (Junk



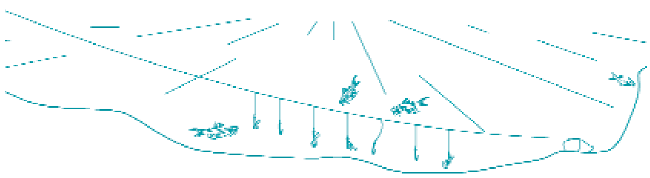
■ **Figure 2.** A conceptual model illustrating the importance of spatiotemporal heterogeneity in maintaining biological diversity in floodplain rivers. This model is derived from the intermediate disturbance hypothesis (Connell 1978; Shiel and Burslem 2003) and the "patch dynamics concept" (Townsend 1989) and is supported by fish data collected from the Cinaruco River, Venezuela, an unregulated, tropical lowland river. Anthropogenic alterations such as channelization and flow regulation are expected to result in compromised heterogeneity; direction of impact is indicated by dotted lines.

et al. 1989; Bayley 1995), but impoverish regional species pools (Grossman *et al.* 1990; Ward *et al.* 1999). Furthermore, reduction of landscape heterogeneity may impair the resilience typically observed in these systems (Townsend 1989; Meffe and Sheldon 1990; Townsend *et al.* 1997). Consequently, restoration strategies for floodplain rivers must emphasize the return of hydrologic variability characteristic of the pre-impacted system (e.g. Toth, Arrington and Begue 1997) as well as re-establishing among-habitat connectivity (Toth *et al.* 1998).

Interactions among seasonal hydrology, variability in habitat structural complexity and landscape heterogeneity appear to maintain high aquatic species richness in these lowland rivers. It follows that alteration of seasonal water level fluctuation (e.g. damming) and habitat heterogeneity (e.g. channelization) should have substantial and negative consequences on the maintenance of regional biodiversity pools in floodplain rivers. Better ecological understanding is needed to properly manage and preserve biological diversity in tropical floodplain rivers.

ACKNOWLEDGEMENTS

Our research was funded by the National Science Foundation (NSF DEB-0107456), The National Geographic Society, L.T. Jordan Institute and the International Sportfish Fund. This work would not have been possible without the help and assistance of J. Arrington, C. Garcia, J. Garcia, C. Layman, C. Lofgren, C. Marzuola, J. Marzuola, E. Pelaez, A. Stergios, B. Stergios, D. Taphorn and G. Webb. C. Layman and an anonymous reviewer provided helpful comments on this manuscript.



LITERATURE CITED

Allan J.D. & Flecker A.S. 1993. Biodiversity conservation in running waters. *Bioscience*, 43: 32-42.

Amoros C. & Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47: 761-776.

Angermeier P.L. & Winston M.R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, 79: 911-927.

Arrington D.A. 2002. Evaluation of the relationship between habitat structure, community structure, and community assembly in a neotropical blackwater river. Texas A&M University, Texas, College Station. (Doctoral dissertation)

Arrington D.A. & Winemiller K.O. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. *Journal of Fish Biology*, 63: 1-18.

Arrington D.A., Winemiller K.O. & Layman C.A. *In* Review community assembly at the patch scale in a speciose tropical river. *Oecologia*.

Bayley P.B. 1995. Understanding large river-floodplain ecosystems. *Bioscience*, 45: 153-158

Brooks T.M., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A., Rylands B., Konstant A.B., Flick W. R., Pilgrim R., Oldfield J., Magin G. & Hilton-Taylor C. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, 16: 909-923.

Chao A. & Lee S.M. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, 87: 210-217.

Chazdon R.L., Colwell R.K., Denslow J.S. & Guariguata M.R. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Riva. *In* F. Dallmeier & J.A. Comiskey eds. *Forest biodiversity research, monitoring and modeling: Conceptual background and old world case studies*. Paris, Parthenon Publishing. pp. 285-309.

Chesson P. & Huntly N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, 150: 519-553.

Colwell R.H. 1997. Estimate S: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published. (Available at: http://viceroy.eeb.uconn.edu/estimates.)

Colwell R.H. & Coddington J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London* Series B, 345:101-118.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302-1310.

Cornell H.V. & Lawton J.H. 1992. Species interactions, local and regional processes and limits to the richness of ecological communities: A theoretical perspective. *Journal of Animal Ecology*, 61: 1-12.

Cox Fernandes C. 1999. Detrended canonical correspondence analysis (DCCA) of electric fish assemblages in the Amazon. *In* A.L. Val & V.M.F. Almeida-Val eds. *Biology of Tropical Fishes*. Manaus, INPA. pp. 21-39.

Crisman T.L., Chapman L.J., Chapman C.A. & Kaufman L.S. eds. 2003. Conservation, ecology, and management of African fresh waters. Gainesville, Fl., University Press of Florida.

Dudgeon D. 2000. Large-scale hydrological changes in tropical Asia: Prospects for riverine biodiversity. *Bioscience*, 50: 793-806.

Duque A.B., Taphorn D.C. & Winemiller K.O. 1998. Ecology of the coporo, *Prochilodus mariae* Characiformes, Prochilodontidae, and status of annual migrations in western Venezuela. *Environmental Biology of Fishes*, 53: 33-46.

Fernandes C.C. 1997. Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish*, 6: 36-44.

Garcia A.M., Vieira J.P. & Winemiller K.O. 2001. Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary Brazil during cold and warm ENSO episodes. *Journal of Fish Biology*, 59: 1218-1238.

Goulding M., Carvalho M.L. & Ferreira E.G. 1988. *Río Negro: Rich life in poor water*. The Hague: SPB Academic Publishing.

Goulding M., Smith N.J.H. & Mahar D.J. 1996. *Floods of fortune: Ecology and economy along the Amazon*. New York, Columbia University Press.

Griffiths D. 1997. Local and regional species richness in North American lacustrine fish. *Journal of Animal Ecology*, 66: 49-56

Grossman G. D., Dowd J.F. & Crawford M. 1990. Assemblage stability in stream fishes: A review. *Environmental Management*, 14: 661-671.

Grossman G.D., Moyle P.B. & Whitaker J.O. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: A test of community theory. *American Naturalist*, 120: 423-454.

Grossman G.D., Ratajczak R.E. Jr., Crawford M. & Freeman M.C. 1998. Assemblage organization in stream fishes: Effects of environmental variation and interspecific interactions. *Ecological Monographs*, 68: 395-420.

Guégan J., Lek S. & Oberdorff T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, 391: 382-384.

Hoeinghaus D.J., Layman C.A., Arrington D.A. & Winemiller K.O. 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes* 49: 421-433.

Hubbell S.P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs 16: Suppl., S9-S21.

Hubbell S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ., Princeton University Press.

Hugueny, B. & Cornell H.V. 2000. Predicting the relationship between local and regional species richness from a patch occupancy dynamics model. *Journal of Animal Ecology*, 69:194-200.

Hugueny, B. & Paugy D. 1995. Unsaturated fish communities in African rivers. *American Naturalist*, 146: 162-169.

Hurtt G.C. & Pacala S.W. 1995. The consequences of recruitment limitations: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, 176: 1-12.

Ibarra M. & Stewart D.J. 1989. Longitudinal zonation of sandy beach fishes in the Napo River Basin, Eastern Ecuador. *Copeia*, 1989: 364-381.

Jackson D.A., Sommers K.M. & Harvey H.H. 1992. Null models and fish communities: Evidence of nonrandom patterns. *American Naturalist*, 139: 930-951.

Jenkins D.G. & Buikema Jr. A.L. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs*, 68: 421-433.

Jepsen D.B. 1997. Fish species diversity in sand bank habitats of a Neotropical river. *Environmental Biology of Fishes*, 49: 449-460.

Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 110-127.

Lamouroux N., Poff N.L. & Angermeier P.L. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, 83: 1792-1807.

Levin S.A. & Paine R.T. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences USA* 71, 2744-2747.

Lundberg J. 2001. Freshwater riches of the Amazon. *Natural History*, 110: 36-43.

Lundberg J.G., Lewis Jr. W.M., Saunders J.F. III & Mago-Leccia F. 1987. A major food web component in the Orinoco River Channel: Evidence from planktivorous electric fishes. *Science*, 237: 81-83.

MacArthur R.H. & Wilson E.O. 1967. The Theory of island biogeography. Princeton, NJ., Princeton University Press.

Matthews W.J. 1998. *Patterns in Freshwater Fish Ecology*. New York, Chapman and Hall.

Meffe G.K. & Sheldon A.L. 1990. Post-defaunation recovery of fish assemblages in southeastern blackwater streams. *Ecology*, 71: 657-667.

Meyers N., Mittermeier R.A., Mittermeier C. G., da Fonseca G.A.B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.

Oberdorff T., Hugueny B., Compin A. & Belkessam D. 1998. Non-interactive fish communities in the coastal streams of North-western France. *Journal of Animal Ecology*, 67: 472-484.

Oberdorff T., Hugueny B. & Vigneron T. 2001. Is assemblage variability related to environmental variability? An answer for riverine fish. *Oikos*, 93: 419-428.

Petry P., Bayley P.B. & Markle D.F. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, 63.

Poff N.L. & Allan J.D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, 76: 606-627.

Pringle C.M., Freeman M.C. & Freeman B.J. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical-temperate comparisons. *Bioscience*, 50: 807-823.

Rahel F.J. 1990. The hierarchical nature of community persistence: A problem of scale. *American Naturalist*, 136: 328-344.

Resetarits W.J., & Bernardo J. eds. 2001. *Experimental Ecology: Issues and perspectives*. New York, Oxford University Press.

Robinson C., Tockner K. & Ward J.V. 2002. The fauna of dynamic riverine landscapes. *Freshwater Biology*, 47: 661-677.

Rodríguez M.A. & Lewis W.M. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, 67: 109-128.

Saint-Paul U., Zuanon J., Villacorta Correa M.A., García M., Noemi Fabré N., Berger U. & Junk W.J. 2000. Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes*, 57: 235-250.

Schlosser I.J. 1987. A conceptual framework for fish communities in small warmwater streams. *In* W.J. Matthews and D.C. Heins eds. *Community and evolutionary ecology of North American stream fishes*. Norman, OK, USA, University of Oklahoma Press. pp. 17-24.

Schlosser I.J. & Kallemeyn L.W. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology*, 81: 1371-1382.

Schmidt J.C., Webb R.H., Valdez R.A., Marzolf R. & Stevens L.E. 1998. Science and values in river restoration in the Grand Canyon. *Bioscience*, 48: 735-747.

Sheil D. & Burslem D.F.R.P. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution*, 18: 18-26.

Shurin J.B., Havel J.E., Leibold M.A. & Pinel-Alloul B. 2000. Local and regional zooplankton species richness: A scale-independent test for saturation. *Ecology*, 81: 3062-3073

Southwood T.R.E. 1988. Tactics, strategies and templets. *Oikos*, 52: 3-18.

Stewart D.J., Ibarra M. & Barriga-Salazar R. 2002. Comparison of deep-river and adjacent sandy-beach fish assemblages in the Napo River Basin, Eastern Ecuador. *Copeia*, 2002: 333-343.

Taylor C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: Local processes and regional patterns. *Freshwater Biology*, 36: 385-396.

Taylor C.M. & Warren M.L. 2001. Dynamics in species composition of stream fish assemblages: Environmental variability and nested subsets. *Ecology*, 82: 2320-2330.

Tockner K., Schiemer F., Baumgartner C., Kum G., Weigand E., Zweimüller I. & Ward J.V. 1999. The Danube restoration project: Species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers: Research & Management*, 15: 245-258.

Tonn W.M. 1990. Climate change and fish communities: a conceptual approach. *Transactions of the American Fisheries Society, 1*19: 337-352.

Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. 1990. Intercontinental comparison of small-lake fish assemblages: The balance between local and regional processes. *American Naturalist*, 136: 345-375.

Toth L.A., Arrington D.A. & Begue G. 1997. Headwaters restoration and reestablishment of natural flow regimes: Kissimmee River of Florida. *In* J.E. Williams, C.A. Wood & M.P. Dombeck eds. *Watershed restoration: Principles and practices*. Bethesda, MY., American Fisheries Society. pp. 425-444.

Toth L.A., Arrington D.A., Brady M.A. & Muszick D.A. 1995. Conceptual evaluation of factors potentially affecting restoration of habitat structure within the channelized Kissimmee River ecosystem. *Restoration Ecology,* 3: 160-180.

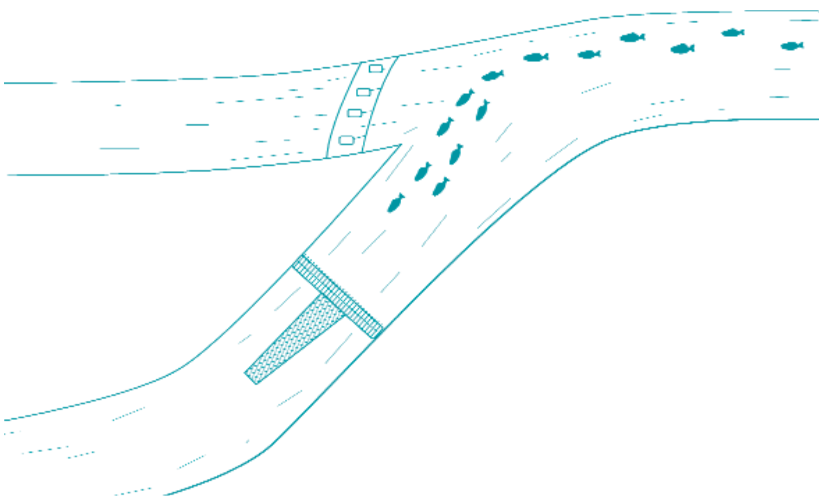
Toth L.A., Melvin S., Arrington D.A. & Chaimberlain J. 1998. Hydrologic manipulations of the channelized Kissimmee River. *Bioscience*, 48: 757-764.

Townsend C.R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society,* 8: 36-50.

Townsend C.R., Scarsbrook M.R. & Dolédec S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography,* 42: 938-949.

Ward J.V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society,* 8: 2-8.

Ward J.V. 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation,* 83: 269-278., 47: 517-539.



ENVIRONMENTAL FLOW ASSESSMENT WITH EMPHASIS ON HOLISTIC METHODOLOGIES

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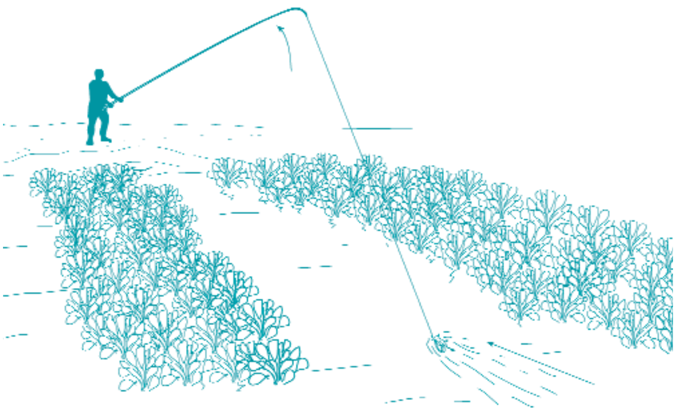


Key words: Environmental Flow Assessment, holistic methodologies, rivers, floodplains, fisheries models, flow experiments, research priorities

ABSTRACT

Worldwide there is growing awareness of the pivotal role of the flow regime (hydrology) as a key 'driver' of the ecology of rivers and their associated floodplain wetlands. Ecological processes related to flow and other factors govern the ecosystem goods and services that rivers provide to humans, such as flood attenuation, water purification, production of fish and other foods and marketable goods. Protecting and restoring river flow regimes and hence the ecosystems they support by providing environmental flows has become a major aspect of river basin management. Over 200 approaches for determining environmental flows now exist and they are used or proposed for use in more than 50 countries

worldwide. Most methodologies currently used in Australia and southern Africa and increasingly in other countries, are holistic in their scope, recognising that it is necessary to provide water for aquatic ecosystems from source to sea and for all water-dependent ecological components. This paper provides a brief history of the development of environmental flow methods and identifies the main features and strengths of each, giving most emphasis to holistic or ecosystem methodologies. We then present an overview of research initiatives needed to enhance these approaches and improve their capacity to predict the ecological, social and economic consequences of change in river flow regimes.

INTRODUCTION

In many parts of the world there is growing awareness of the pivotal role of the flow regime (hydrology) as a key 'driver' of the ecology of rivers and their associated floodplains (see Richter *et al.* 1996; Poff *et al.* 1997; Puckridge *et al.* 1998; Bunn and Arthington 2002; Naiman *et al.* 2002 for reviews). Every river system has an individual or 'signature' flow regime with particular characteristics relating to flow quantity and temporal attributes such as seasonal pattern of flows, the timing, frequency, predictability and duration of extreme events (e.g. floods and droughts), rates of change and other aspects of flow variability (Richter *et al.* 1996; Poff *et al.* 1997; Olden and Poff 2002). Each of these hydrological characteristics has individual as well as interactive regulatory influences on the biophysical structure and functioning of river and floodplain ecosystems, including the physical nature of river channels, sediment regime and water quality, biological diversity/riverine biota and key ecological processes sustaining the aquatic ecosystem (Naiman *et al*. 2002). These processes in turn govern the ecosystem goods and services that rivers provide to humans (e.g. flood attenuation, water purification, production of fish and other foods and marketable goods).

In large part, recognition of the importance of flow and its interactions with other driving variables has stemmed from an increasing body of information describing the negative impacts to riverine ecosystems that are clearly attributable, either directly or indirectly, to the alteration of natural flow regimes (Rosenberg, McCully and Pringle 2000; Bunn and Arthington 2002).

Recognition of the escalating hydrological alteration of rivers on a global scale and the resultant environmental degradation has led to the gradual establishment of a field of scientific research termed environmental flow assessment (EFA) (Tharme 2003). In simple terms, such an assessment addresses how much and which specific temporal characteristics, of the original flow regime of a river should continue to flow down it and onto its floodplains in order to maintain specified features of the riverine ecosystem (Arthington *et al*. 1992; Tharme and King 1998; King, Tharme and De Villiers 2002). An EFA produces one or more descriptions of possible modified hydrological regimes for the river, the environmental flow requirement(s) (EFRs) or environmental water allocation(s), each regime linked to a predetermined objective in terms of the ecosystem's future condition.

Environmental flow assessments are directed at two main types of management response to the potential and extant impacts of altered flow regimes:

(1) A proactive response, intended to maintain the hydrological regimes of undeveloped rivers as close as possible to the un-regulated condition, or at least to offer some level of protection of natural river flows and ecosystem characteristics, and (2) A reactive response, intended to restore certain characteristics of the pre-regulation flow regimeand ecosystem in developed rivers with modified/regulated flow regimes. Both of these circumstances can be addressed using the environmental flow assessment methods currently available.

The level of resolution of the EFR produced may range from a single annual flow volume through to, more commonly nowadays, a comprehensive, modified flow regime where the overall volume of water allocated for environmental purposes is a combination of different monthly and more frequent, event-based flow quantities such as within-channel or floodplain flood pulses (Tharme 2003). The scale at which the assessment is undertaken may also vary widely, for instance, from an entire large river basin that includes a regulated main channel and/or several regulated tributaries, to a flow restoration project for a single flow-impacted river reach (Arthington, Brizga and Kennard 1998; King, Tharme and Brown 1999). Different methodologies are appropriate at each particular spatial scale as well as in relation to typical project constraints, including the time frame for assessment, the availability of data, technical capacity and finances (Tharme 1996; Arthington *et al.* 1998; Arthington, *et al.* 2003a; Kennard *et al.* 2003b). Methodologies accordingly range from rapid, reconnaissance-level approaches for regional, national or basin wide water resources planning, to resource intensive methodologies for highly exploited, individual river sites subject to multiple uses or rivers of high conservation significance.

This paper describes the origins of methods for environmental flow assessment and the different types of approaches presently available. It does not describe individual methods in detail, as many reviews, case studies and manuals are available (*inter alia* Bovee 1982, 1998; Milhous, Updike and Schneider 1989; Arthington and Pusey 1993; Stalnaker *et al*.; Tharme 1996; Jowett 1997; Stewardson and Gippel 1997; Dunbar *et al.* 1998; Arthington 1998; Arthington and Zalucki 1998; Dunbar *et al.* 1998; Milhous 1998; King *et al.* 2002, 2003, 1999; Tharme 2003). Further information on recent world developments in the field of environmental flow assessment can be found in *River Research and Applications* Volume 19 (2003) containing selected papers from the *International Working Conference on Environmental Flows for River Systems and the Fourth International Ecohydraulics Symposium* (held in Cape Town, South Africa, March 2002).

The main focus of this paper is the category of techniques termed holistic methodologies (*sensu* Tharme 1996) and their diversification to address both river ecosystem protection (i.e. proactive approaches) and river ecosystem restoration (i.e. reactive approaches). We outline the characteristics, strengths and limitations of the main holistic methodologies in use today and comment on shared features and best practices that commend these methods for use in developed as well as developing countries. We conclude with a brief overview of the modelling and research initiatives needed to enhance these holistic methodologies and increase their capacity to produce quantitative predictions of the effects of altering a river's flow regime outcomes and eventually, predictive models of the ecological and knock-on socio-economic consequences of changes in river flow regimes.

THE ORIGINS OF ENVIRONMENTAL FLOW ASSESSMENT

Tharme (1996) traced the evolution of environmental flow methodologies worldwide, observing that historically, the United States of America was at the forefront of research with the first *ad hoc* methods appearing in the late 1940s and a series of more formally documented techniques emerging in the late 1970s. In most other parts of the world, EFA processes became established far later, with approaches to determine environmental water allocations only beginning to appear in the literature in the 1980s. Early on and still today in some countries, the focus of environmental flow assessment was the maintenance of economically important freshwater fisheries, especially salmonid fisheries, in regulated rivers. The main objective was to define a minimum acceptable flow based almost entirely on predictions of instream habitat availability matched against the habitat preferences of one or a few species of fish (see Jowett 1997; Pusey 1998 for reviews). It was assumed that the flows recommended to protect target fish populations, habitats and food resources would ensure maintenance of the river ecosystem. From these early attempts to quantify appropriate stream flows for fish, many new methods and innovations have evolved and recently, a much more comprehensive approach to EFAs has been adopted in both theory and practice.

DESCRIPTION OF METHODOLOGIES

Tharme (1996, 2003) has recognised four relatively discrete types of environmental flow methodology: (1) hydrological, (2) hydraulic rating, (3) habitat simulation and (4) holistic methodologies; among other techniques occasionally applied during EFAs. The four types are briefly described below.

HYDROLOGICAL METHODOLOGIES

These represent the simplest set of techniques where, at a desktop level, hydrological data, as naturalised, historical monthly or average daily flow records, are analysed to derive standard flow indices which then become the recommended environmental flows. Commonly, the EFR is represented as a proportion of flow (often termed the 'minimum flow', e.g. Q_{95} – the flow equalled or exceeded 95 percent of the time) intended to maintain river health, fisheries or other highlighted ecological features at some acceptable level, usually on an annual, seasonal or monthly basis. In a few instances, secondary criteria in the form of catchment variables, hydraulic, biological or geomorphological parameters are also incorporated. As a result of the rapid and non-resource intensive provision of low resolution flow estimates, hydrological methodologies are generally used mainly at the planning stage of water resource developments, or in situations where preliminary flow targets and exploratory water allocation trade-offs are required (Tharme 1996; Arthington *et al.* 1998; Tharme 2003).

HYDRAULIC RATING METHODOLOGIES

Hydraulic rating methodologies use changes in simple hydraulic variables, such as wetted perimeter or maximum depth, usually measured across single, flow-limited river cross-sections (commonly riffles), as a surrogate for habitat factors known or assumed to be limiting to target biota. Environmental flows are determined from a plot of the hydraulic variable(s) against discharge, commonly by identifying curve breakpoints where significant percentage reductions in habitat quality occur with decreases in discharge. It is assumed that ensuring some threshold value of the selected hydraulic parameter at a particular level of altered flow will maintain aquatic biota and thus, ecosystem integrity. These relatively low-resolution hydraulic techniques have been superseded by more advanced habitat modelling tools, or assimilated into holistic methodologies (Tharme 1996; Jowett 1997; Arthington and Zalucki 1998; Tharme 2003). However, select approaches continue to be applied and evaluated, notably the Wetted Perimeter Method (e.g. Gippel and Stewardson 1998).

HABITAT SIMULATION OR MICROHABITAT MODELLING METHODOLOGIES

Habitat simulation methodologies also make use of hydraulic habitat-discharge relationships, but provide more detailed, modelled analyses of both the quantity and suitability of the physical river habitat for the target biota. Thus, environmental flow recommendations are based on the integration of hydrological, hydraulic and biological response data. Flow-related changes in physical microhabitat are modelled in various hydraulic programs, typically using data on depth, velocity, substratum composition and cover; and more recently, complex hydraulic indices (e.g. benthic shear stress), collected at multiple cross-sections within each representative river reach. Simulated information on available habitat is linked with seasonal information on the range of habitat conditions used by target fish or invertebrate species (or life-history stages, assemblages and/or activities), commonly using habitat suitability index curves (e.g. Groshens and Orth 1994). The resultant outputs, in the form of habitat-discharge curves for specific biota, or extended as habitat time and exceedence series, are used to derive optimum environmental flows. The habitat simulation-modelling package PHABSIM (Bovee 1982, 1998; Milhous 1998, 1982; Milhous *et al.* 1989; Stalnaker *et al.* 1994), housed within the Instream Flow Incremental Methodology (IFIM), is the pre-eminent modeling platform of this type. The relative strengths and limitations of such methodologies are described in King and Tharme (1994); Tharme (1996); Arthington and Zalucki (1998); Pusey (1998) and they are compared with the other types of approach in Tharme (2003).

HOLISTIC METHODOLOGIES

Over the past decade, river ecologists have increasingly made the case for a broader approach to the definition of environmental flows to sustain and conserve river ecosystems, rather than focusing on just a few target fish species (Arthington and Pusey 1993; King and Tharme 1994; Sparks 1992, 1995; Richter *et al*. 1996; Poff *et al*. 1997). From the conceptual foundations of a holistic ecosystem approach (proposed by Arthington *et al*. 1992), a wide range of holistic methodologies has been developed and applied, initially in Australia and South Africa and more recently in the United Kingdom. This type of approach reasons that if certain features of the natural hydrological regime can be identified and adequately incorporated into a modified flow regime, then, all other things being equal, the extant biota and functional integrity of the ecosystem should be maintained (Arthington *et al*. 1992; King and Tharme 1994). Likewise, Sparks (1992, 1995) suggested that rather than optimising water regimes for one or a few species, a better approach is to try to approximate the natural flow regime that maintained the "entire panoply of species".

Importantly, holistic methodologies aim to address the water requirements of the entire "riverine ecosystem" (Arthington *et al*. 1992) rather than the needs of only a few taxa (usually fish or invertebrates). These methodologies are underpinned by the concept of the "natural flows paradigm" (Poff *et al.* 1997) and basic principles guiding river corridor restoration (Ward *et al*. 2001,;Uehlinger *et al.* 2001). They share a common objective - to maintain or restore the flow-related biophysical components and ecological processes of in-stream and groundwater systems, floodplains and downstream receiving waters (e.g. terminal lakes and wetlands, estuaries and near-shore marine ecosystems).

Ecosystem components that are commonly considered in holistic assessments include geomorphology, hydraulic habitat, water quality, riparian and aquatic vegetation, macroinvertebrates, fish and other vertebrates with some dependency upon the river/riparian ecosystem (i.e. amphibians, reptiles, birds, mammals). Each of these components can be evaluated using a range of field and desktop techniques (see Tharme 1996; Arthington and Zalucki 1998; Tharme 2003; for reviews) and their flow requirements are then incorporated into EFA recommendations, using various systematic approaches as discussed in more detail below.

Holistic environmental flow assessments may include evaluation of a range of other mitigation measures, for example, how to restore longitudinal and lateral connectivity by providing fish passes or altering the configuration of levee banks on a floodplain. Management of storage water levels may also be examined and recommendations made on the benefits of more, or less, stable water levels. Some holistic methodologies also take into consideration the influence of threatening processes and disturbances unrelated (or less directly related) to flow regulation and advise on possible mitigation measures such as riparian and habitat restoration, or the management of invasive vegetation and fish.

TYPES OF HOLISTIC METHODOLOGY

Holistic methodologies currently represent around 8 percent of the global total, with at least 16 extant methodologies based on the holistic principles described above having been developed over the last ten years (Tharme 2003). Although predominantly developed and used in South Africa and Australia, recently such methods have begun to attract growing international interest in both developed and developing regions of the world, with strong expressions of interest from in excess of 12 countries in Europe, Latin America, Asia and Africa (Tharme 2003).

These approaches have been described (see Arthington *et al.* 1998) as either 'bottom-up' methods (designed to 'construct' a modified flow regime by adding flow components to a baseline of zero flows), or 'top-down' methods (addressing the question, "How much can we modify a river's flow regime before the aquatic ecosystem begins to noticeably change or becomes seriously degraded?").

For comparative purposes, selected holistic methodologies are summarised in Table 1, in terms of their origins, key features, strengths, limitations and present stage of development and application (adapted from Tharme 2003). Further details of the various methodologies are available in the source references provided in Table 1, as well as in the review papers listed herein.

The South African Building Block Methodology or BBM (King and Tharme 1994; King and Louw 1998; King *et al*. 2002) was the first structured approach of this type. It began as a bottom-up method, more recently incorporating the Flow Stress-Response Method (O'Keeffe and Hughes 2002). In this modified form, the BBM is legally required for intermediate and comprehensive determinations of the South African Ecological Reserve (DWAF 1999). Other essentially bottom-up methodologies include 'expert' and 'scientific panel' methods developed and applied in Australia (reviewed in Cottingham, Thoms and Quinn 2002).

There are several so-called 'top-down' methods. Examples of top-down methods are the Benchmarking Methodology (Brizga *et al*. 2001) used routinely in Queensland (Australia) at the planning stage of new developments to assess the environmental impacts likely to result from future water resource developments and DRIFT - Downstream Response to

Table 1: Summary of holistic environmental flow methodologies presented in approximate sequence of development, highlighting salient features, strengths and limitations, as well as their current status in terms of development and application (adapted from Tharme 2003). Further information on the strengths and deficiencies of individual holistic methodologies is provided in Tharme (1996); Arthington (1998); Cottingham *et al*. (2002); Arthington *et al*. (2003a); King *et al*. (2003); Tharme (2003). Abbreviations: DNR – Queensland Department of Natural Resources; DWAF – South African Department of Water Affairs and Forestry; EAFR – ecologically acceptable flow regime; EF – environmental flow; EFA – EF assessment; EFR(s) – EF requirement(s); EFM – EF methodology; TAP – technical advisory panel; WAMP – water allocation and management planning; WRD(s) – water resource development(s); abbreviations for methodology names are given in the first table column.

Methodology	Origins	Features, strengths and limitations	Status
Holistic Approach: (Arthington *et al*. 1992; Davies *et al*. 1996; Arthington 1998; Petit *et al*. 2001).	Developed in Australia to address EFRs of entire riverine ecosystem; shared conceptual basis with BBM and the theoretical and conceptual basis of the Benchmarking Methodology and Flow Restoration Methodology.	Conceptual and theoretical approach for bottom-up construction of EF regime for whole riverine ecosystem from headwaters to floodplains, including groundwater and estuary or coastal waters; describes systematic construction of a modified flow regime, on a month-by-month (or shorter time scale) flow element-by-element basis and based on best available scientific data, to achieve predetermined objectives for future river condition of rivers; principally represents a flexible conceptual framework, elements of which have been adapted in a variety of ways into several Australian holistic methodologies and for individual studies; basic tenets and assumptions as per BBM, which was derived from it; incorporates more detailed assessment of flow variability than early BBM studies; includes method for generating trade-off curves for examining alternative water use scenarios; some risk of inadvertent omission of critical flow events (common to all holistic methodologies); applicable to regulated or unregulated rivers and for flow restoration; high potential for application to other aquatic ecosystems; recommends a monitoring programme as a crucial component of holistic flow assessments; lack of structured set of procedures and clear identity for EFM hinders rigorous routine application (but routinely used in customized format in Western Australia).	Represents conceptual and theoretical basis of most other holistic EFMs; developed and applied in various forms in Australia, e.g. expert panel assessments, Flow Events Method, Benchmarking Methodology and Flow Restoration Methodology

Methodology	Origins	Features, strengths and limitations	Status
Building Block Methodology (BBM): (King and Louw 1998; King *et al*. 2000).	Developed in South Africa by local researchers and DWAF, through application in numerous water resource development projects to address EFRs for entire riverine ecosystems under conditions of variable resources; adapted for intermediate and comprehensive determinations of the ecological Reserve under the new SA Water Law.	Rigorous and extensively documented (manual and case studies available); prescriptive bottom-up approach with interactive scenario development; moderate to highly resource intensive; shared conceptual basis with Holistic Approach; developed to differing extents for both intermediate-level (2 months) or comprehensive (1-2 years) EFAs, within South Africa's Reserve framework; based on a number of sites within representative and/or critical river reaches; includes a well established social component (dependent livelihoods); functions in data poor or rich situations; comprises 3-phase approach : (1) preparation for workshop, including stakeholder consultation, desktop and field studies for site selection, geomorphological reach analysis, river habitat integrity and social surveys, objectives setting for future river condition, assessment of river importance and ecological condition, hydrological and hydraulic analyses, (2) multidisciplinary workshop-based construction of modified flow regime through identification of ecologically essential flow features on a month-by-month (or shorter time scale), flow element-by-flow element basis, for maintenance and drought years, based on best available scientific data, (3) linking of EFR with water resource development engineering phase, through scenario modelling and hydrological yield analysis; EFM exhibits limited potential for examination of alternative scenarios relative to DRIFT, as BBM EF regime is designed to achieve a specific predefined river condition; incorporates a monitoring programme and additional research on important issues, as crucial components of EF implementation; some risk of inadvertent omission of critical flow events (common to all holistic methodologies), high potential for application to other aquatic ecosystems; links to external stakeholder and public participation processes; flexible and amenable to simplification for more rapid assessments; less time, cost and resource intensive than DRIFT; applicable to regulated or unregulated rivers and in flow restoration context; now incorporates Flow Stressor-Response Method facilitating top-down, scenario-based assessments of alternative flow regimes, each with expression of the potential risk of change in river ecological condition.	Most frequently used holistic EFM globally, applied in 3 countries; adopted as the standard EFM for South African Reserve determinations
Expert Panel Assessment Method (EPAM): (Swales and Harris 1995).	First multidisciplinary panel based EFM used in Australia, developed jointly by the New South Wales Departments of Fisheries and Water Resources.	Bottom-up, reconnaissance-level approach for initial assessment of proposed WRDs with many conceptual features and methodological procedures in common with the Holistic Approach and BBM; rapid and inexpensive, with limited field data collection; site-specific focus; applicable primarily for sites where dam releases are possible; relies on field-based ecological interpretation, by a panel of experts, of different multiple trial flow releases (ranked in terms of scored ecological suitability) from dams, at one or	Applied only in Australia; several applications, both in original and variously modified forms

Methodology	Origins	Features, strengths and limitations	Status
		a few sites, to determine EFR (typically expressed as flow percentiles); low resource intensity; limited resolution of EF output; aims to address river ecosystem health (using fish communities as indicators), rather than to assess multiple ecosystem components; strongly reliant on professional judgement; limited subset of expertise represented by panel (e.g. fish, invertebrates, geomorphology); simplistic in terms of the range of ecological criteria and components assessed (but scope for inclusion of additional ones) and the focus on fish; no explicit guidelines for application; poor congruence in opinion of different panel members (e.g. due to subjective scoring approach, individual bias); requires further validation; led to development of more advanced, but similar SPAM, Snowy Inquiry Methodology and other expert panel approaches.	
Scientific Panel Assessment Method (SPAM): (Thoms *et al*. 1996; Cottingham *et al*. 2002).	Developed during an EFA for the Barwon-Darling River System, Australia.	Bottom-up field (multiple sites) and desktop approach appropriate for provision of interim or intermediate level EFAs with many conceptual features and methodological procedures in common with the Holistic Approach and BBM; evolved from EPAM as more sophisticated and transparent expert-panel approach; aims to determine a modified flow regime that will maintain ecosystem health; differs from EPAM in that key features of the ecosystem and hydrological regime and their interactions at multiple sites are used as basis for EFA; EFR process includes: (1) identification of management performance criteria by panel of experts for 5 main ecosystem components: fish, trees, macrophytes, invertebrates and geomorphology, (2) application of the criteria for three elements (and associated descriptors) identified as exerting an influence on the ecosystem components (viz. flow regime, hydrograph and physical structure at 3 spatial scales), (3) workshop-based cross-tabulation approach to identify and document generalised responses and/or impacts for each ecosystem components to each specific descriptor (for each element), so as to relate flow regime attributes to ecosystem responses and EFRs; incorporates system hydrological variability and elements of ecosystem functioning; includes stakeholder-panel member workshop for EFR refinement; well defined EFA objectives; some potential for inclusion of other ecosystem components; led to the evolution of other expert-panel approaches; limited use of field data; poor definition of output format for EFR; moderately rapid, flexible and resource-intensive; simpler, less quantitative supporting evidence and less rigorous than Flow Restoration Methodology, BBM and DRIFT; recent applications and limitations reviewed, need for a Best Practice Framework identified.	Appears limited to a single application in Australia in its original form; general approach variously modified for other expert-panel based EFAs

Methodology	Origins	Features, strengths and limitations	Status
Habitat Analysis Method: (Walter *et al*. 1994; Burgess and Vanderbyl 1996; Arthington 1998).	Developed by former Queensland Department of Primary Industries, Water Resources (now DNR), Australia, as part of water allocation and management planning initiative.	Relatively rapid, inexpensive, basin-wide reconnaissance method for determining preliminary EFRs at multiple points in catchment (rather than at a few critical sites); superior to simple hydrological EFMs, but inadequate for comprehensive EFAs; field data limited or absent; bottom-up process of 4 stages using TAP: (1) identification of generic aquatic habitat types existing within the catchment, (2) determination of flow-related ecological requirements of each habitat (as surrogate for EFRs for aquatic biota), using small group of key flow statistics, plus select 'biological trigger' flows and floods for maintenance of ecological and geomorphological processes, (3) development of bypass flow strategies to meet EFRs, (4) development of EFR monitoring strategy; EFM represents an extension of expert panel approaches (EPAM, SPAM), with conceptual basis and assumptions adapted from Holistic Approach; little consideration of specific flow needs of individual ecological components; requires standardisation of process, refinement of flow bands linked to habitats and addition of flow events related to needs of biota; represents a simplified version of the Holistic Approach; largely superseded by Benchmarking Methodology.	Precursor of Benchmarking Methodology within WAMP initiatives; several applications within Australia
Benchmarking Methodology: (Brizga *et al*. 2001, 2002).	Developed in Queensland, Australia, by local researchers and DNR, to provide a framework for assessing risk of environmental impacts due to WRDs, at basin scale.	Rigorous and comprehensive, scenario-based, top-down approach for application at basin scale; using field and desktop data for multiple river sites; same conceptual basis as BBM and Holistic Approach, EFM has 4 main stages: (1) establishment: formation of multidisciplinary expert panel (TAP) and development of hydrological model for catchment, (2) ecological condition and trend assessment: development of spatial reference framework (multiple river sites within representative and critical river reaches), assessment of ecological condition for suite of ecosystem components (using 3-point rating of degree of change from reference condition and appropriate methods for assessing each component), development of generic models (conceptual, empirical) defining links between flow regime components and ecological processes, selection of key flow indicators and statistics with relevance to these relationships, modelling-based assessment of hydrological impacts, (3) development of risk assessment framework to guide evaluation of potential impacts of future water resource development and management scenarios: benchmark models are developed for all or some key flow indicators showing levels of risk of geomorphological and ecological impacts associated with different degrees of flow regime change, risk levels are defined by association with benchmark sites which have undergone different degrees of flow-related change in con-	Sole holistic EFM for basin-scale assessment and assessing risk of environmental impacts due to WRD; adopted for routine application in Queensland with applications in 15 basins; under consideration for use in Western Australia; only applied in Australia to date

Methodology	Origins	Features, strengths and limitations	Status
		dition, link models are used to show how the modelled flow indicators affect ecological condition, (4) evaluation of future WRD scenarios, using risk assessment and link models, ecological implications of scenarios and associated levels of risk readily expressed in graphical form; EFM is particularly suited to data poor situations; potential for use in developing countries and for application to other aquatic ecosystems (e.g. wetlands, estuaries); utilises a wide range of specialist expertise; presents a comprehensive benchmarking process and transparent reporting system; provides several ways of developing risk assessment models, guidance on key criteria for assessing condition and key hydrological and performance indicators; a recent approach built on several preceding EFA initiatives; no explicit consideration of social component, but with scope for inclusion of socio-economic assessments (note that socio-economic issues are evaluated separately by DNR and considered when the final EF recommendations are being decided); requires evaluation of several aspects (e.g. applicability or sensitivity of key flow statistics, degree to which benchmarks from other basins or sites within basins are valid considering differences in river hydrology and biota); recommends a monitoring programme and additional research on important issues, as crucial components of EF implementation; requires documentation of generic procedure for wider application.	
Environmental Flow Management Plan Method (FMP): (Muller 1997; DWAF 1999).	Developed in South Africa by the Institute for Water Research, for use for intensively regulated river systems.	Simplified bottom-up approach, applicable in highly regulated and managed systems with considerable operational limitations; considered for use within South Africa Reserve determination process only where BBM or equivalent approach cannot be followed; workshop-based, multidisciplinary assessment including ecologists and system operators; 3-step process: (1) definition of operable reaches for study river and site selection, establishment of current operating rules, (2) determination of current ecological status and desired future state, (3) identification of EFRs using similar procedures to BBM; EFM has limited scope for application; structure and procedures for application are not formalised or well documented; poorly established post-workshop scenario phase; no evaluation undertaken; considerably more limited approach than Flow Restoration Methodology.	Limited to 3 applications; only used in South Africa to date; uncertain status within the national Reserve framework

Methodology	Origins	Features, strengths and limitations	Status
River Babingley (Wissey) Method: (Petts *et al*. 1999).	First developed for application in groundwater-dominated rivers, Anglian Region of England.	Bottom-up field and desktop approach; EAFR (the EF regime) defined in 4 stages: (1) ecological assessment of river and specification of an ecological objective comprising specific targets (for river components and biota), (2) determination of 4 general and 2 flood benchmark flows to meet the specified targets, (3) use of flows to construct 'ecologically acceptable hydrographs', which may include provision for wet years and drought conditions, (4) assignment of acceptable flow frequencies and durations to the hydrographs and their synthesis into a flow duration curve, the EAFR; EFM uses hydro-ecological models, habitat and hydrological simulation tools to assist in identification of benchmark flows and overall EAFR; allows for flexible examination of alternative EF scenarios; loosely structured approach, with limited explanation of procedures for integration of multidisciplinary input; risk of omission of critical flow events from EAFR; specific to baseflow-dominated rivers and requires further research for use in flashy catchments; requires documentation of generic procedure for wider application.	Relatively limited application to date; general approach appears to have been extended to other EFA studies in the UK
Downstream Response to Imposed Flow Transformations (DRIFT): (King *et al*. 2003; Arthington *et al*. 2003a).	Developed in southern Africa by Southern Waters and Metsi Consultants (with inputs from Australian and southern African researchers) as an interactive scenario-based holistic EFM with explicit socio-economic component.	Rigorous and well-documented top-down, scenario-based process with interactive scenario development; same conceptual basis as BBM and Holistic Approach; appropriate for comprehensive EFAs (1-3 years) based on several sites within representative and critical river reaches; comprised of 4 modules: (1) biophysical module: used to describe present ecosystem condition, to predict how it will change under a range of different flow alterations, uses generic lists of links to flow and relevance for each specialist component, each prediction and the direction and severity of change are recorded in a database, to quantify each flow-related impact, (2) sociological module: used to identify subsistence users at risk from flow alterations and to quantify their links with the river in terms of natural resource use and health profiles, (3) scenario development module: links first 2 modules through querying of database, to extract predicted consequences of altered flows (with potential for presentation at several levels of resolution); this process is used to create flow scenarios (typically 4 or 5), (4) economic module: generates description of costs of mitigation and compensation for each scenario; well developed ability to address socio-economic links to ecosystem; considerable scope for comparative evaluation of alternative modified flow regimes; high potential for application to other aquatic ecosystems; resource intensive but amenable to simplification for more rapid assessments; uses many successful features of other holistic EFMs; exhibits parallels with	EFM with most developed capabilities for scenario analysis and explicit consideration of social and economic effects of changing river condition on subsistence users; limited application to date, within southern Africa

Methodology	Origins	Features, strengths and limitations	Status
		Benchmarking Methodology; output is more suitable for negotiation of tradeoffs than in BBM or other bottom-up approaches, as implications of not meeting the EFR are readily accessible; links to external public participation process and macro-economic assessment; generic lists provide clear parameters for inclusion in a monitoring programme; applicable to regulated or unregulated rivers and for flow restoration; EFM modules require refinement; approach provides limited consideration of synergistic interactions among different flow events and ecosystem components; limited inclusion of flow indices describing system variability; recommends a monitoring programme and additional research on important issues, as crucial components of EF implementation; requires documentation of generic procedure for wider application.	
Adapted BBM-DRIFT Methodology: (Steward *et al*. 2002).	Developed in Zimbabwe by Mott MacDonald Ltd. in collaboration with Zimbabwe National Water Authority (with input from South Africa) through adaptation of key elements of BBM and DRIFT, in response to requirements in new Water Act for EFAs.	Simplified top-down, multidisciplinary team approach, for use in highly resource-limited (including data limited) situations and with direct dependencies by rural people on riverine ecosystems; combines pre-workshop data collection phase of BBM with DRIFT's scenario-based workshop process; comprises 3 phases: (1) preparation for workshop as per BBM and DRIFT, but excluding certain components (e.g. habitat integrity and geomorphological reach analyses) and with limited field data collection, (2) workshop, with simplified DRIFT process linking the main geomorphological, ecological and social impacts with elements of the flow regime (based on assessments of impact and severity for component-specific generic lists), used to construct a matrix, (3) use of matrix in evaluating development options, where the matrix indicates ecosystem aspects that are especially vulnerable or important to rural livelihoods, socially and ecologically critical elements of the flow regime and EF recommendations for mitigation; EFM incorporates more limited ecological and geomorphological assessments than BBM and DRIFT; limited coverage of key specialist disciplines; no link to system for defining target river condition; limited capability for scenario development; especially appropriate in developing countries context; requires further development and validation; would benefit from inclusion of economic data.	Under early development, single documented application to date

Methodology	Origins	Features, strengths and limitations	Status
Flow Restoration Methodology (FLOWRESM): (Arthington *et al*. 1999; Arthington *et al*. 2000).	Developed in a study of the Brisbane River, Queensland, Australia, specifically addressing EFRs in river systems exhibiting a long history of flow regulation and requiring flow restoration.	Primarily bottom-up, field and desktop approach appropriate for comprehensive (or intermediate) EFAs; EFM represents hybrid of Holistic Approach and BBM; designed for use in intensively regulated rivers with emphasis on identification of the essential features that need to be built back into the hydrological regime to shift the regulated river system towards the pre-regulation state; EFM uses an 11-step process in 2 stages, in which the following are achieved: (1) review of changes to the river hydrological regime (focusing on unregulated, present day and future demand scenarios, using hydrological simulation model), (2) series of 8 steps within scenario-based workshop, using extensive multidisciplinary specialist input from field work, literature and expert judgement: determination of flow-related environmental effects for low and high flow months, rationale and potential for restoration of various flow components so as to restore ecological components and functions and establishment of EFRS based on identification of critical flow thresholds or flow bands that meet specified ecological or other objectives, (3) develops series of EF scenarios (quantity, timing, duration of flows) and assesses implications of multiple scenarios for system yield, (4) outlines remedial actions not related to flow regulation, alternatives to flow restoration (e.g. physical habitat restoration, fish passage facilities) are evaluated when some elements of pre-regulation flow regime cannot be restored fully for practical or legal reasons, (5) outlines monitoring strategy to assess benefits of EFRs; particular relevance to rivers regulated by large dams, but applicable to any river system regulated by infrastructure or surface and/or groundwater abstraction; includes well-developed hydrological and ecological modelling tools; more rigorous than expert-panel methods; includes flexible top-down process for assessing ecological implications of alternative modified flow regimes and impacts of not restoring particular flows; potential for adoption of full benchmarking process to rank outcomes of not restoring critical flows; some risk of inadvertent omission of critical flow events (common to all holistic approaches); requires documentation of generic procedure for wider application.	Most comprehensive EFM for flow-related river restoration; single application in Australia to date; EFM case study on Brisbane River used as a procedural guide in other recent EF applications (e.g. Ord River study, Western Australia)

Methodology	Origins	Features, strengths and limitations	Status
Flow Events Method (FEM): (Stewardson and Cottingham 2002).	Developed by Australian Cooperative Research Centre for Catchment Hydrology to provide state agencies with a standard approach for EFAs.	Top-down method for regulated rivers; considers the maximum change in river hydrology from natural or key ecologically relevant flow events, based on empirical data or expert judgement; considered a method of integrating existing analytical techniques and expert opinion to identify important aspects of the flow regime; EFM comprises 4 steps: (1) identification of ecological processes (hydraulic, geomorphic and ecological) affected by flow variations at range of spatial and temporal scales, (2) characterisation of flow events (e.g. duration, magnitude) using hydraulic and hydrological analyses, (3) description of the sequence of flow events for particular processes, using a frequency analysis to derive event recurrence intervals for a range of event magnitudes, (4) setting of EF targets, by minimising changes in event recurrence intervals from natural or reference or to satisfy some constraint (e.g. maximum percent permissable change in recurrence interval for any given event magnitude); EFM's singular development appears to be analysis of changes in event recurrence intervals with altered flow regimes; draws greatly on established procedures of other complex EFMs (e.g. BBM, FLOWRESM and DRIFT); may be used to: (1) assess the ecological impact of changes in flow regimes, (2) specify EF management rules and/or targets, (3) optimise flow management rules to maximise ecological benefits within constraints of existing WRD schemes; possibly places undue emphasis on frequency compared with other event characteristic independent of an associated expert panel method, but could be embedded into one as routine procedure.	Recent approach with few applications in Australia to date; often linked to expert-panel approaches

Imposed Flow Transformations (King, Brown and Sabet 2003), a scenario-based approach that also predicts the probable ecological impacts of various scenarios of flow regime change. These methodologies make such predictions in different ways, as outlined in Table 1 and the background literature cited for each method therein. The Flow Restoration Methodology (Arthington *et al.* 1999; Arthington *et al*. 2000) is a bottom-up approach with the objective of shifting a regulated flow regime and river system more towards its natural state, combined with a simple top-down appraisal of the probable ecological consequences of not restoring certain features of the pre-regulation flow regime. The Flow Events Method (Stewardson and Cottingham 2002) seems to be a rather similar approach, usually linked to a scientific panel method (Table 1).

Additional holistic methodologies developed and applied elsewhere include the River Babingley Method (Petts *et al.* 1999) developed in England and the Adapted BBM-DRIFT methodology developed in Zimbabwe (Steward, Madamombe and Topping 2002).

In applications of holistic methodologies to date, the focus has almost entirely been on river systems, with most effort addressed to the main river channel and its tributaries and it is only relatively recently that specialist methods have been proposed to address the freshwater flow requirements of downstream receiving waterbodies (e.g. floodplains and terminal lakes in large arid-zone and tropical rivers) and estuaries (e.g. Loneragan and Bunn 1999). Further, methodologies to integrate the dynamic interactions of surface and groundwater systems into existing holistic methodologies are at a fairly immature stage of development, with none routinely applied as part of holistic assessments (King *et al.* 1999).

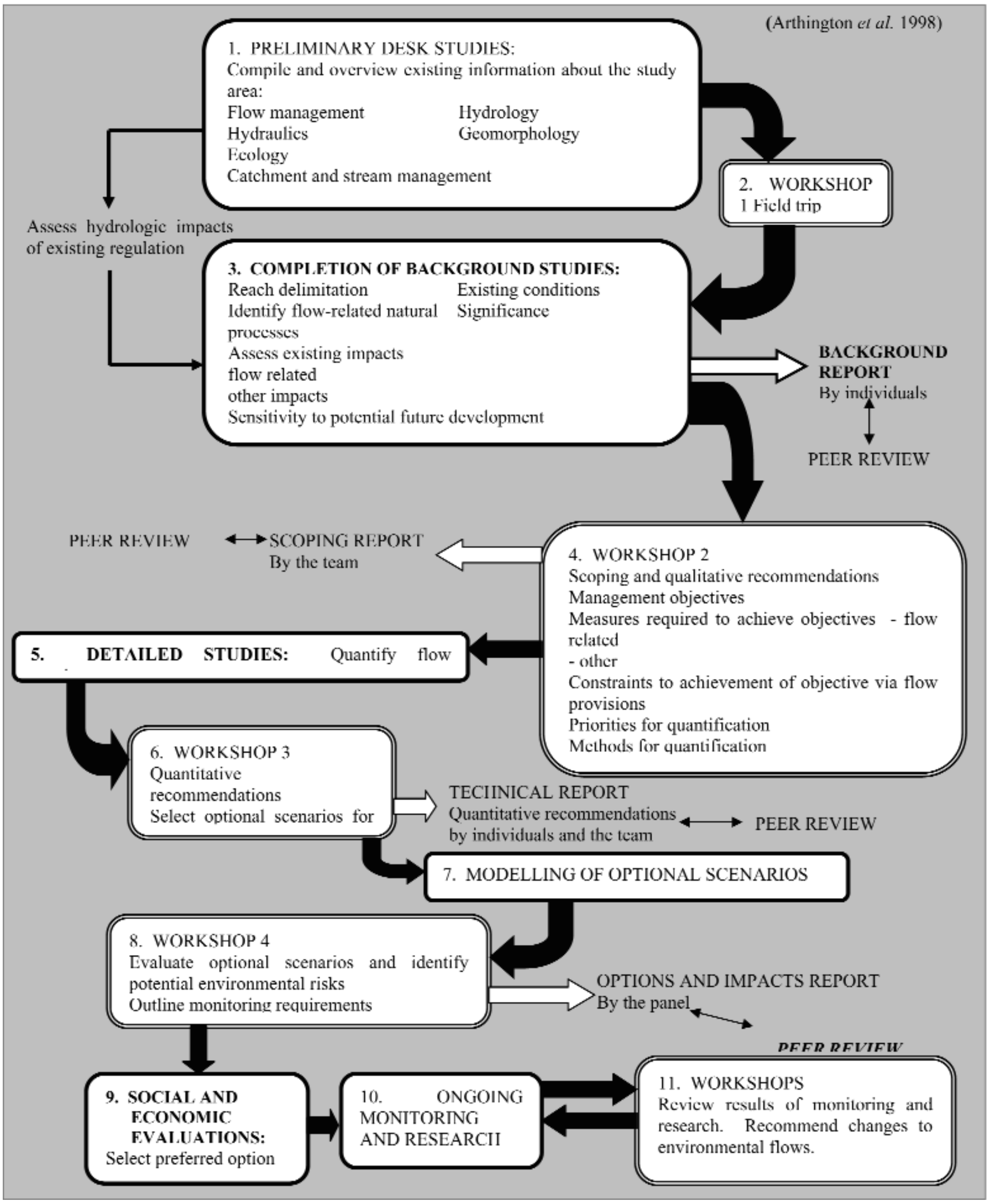
SHARED STRENGTHS OF HOLISTIC METHODOLOGIES

Most holistic methodologies employ some form of expert panel-based approach in the derivation of the EFRs of rivers, including those that are specifically termed ‘expert panel’ methods in their own right themselves (e.g. Expert Panel Assessment Method and Scientific Panel Assessment Method, see Table 1). In a review of the use and utility of Australian expert panel methods, Cottingham *et al.* (2002) commented that environmental flow methods using scientific panels have been “an excellent knowledge exchange mechanism”, many are “rapid and inexpensive compared to empirical investigations” (but note that the most recent holistic methodologies use empirically derived, as well as other, knowledge sources), have “the flexibility to adapt the most appropriate and up-to-date assessment methods”, and can “ make use of information ranging from anecdotal to theoretical”. Their shortcomings are judged to fall into two categories: those relating to the scope and quality of field assessments and “problems relating to panel discussions and recommendations” (Cottingham *et al.* 2002).

To offset these shortcomings, Cottingham *et al*. (2002) suggest that scientific panel methods would be bolstered by the development of a flexible “best practice” approach suitable for wide application and including the following major features:

- Clear processes for selecting panel members and protocols to guide the conduct of panels and the interactions between members;
- Guidelines for developing a “vision statement” and explicit ecological objectives, so that any ecosystem response to environmental flow provisions can be measured against the desired outcomes in an adaptive management framework;
- More explicit guidelines regarding the selection of field sites and the collection of new field data;
- Procedures for recording the strengths and limitations of evidence used to make environmental flow recommendations;
- Consideration of the social and economic implications of environmental flow recommendations;
- A standard process for presentation and documentation of findings; and
- An opportunity to make recommendations on the additional information required to support or improve decisions relating to water management and particularly, to strengthen the scientific basis of environmental flow assessments.

It is worth noting that a “Best Practice Framework” (see Figure 1) for the conduct of holistic environmental flow assessments is already available in Australia (Arthington *et al*. 1998) but was not discussed in the review by Cottingham *et al*. (2002) even though it appears to offer most of the recommended elements of good practice for ‘scientific panel’ methods. (2002). In the following sections of this paper, we show how the more sophisticated and structured holistic methodologies share common features that address the best practices recommended above (points 1-7) and the common and additional features proposed by Arthington *et al*. (1998). We focus particularly on the BBM, DRIFT and the Benchmarking and Flow Restoration methodologies, as these represent the most recent developments in holistic methodologies familiar to us and were not included in the appraisal of Cottingham *et al*. (2002).



■ Figure 1. Best Practice Framework for assessing environmental flows in regulated and unregulated river systems (from Arthington *et al*. 1998).

1) Protocols for selecting scientific/expert panels

Guidelines for selecting scientific or technical panel members were established as part of the BBM (King *et al*. 2000) and these formal procedures have been incorporated into all of the more recent holistic methodologies often based upon the well-established protocols of the BBM (King *et al*. 2000). Each assessment using the BBM, DRIFT, Benchmarking and Flow Restoration methodologies involves one or more scientists in the fields of hydrology (and occasionally, geohydrology), hydraulics, geomorphology, water quality and aquatic ecology (algae and aquatic plants, riparian vegetation, invertebrates, fish, and wildlife and occasionally, estuarine ecology). Each scientist is expected to be familiar with the river system under study or similar types of rivers and/or EFA procedures.

The roles, responsibilities and interactions of panel members during EFA studies and associated workshops are governed by the particular step-by-step procedures built into each methodology. These procedures generally circumvent outright dominance of workshops and discussions by any one member of the team. Each member has equal opportunity to contribute as fully as they wish and it is usually not possible for any one member to dominate the workshops or bias the outcomes of the evaluations of environmental flow evaluations. Furthermore, workshops forming part of the BBM, DRIFT, Benchmarking and Flow Restoration methodologies are structured and facilitated in such a way that there are frequent comparisons of results and EFA evaluations and results among the participating scientists. These comparisons generally reveal any inconsistencies of approach, or vastly different rankings of flow-related impacts in terms of one or other ecosystem component (other than inherent differences) and/or areas of personal bias. If such issues can be identified early in the workshop process, they can usually be resolved before any consistent patterns of bias affect the entire EFA process. Sensitivity analysis can also be used to identify the influence of particular components of the overall outcome of an EFA.

2) Guidelines for developing objectives

The BBM, DRIFT, Benchmarking and Flow Restoration methodologies all address clear working objectives established as part of the study design, and formalized in design and the contracts signed between the client and each scientific or technical panel member. One or more shared, broad river visions (desired future states in the BBM) may be established, or several more common water resource development or flow restoration objectives may be set, and EFAs evaluated to achieve these objectives. The common practice is to evaluate the ecological consequences of several well-defined scenarios of change in flow regime (either flow reductions, or degrees of flow restoration). These scenarios may be defined using various hydrological statistics, plots and/or indices describing important features of the flow regime modified *versus* the natural (unregulated) flow regime. Hydrological statistics generally related to flow quantity, timing, duration, frequency of floods and low flow spells, rates of change (e.g. hydrograph rise and fall) and other aspects of variability, including the presence/absence of definite patterns of flow seasonality (after Richter *et al*. 1996, 1997), as well as ill-defined objectives leading to weak EF recommendations are less likely when the scenarios of hydrological change are explicitly and statistically defined, and/or desired ecological endpoints are stated at the outset of the study. To aim simply for 'improved river health' or 'a sustainable river ecosystem' is too imprecise an objective for sound scientific assessment.

3) Guidelines for field work

Cottingham *et al*. (2002) noted that many scientific panel assessments on rivers of southern Australia are based only on desk-top methods and best-available information (often very limited or of poor quality), or involve little more than a rapid field assessment and single spatial/temporal "snap-shot" of the river system conducted at sites "assumed to be representative of the river system under consideration". In contrast, the site selection procedures of the BBM, DRIFT, Flow Restoration and Benchmarking methodologies have a sound, well-documented rationale and they all offer an explicit and transparent framework and methods, for evaluating the ecological implications of many alternative flow scenarios. A range of quantitative procedures can be applied within any of these methodologies to relate flow changes to ecological responses (e.g. wetted perimeter analysis, vegetation transect analysis, water and sediment budget analyses, empirical statistical models, multivariate statistical analyses, predictive population models). For example, the fish components of the Flow Restoration Methodology and DRIFT involve a year of field studies designed to enable consideration of a core set of flow-related aspects of fish biology/ecology (see Pusey 1998; Pusey *et al.* 1998; Kennard, Arthington and Thompson 2000; Pusey, Kennard and Arthington 2000; Rall 1999; Arthington *et al.* 2003a). The Benchmarking Methodology, in contrast, relies heavily on the interpretation of data from past field studies, the literature and professional judgement rather than new field studies to relate the ecological condition of fish communities to the level and type of flow modification (Brizga *et al.* 2002).

4) Procedures for rating confidence levels

The level of confidence in the BBM, DRIFT and Benchmarking assessments is rated according to the information sources available and their scientific quality, thus providing the water manager with an explicit means to undertake his/her own assessment of the risks associated with management actions based on limited or low quality information. The rating scheme applied in DRIFT closely resembles that recommended by Downes *et al*. (2000) and adapted by Cottingham *et al*. (2002) into “levels of evidence that support environmental flow assessments”. In addition to confidence ratings, the application of DRIFT in the Lesotho Highlands Project involved several phases of peer review (see King *et al.* 2003), which parallel the sequence of reviews proposed by Arthington *et al.* (1998) in their Best Practice Framework for environmental flow assessments.

5) Estimating social and economic consequences

The DRIFT methodology includes an explicit process for evaluating the social consequences of each flow scenario stemming from earlier, less clearly defined procedures applied within the BBM (King *et al*. 2002) and thereby a means to estimate the economic costs of flow regulation in terms of changes in fish and other natural resources or services used by local rural communities (King *et al*. 2003). This represents a significant advance of DRIFT over other holistic methodologies and avoids the charge that “scientific panels have only ‘green’ value-systems and that they are an alternative environmental lobby” (Cottingham *et al*. 2002). The Flow Restoration Methodology (Arthington *et al*. 2000) and the Best Practice Framework also incorporate socio-economic considerations, the former by including a process for evaluating the ‘cost’ of many different environmental flow scenarios generated by releasing flows from storage. In that study, costs were represented in terms of water yields foregone from a large storage reservoir if particular environmental flow scenarios were to be implemented (Arthington *et al*. 1999; 2000).

6) Documentation

The BBM, DRIFT, Flow Restoration and Benchmarking methodologies all produce comprehensive literature reviews and data reports describing the study area and its ecological systems, EFA methods, results and recommendations, thereby providing major reference documents and benchmarks upon which to base the planning and design of any river restoration activities and future assessments or post-implementation monitoring of river condition. The collation of historic information and preparation of a sequence of refereed reports is a fundamental aspect of the Best Practice Framework (Arthington *et al*. 1998).

7) Monitoring and further research

Cottingham *et al*. (2002) did not recommend the incorporation of an explicit monitoring phase as part of scientific panel assessments, although they alluded to the principles of adaptive environmental management (Walters 1987). These principles and rigorous monitoring protocols are built into most other holistic methodologies (see Table 1) and the Best Practice Framework (Figure 1). For example, all components of DRIFT include a detailed rationale and protocol for monitoring the geomorphological or ecological outcomes of environmental flow allocations and water management scenarios (King *et al.* 2003; Metsi Consultants 2000). With regard to the application of DRIFT in Lesotho rivers, the predictions of fish responses to each environmental flow scenario have formed the basis of hypotheses for testing by monitoring and longer-term research (J. Rall, pers. comm. 2003). Benchmarking Methodology reports always include a section describing key knowledge gaps and research priorities for the catchment under study and the Flow Restoration Methodology devotes a chapter to research and monitoring requirements.

In considering the recommendations of Cottingham *et al*. (2002) as to the desirable elements of best practice in holistic EFAs based on 'scientific panel' approaches, we suggest that the most recent holistic methodologies developed and applied in Australian and southern Africa already address the main concerns and limitations raised above, as does the Best Practice Framework (Arthington *et al*. 1998). Even so, all such methodologies can be enhanced in many ways and in the next section of this paper we discuss opportunities for the further development of this type of approach to EFAs, particularly in relation to the methods and models used to predict the ecological consequences of flow regime change.

Further development of holistic methodologies

King *et al*. (1999) and Tharme (2003) consider holistic methodologies to be especially appropriate for use in developing countries, due to the need for resource protection at an ecosystem scale and the direct dependence of local people on the goods and services provided by aquatic ecosystems for food and broader livelihood security. Arthington *et al.* (2003a) place holistic methodologies at the second level of a three-tiered hierarchy of EFA methods, reflecting recognition by several colleagues (Tharme 1996; Dunbar *et al*. 1998) of the levels of complexity, confidence in outcomes and risk of error at which EFAs are needed and applied. These are Level 1: precautionary hydrological approaches; Level 2: Holistic scientific panel methodologies using all types of data, information and professional judgement in a structured framework, usually applied when time/resource constraints preclude lengthy investigations and predictive model development; and, Level 3: EFA assessments based on detailed studies and predictive flow-ecology models. Tharme (2003) rated holistic methodologies as having moderate to high resource intensity, complexity and resolution and high flexibility (Table 1) and recommended their use when assessing water resource developments, typically of large-scale, involving rivers of high conservation and/or strategic importance and/or with complex user tradeoffs.

In assessing the utility of DRIFT and other holistic methodologies, Arthington *et al.* (2003a) and King *et al.* (2003) considered the gravest risk to be that such approaches "may be used routinely and become all that is sought and used, rather than investing in securing new knowledge of river ecology to guide sound decision-making in the future". They caution that "DRIFT and other scientific panel methods should only be used where there is a genuine commitment to implement and monitor the recommended environmental flows, to support knowledge development and to adapt water management strategies when better information about the river's responses to flow modification becomes available through monitoring and research".

Clearly, holistic methodologies can be enhanced by integrating modelled responses of river ecosystems to flow change, be it regulation or restoration, that is, by moving towards Level 3 of the EFA hierarchy outlined above. At this level of resolution, environmental water requirements would be defined and alternative water resource developments or restoration scenarios evaluated, by means of quantitative predictive models describing relationships between hydrology and the flow-related ecological processes governing biological diversity and river ecosystem integrity (Arthington *et al.* 2003).

Quantitative models that describe associations between flow and geomorphological or ecological parameters are available for some ecosystem components (see Arthington and Zalucki 1998 and literature cited therein). For example, hydraulic geometry models can be used to provide an indication of the likely net change in channel dimensions resulting from flow regime change (Brizga *et al.* 2001). Sediment transport models can provide an indication of the likely implications of flow regime change for sediment processes. Wetland and riparian water budget analyses have proved useful in environmental flow studies designed to restore regulated stream ecosystems (e.g. Pettit, Froend and Davies 2001).

It is useful to briefly review existing techniques and models that predict the responses of fish to changes in river flow regime and the extent of their application in EFAs and river flow management in general.

Hydraulic rating and habitat simulation methods and modelling packages (e.g. PHABSIM - part of IFIM) have been discussed above, so we confine this review to some of the more advanced approaches. Over a decade ago, O'Brien (1987) defined the minimum stream flow hydrograph to maintain existing habitat, food supplies and spawning potential of the endangered Colorado River squawfish (*Ptychocheilus lucius*) in terms of four flow characteristics. To develop this minimum hydrograph, O'Brien (1987) combined the results of a two-year field study, a physical model, laboratory simulation of flows over cobble substrate and a mathematical sediment transport model. Hill, Platts and Beschta (1991) developed a method linking the timing and magnitude of the low and high flow attributes of annual flow hydrographs to in-stream and out of channel physical habitat availability and suitability for fish. In a more ambitious program of studies, Williamson, Bartholow and Stalnaker (1993) developed a conceptual framework and a suite of interactive mathematical models of salmon production (SALMOD) simulating the dynamics of resident and anadromous freshwater populations. Milhous (2003) applied a time series analysis of predicted changes in spawning, incubation, fry and juvenile habitat of brown trout to model temporal changes in abundance associated with discharge. This approach was also used to model the effect of reservoir construction on riparian dynamics.

The most recent developments in fisheries modelling in relation to river hydrology and flow management are outlined in Arthington *et al.* (2003b) and Halls and Welcomme (2003). Fisheries models can be broadly categorised as empirical, population dynamics and holistic. Empirical models are statistical representations of variables or relationships of interest, without reference to the underlying processes. They have been used to describe the response of fish yield to one or more explanatory variables including measures of river morphology, such as drainage basin or floodplain area (e.g. Welcomme 1985), morpho-edaphic indices (Bayley 1988; Pusey *et al.* 2000) and fishing intensity (Welcomme 1985; Bayley 1988). Other models of this type describe the relationship between fish catches and freshwater flows into estuaries (Loneragan and Bunn 1999), an approach now forming part of Australian environmental flow assessments in coastal rivers.

Fish population dynamics models attempt to describe the response of fish populations to exploitation and environmental variation based upon established theories of population regulation and upon recent advances in understanding of floodplain-river fisheries ecology and biology (Welcomme and Hagborg 1977; Halls, Kirkwood and Payne 2001; Halls and Welcomme 2003). They have yet to be incorporated into holistic environmental flow assessments in any routine fashion, although efforts to do so are in progress (P. Dugan, pers. comm. 2003). Nevertheless, recent applications have informed river flow management. For example, Minte-Vera (2003) developed a lagged recruitment, survival and growth model for the migratory curimba *Prochilodus lineatus* (Valenciennes, 1847) in the high Paraná River Basin (Brazil), with recruitment as a function of flooding and stock size. Results obtained were used to evaluate the risk to the population from various fisheries and dam-operation management decisions.

In the field of inland and floodplain fisheries, the term 'holistic' applies to models that address fish production or yield in the broader context of environmental management and therefore integrate a diversity of variables of hydrological, environmental or social nature (e.g. fishing methods and effort). Holistic models can be broadly classified into ecological models (e.g. Ecopath, see www.ecopath.org), multi-agent models (e.g. FIRMA 2000; see http://cormas.cirad.fr/indexeng.htm) and Bayesian networks. Baran, Makin and Baird (2003) used a Bayesian network model to assess impacts of environmental factors, fish migration patterns and land use options on fisheries production in the Mekong River. Bayesian network models are slowly being incorporated into decision support systems for the determination of river flow regimes that will sustain river ecosystems and their fish populations.

Despite these advances in fisheries modelling (see also Arthington *et al.* 2003b; Halls and Welcomme 2003) and modelling developments for other ecosystem components (beyond the scope of this paper), the range of available quantitative models is generally too narrow, or too limited in transferability across river ecotypes, to provide a comprehensive basis for environmental flow determinations. Therefore, models generally need to be used in conjunction with/or as a component within other knowledge-based methodologies. Furthermore, many of the ecological models remain black-box (empirical) models and the ecological processes they represent are not well understood. Quantitative models of the secondary effects of flow regime change (e.g. impacts of channel contraction for vegetation and in-stream biota) are generally not available.

IMPROVING THE KNOWLEDGE BASE FOR ENVIRONMENTAL FLOW ASSESSMENTS

Although major advances have been achieved in the broad field of river ecology in recent decades, substantial information gaps characterize every fundamental aspect of aquatic biology and the ecological processes sustaining aquatic ecosystems are still poorly understood (e.g. Walker, Sheldon and Puckridge 1995; Winemiller 2003), particularly in large floodplain river systems that are most threatened by water resource development, fishing pressure and catchment disturbance (Tockner and Stanford 2003). The main knowledge gaps and research priorities for riverine fish and fisheries have been reviewed by Arthington *et al.* (2003b) and for aquatic systems more generally by Dugan *et al*. (2002).

In the following section, we comment on the value of experimental studies and long-term research to inform river management and environmental flow decision-making in particular.

Flow manipulation experiments

Experimental manipulation of river flow can provide useful information informing environmental flow assessments and some experimental releases from dams have been made in this context (e.g. Harris and Gherke 1995). For example, King, Cambray and Impson (1998) demonstrated that experimental releases from the Clanwilliam Dam on the Olifants River, western South Africa, resulted in spawning and larval recruitment of the Clanwilliam Yellowfish (*Barbus capensis)*, provided that water temperatures were suitable for spawning activity, egg survival and larval development. Additional examples, focused on the effects of managed floods on the floodplain wetlands of large rivers, are provided in Acreman, Farquharson, McCartney et *al*. (2000).

Environmental flows as ecological experiments

There are few opportunities for experimentation in unregulated river systems and the high cost of water has precluded widespread experimentation in many regulated systems. Infrastructure constraints (e.g. size of outlet valves, number of flood control gates) also limit the scope of flow experimentation that is possible. Nevertheless, many scientists argue that the implementation of environmental flow regimes and river restoration projects should be regarded as opportunities to conduct ecological experiments (Kingsford 2000; Lake 2001; Bunn and Arthington 2002) and have called for rigorous and comprehensive monitoring of the ecological outcomes of environmental flows to guide river flow management in the future. Poff *et al.* (2003) have outlined how large scale demonstration flow restoration projects in focus catchments that have significant problems due to flow regime modification and realistic opportunities for flow restoration, could inform river science and management. Although there are likely to be significant experimental design issues (few suitable reference systems and limited opportunities for replication), ecologists believe that turning flow restoration projects into experiments in restoration ecology should be part of the research agenda informing river flow management and are long overdue (Kingsford 2000; Lake 2001; Bunn and Arthington 2002).

Long-term ecological research

Long-term research in relative undisturbed catchments appears essential to improve our understanding of river ecosystem functioning in relation to hydrological history and flow events such as floods and droughts. From appropriate spatial and time series investigations it may eventually be possible to develop suites of models predicting how rivers will respond to natural flow variations (and climate change) and various types of flow regulation (Kingsford 2000; Bunn and Arthington 2002; Arthington and Pusey 2003). Such research is also needed to strengthen predictions of restoration trajectories after flows are restored to regulated rivers and their floodplains (Petts 1987; Ward *et al*. 2001; Lake 2001). With further climate change likely, river flow regimes will change in response to altered thermal and rainfall distributions, increasing evaporation rates, more extreme floods and droughts and increasing water stress. Water shortages and increasing competition for the available water will place even greater demands on the scientific community to define (and defend) the flow requirements of rivers and floodplains.

CONCLUSIONS AND RECOMMENDATIONS

This paper has outlined the origins and development of four types of environmental flow methodology recognised by Tharme (1996; 2003), namely hydrological, hydraulic rating, habitat simulation and holistic approaches. The latter category of methods, of which there are now 16 different types, have many features and strengths in common, particular the use of a multi-disciplinary team of scientists and the structured analysis of EFRs, usually in a workshop setting. We have shown that the most recent holistic methodologies – BBM, DRIFT, Benchmarking and Flow Restoration - already address and in some aspects improve upon, the main elements of best practice in holistic EFAs recommended by Cottingham *et al*. (2002). An existing Best Practice Framework (Arthington *et al.* 1998) sums up the most desirable elements of holistic EFAs and most of the new generation holistic EFAs conform to this model.

Nevertheless, holistic methodologies could be vastly enhanced by applying a wider range of quantitative techniques to relate flow alterations to ecological responses and by integrating models that facilitate prediction of the responses of river ecosystems to flow change, that is, by moving towards Level 3 of the EFA hierarchy proposed originally by Tharme (1996) and adapted by Arthington *et al.* (1998, 2003a). At this level of resolution, environmental water requirements would be defined and alternative water resource developments or restoration scenarios evaluated, by means of detailed studies and quantitative predictive models of the relationships between hydrology, biophysical processes and ecosystem functioning (Arthington *et al.* 2003a).

Several types of modelling facilitate prediction of the responses of fish and fisheries to river hydrology and changes in flow regime, as well as other environmental and social factors. Recent developments in empirical, population and multi-agent modelling are increasingly being applied in river basin studies and projections of the consequences of river flow change. The integration of such modelling tools into existing and enhanced holistic decision support systems is a priority.

Review and synthesis papers contributed to LARS2 (e.g. Arthington *et al*. 2003b; Junk and Wantzen 2003; Winemiller 2003) have revealed substantial information gaps in every fundamental aspect of aquatic biology and also show that the ecological processes sustaining aquatic ecosystems are still poorly understood, particularly the functioning of large floodplain river systems. Increasing threats to these systems from water resource development, interacting with fishing pressure, catchment disturbance and climate change, highlight the urgency of establishing experimental research and long-term research programs to inform river management and environmental flow decision-making.

We suggest that there is a role for an international research program to advance the scientific basis of environmental flow assessments in rivers intended for future water infrastructure development and in regulated rivers where there are opportunities for partial restoration of the flow regime. The key elements of existing holistic methodologies discussed in this paper could provide the foundations for new and improved decision support systems, featuring bottom-up and top-down environmental flow methodologies that embody predictive models describing the relationships between river hydrology and flow-related geomorphological and ecological responses. Predictive models of biophysical processes already in use in fisheries management, for example, could be incorporated into EFAs and decision support systems. These models should be linked to processes for assessing the social and livelihoods (and ultimately economic) consequences of changes in flow regimes, for people dependent upon rivers for, among other things, clean water supplies, food resources, fibres, recreational opportunities and spiritual values.

Many features of DRIFT in its current, or variously adapted forms and several Australian holistic methodologies, provide suitable platforms and techniques for the further development of enhanced environmental flow decision support systems. The application of these new generation decision support tools within large scale demonstration flow restoration projects in focus catchments could inform river science and management in both the short and longer term.

ACKNOWLEDGEMENTS

Financial support to Angela Arthington from the organisers of LARS 2 is gratefully acknowledged. Angela and Brad Pusey also thank Griffith University for support to attend LARS 2. Comments from Robin Welcomme and an anonymous reviewer on an early draft of this paper are appreciated and thanks are due also to colleagues who assisted with final revisions and to Samantha Capon for drawing Figure 1.

REFERENCES

Acreman M.C., Farquharson F.A.K., McCartney M.P., Sullivan C., Campbell K., Hodgson N., Morton J., Smith D., Birley M., Knott D., Lazenby J., Wingfield R. & Barbier E.B. 2000. Managed flood releases from reservoirs: Issues and guidance. *Report to DFID and the World Commission on Dams*. Wallingford, UK, Centre for Ecology and Hydrology. 86 pp.

Arthington A.H. 1998. Comparative evaluation of environmental flow assessment techniques: Review of holistic methodologies. *LWRRDC Occasional Paper 26/98*. Canberra, Land and Water Resources Research and Development Corporation. 46 pp.

Arthington A.H., Brizga S.O. & Kennard M.J. 1998. Comparative Evaluation of Environmental Flow Assessment techniques: Best practice framework. LWRRDC *Occasional Paper 25/98.* Canberra, Land and Water Resources Research and Development Corporation. 26 pp.

Arthington A.H., Brizga, S.O., Kennard M.J., Mackay S.J., McCosker R.O., Choy S.C., Ruffini J.L. 1999. Development of a flow restoration methodology (FLOWRESM) for determining environmental flow requirements in regulated rivers using the Brisbane River as a case study. *In Proceedings of Hydrology 1999, the 24th Hydrology and Water Resources Symposium*. Barton, ACT, Australian Institution of Engineers. pp. 449-454.

Arthington A.H., Brizga S.O., Choy S.C., Kennard M.J., Mackay S.J., McCosker R.O., Ruffini J.L. & Zalucki J.M. 2000. *Environmental flow requirements of the Brisbane River downstream from Wivenhoe Dam. Brisbane, Australia, South East Queensland Water Corporation and Centre for Catchment and In-Stream Research*. Griffith University. 536 pp.

Arthington A.H., King J.M., O'Keefe J.H., Bunn S.E., Day J.A., Pusey B.J., Bluhdorn D.R. & Tharme R. 1992. Development of an holistic approach for assessing environmental flow requirements of riverine ecosystems. *In* J.J. Pigram & B.P. Hooper eds. *Proceedings of an International Seminar and Workshop on Water Allocation for the Environment.* Armidale, USA, Centre for Water Policy Research, University of New England. pp. 69-76.

Arthington A.H., Lorenzen K., Pusey B.J., Abell R., Halls A.S., Winemiller K.O., Arrington D.A., Baran E. 2003b. River fisheries: Ecological basis for management and conservation. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 1.* Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/16. pp. 21-60.

Arthington A.H. & Pusey B.J. 1993. In-stream flow management in Australia: Methods, deficiencies & future directions. *Australian Biologist,* 6: 52-60.

Arthington A.H. & Pusey B.J. 2003. Flow restoration and protection in Australian rivers. *River Research and Applications,* 19: 377-395.

Arthington A.H., Rall J.L., Kennard M.J. & Pusey B.J. 2003b2. Assessment of the environmental flow requirements of fish in Lesotho rivers using the DRIFT methodology. *River Research and Applications,* 19: 641-666.

Arthington A.H. & Zalucki J.M. eds. 1998. Comparative evaluation of environmental flow assessment techniques: Review of methods. *LWRRDC Occasional Paper Series 27/98.* Canberra, Land and Water Resources Research and Development Corporation. 141 pp.

Baran E., Makin I. & Baird I.G. 2003. Bayfish: A model of environmental factors driving fish production in the lower Mekong Basin. *Abstract submittted to the Second International Symposium on the Management of Large Rivers for Fisheries. Phnom Penh, Mekong River Commission.*

Bayley P.B. 1988. Accounting for effort when comparing tropical fisheries in lakes, river-floodplains and lagoons. *Limnology & Oceanography*, 33: 963-972.

Bovee K.D. 1982. A Guide to stream habitat analysis using the instream flow incremental methodology. *Instream Flow Information Paper 12.* Fort Collins, US Department of Fisheries and Wildlife Service. 248 pp.

Brizga S.O., Arthington A.H., Choy S., Craigie N.M., Mackay S., Poplawski W., Pusey B.J. & Werren G. 2001. Pioneer valley water resource plan: Proposed environmental flow assessment framework. Brisbane, Australia, Department of Natural Resources and Mines, 2 Volumes.

Brizga S.O., Arthington A.H., Pusey B.J., Kennard M.J., Mackay S.J., Werren G.L., Craigie N.M., Choy S.J. 2002. Benchmarking, a 'top-down' methodology for assessing environmental flows in Australian rivers. *Proceedings of International Conference on Environmental Flows for Rivers*. Cape Town, SA, University of Cape Town (Available on CD)

Bunn S.E. & Arthington A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30: 492-507.

Burgess G.K. & Vanderbyl T.L. 1996. Habitat analysis method for determining environmental flow requirements. *In Proceedings of Water and the Environment, the 23rd Hydrology and Water Resources Symposium*. Barton, ACT, Australian Institution of Engineers. 203-206.

Cottingham P., Thoms M.C. & Quinn G.P. 2002. Scientific panels and their use in environmental flow assessment in Australia. *Australian Journal of Water Resources*, 5: 103-111.

Davies P.M., Bunn S.E. & Arthington A.H. 1996. Environmental water requirements for lowland river systems on the Swan Coastal Plain. Unpublished report to the Water and Rivers Commission, Western Australia. Perth, University of Western Australia, Department of Zoology. 114 pp.

Downes B., Barmuta L., Fairweather P., Faith D.P., Keought M.J., Lake P.S., Mapstone B.D. & Quinn G.P. 2002. Monitoring ecological impacts: Concepts and practice in flowing waters. Cambridge, UK, Cambridge University Press. 434 pp.

Dugan P.J., Baran E., Tharme R., Prein M., Ahmed M., Amerasinghe P., Bueno P., Brown C., Dey M., Jayasinghe G., Niasse M., Nieland A., Smakhtin V., Tinh N., Viswanathan K. & Welcomme R.L. 2002. The contribution of aquatic ecosystems and fisheries to food security and livelihoods: A research agenda. *In Background papers of the Challenge Programme on Water and Food*. CGIAR. 87-113.

Dunbar M.J., Gustard A., Acreman M. & Elliott C.R.N. 1998. *Overseas approaches to setting river flow objectives. R & D Technical Report W6B964*. Wallingford, UK, Institute of Hydrology. 80 pp.

DWAF 1999. Resource directed measures for protection of water resources. Volume 2: Integrated manual. Version 1.0. Pretoria, SA, Department of Water Affairs and Forestry, Institute for Water Quality Studies. 45 pp.

Gippel C.J. & Stewardson M.J. 1998. Use of wetted perimeter in defining minimum environmental flows. *Regulated Rivers: Research & Management*, 14: 53-67.

Groshens T.P. & Orth D.J. 1994. Transferability of habitat suitability criteria for smallmouth bass, *Micropterus dolomieu*. *Rivers*, 4: 194-212.

Halls A.S., Kirkwood G.P. & Payne A.I. 2001. A dynamic pool model for floodplain river fisheries. *Ecohydrology and Hydrobiology*, 1: 323-339.

Halls A.S. & Welcomme R.L. 2003. Dynamics of river fish populations in response to hydrological conditions: A simulation study. *Abstract submittted to the Second International Symposium on the Management of Large Rivers for Fisheries. Phnom Penh, Mekong River Commission.*

Hill M.T., Platts S. & Beschta R.L. 1991. Ecological and geomorphological concepts for instream and out-of-channel flow requirements. *Rivers*, 2: 198-210.

Jowett I.G. 1997. Instream flow methods: A comparison of approaches. *Regulated Rivers: Research & Managemen*t, 13: 115-127.

Junk W.J. & Wantzen K.M. 2003. The Flood Pulse Concept: New aspects, approaches and applications, an update. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 1.* Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/16. pp. 117-140.

Kennard M.J., Arthington A.H. & Thompson C. 2000. Flow requirements of freshwater fish. *In Environmental flow requirements of the Brisbane River downstream from Wivenhoe Dam, Brisban.* South East Queensland Water Corporation and Centre for Catchment and In-Stream Research.

King J.M., Brown C.A. & Sabet H. 2003. A scenario-based holistic approach to environmental flow assessments for rivers. *River Research and Applications*, 19: 619-640.

King J.M., Cambray J.A. & Dean Impson N. 1998. Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish *Barbus capensis*. *Hydrobiologia*, 384: 245-265.

King J.M. & Louw D. 1998. Instream flow assessments for regulated rivers in South Africa using the building block methodology. *Aquatic Ecosystem Health and Restoration*, 1: 109-124.

King J.M. & Tharme R.E. 1994. *Assessment of the Instream Flow Incremental Methodology (IFIM) and initial development of alternative instream flow methodologies for South Africa. Water Research Commission, Report No. 295/1/94*. Pretoria, SA. 590 pp.

King J.M., Tharme R.E. & Brown C.A. 1999. *Definition and implementation of instream flows. Thematic Report for the World Commission on Dams*. Cape Town, SA, Southern Waters Ecological Research and Consulting. 63 pp.

King J.M., Tharme R.E. & de Villiers M.S. eds. 2002. *Environmental flow assessments for rivers: Manual for the building block methodology. Water Research Commission Technology Transfer Report No. TT131/00*. Pretoria, SA, Water Research Commission. 340 pp.

Kingsford R.T. 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology,* 25: 109-127.

Lake P.S. 2001. On the maturing of restoration: Linking ecological research and restoration. *Ecological Management and Restoration*, 2: 110-115.

Loneragan N.R. & Bunn S.E. 1999. River flows and estuarine ecosystems: Implications for coastal fisheries from a review and a case study of the Logan River, Southeast Queensland. *Australian Journal of Ecology,* 24: 431-40.

Metsi Consultants. 2000. *Consulting services for the establishment and monitoring of the instream flow requirements for river courses downstream of LHWP dams. Fish. Report No. 648-F-18. Lesotho, Lesotho Highlands Development Authority Contract 648.* 85 pp. plus Appendices.

Milhous R.T., Updike M.A. & Schneider D.M. 1989. *Physical habitat simulation system reference manual, version 2. Instream Flow Information Paper 26. U.S.D.I. Fish Wildlife Service Biological Report* 8916.

Minte-Vera C.V. 2003. Risk assessment of a floodplain migratory fish subject to fisheries and dam-operation procedures. *Abstract submittted to the Second International Symposium on the Management of Large Rivers for Fisheries. Phnom Penh, Mekong River Commission.*

Naiman R.J., Bunn S.E., Nilsson C., Petts G.E., Pinay G. & Thompson L.C. 2002. Legitimizing fluvial ecosystems as users of water. *Environmental Management*, 30: 455-467.

O'Brien J.S. 1987. A case study of minimum streamflow for fishery habitat in the Yampa River. *In* C.R. Thorne, J.C. Bathurst & R.D. Hey RD eds. *Sediment Transport in gravel-bed rivers*. Chichester, UK, John Wiley & Sons. pp. 921-946.

O'Keeffe J.H., Hughes D.A. & Tharme R.E. 2001. Linking ecological responses to altered flows for use in environmental flow assessments: The flow stress-response method. V*erh. Int. Ver. Limnol.* (Available on CD)

O'Keeffe J.H. & Hughes D.A. 2002. The flow stress-response method for analysing flow modifications: Applications and developments. *Proceedings of International Conference on Environmental Flows for Rivers*. Cape Town, SA, University of Cape Town. (Available on CD)

Olden J.D. & Poff N.L. 2003. Redundancy and the choice of hydrological indices for characterising streamflow regimes. *River Research and Applications*, 19: 101-121.

Pettit N.E., Froend R.H. & Davies P.M. 2001. Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting Western Australian rivers. *Regulated Rivers: Research & Management*, 17: 201-215.

Petts G.E. 1987. Time-scales for ecological changes in regulated rivers. *In* J.F. Craig & J.B. Kemper eds. *Regulated streams Advances in ecology*. New York, Plenum Press. pp. 257-266.

Petts G.E., Bickerton M.A., Crawford C., Lerner D.N. & Evans D. 1999. Flow management to sustain groundwater-dominated stream ecosystems. *Hydrological Processes*. 13: 497-513.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. 1997. The natural flow regime, a paradigm for river conservation and restoration. *BioScience*, 47: 769-784.

Poff N. LeRoy, Allan J.D., Palmer M.A., Hart D.D., Richter B.D., Arthington A.H., Rogers K.H., Meyer J.L. & Stanford J.A. 2003. River flows and water wars: Emerging science for environmental decision-making. *Frontiers in Ecology and the Environment*, 1: 298-306.

Puckridge J.T., Sheldon F., Walker K.F. & Boulton A.J. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Researc,h* 49: 55-72.

Pusey B.J. 1998. Methods addressing the flow requirements of fish. *In* A.H. Arthington & J.M. Zalucki eds. *Comparative evaluation of environmental flow assessment techniques: Review of methods. LWRRDC Occasional Paper Series 27/98.* Canberra, Land and Water Resources R & D Corporation. pp. 66-105.

Pusey B.J., Kennard M.J. & Arthington A.H. 2000. Discharge variability and the development of predictive models relating stream fish assemblage structure to habitat in north-eastern Australia. *Ecology of Freshwater Fishes*, 9: 30-50.

Pusey B.J., Kennard M.J., Arthur, J.M. & Arthington A.H. 1998. Quantitative sampling of stream fish assemblages: Single versus multiple pass electroshocking. *Australian Journal of Ecology*, 23: 365-374.

Rall J.L. 1999. Development of a conservation program on *Pseudobarbus quathlambae* in the catchment area of phase 1B of the Lesotho Highlands Water Project. Rand Afrikaans University. (Doctoral dissertation)

Richter B.D., Baumgartner J.V., Powell J. & Braun D.P. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, 10: 1-12.

Richter B.D., Baumgartner J.V., Wigington R. & Braun D.P. 1997. How much water does a river need? *Freshwater Biology*, 37: 231-249.

Rosenberg D.M., McCully P. & Pringle C.M. 2000. Global-scale environmental effects of hydrological alterations: Introduction. *BioScience*, 50: 746-751.

Sparks R.E. 1992. Risks of altering the hydrologic regime of large rivers. *In* J. Cairns, B.R. Niederlehner & D.R. Orvos eds. *Predicting Ecosystem Risk. Vol XX*. Princeton, NJ, Princeton Scientific Publishing Co. pp. 119-152.

Sparks R.E. 1995. Need for ecosystem management of large rivers and floodplains. *BioScience*, 45: 168-182.

Stalnaker C., Lamb B.L., Henriksen J., Bovee K. & Bartholow J. 1994. *The instream incremental methodology. A primer for IFIM. Biological Report, 29.* Washington, DC, U.S. Department of the Interior, National Biological Service.

Steward H.J., Madamombe E.K. & Topping C.C. 2002. Adapting environmental flow methodologies for Zimbabwe. *Proceedings of International Conference on Environmental Flows for Rivers*. Cape Town, SA, University of Cape Town (Available on CD)

Stewardson M.J. & Cottingham P. 2002. A demonstration of the flow events method: Environmental flow requirements of the Broken River. *Australian Journal of Water Resources*, 5: 33-47.

Stewardson M.J. & Gippel C. 1997. In-stream environmental flow design: A review. Victoria, Australia, Cooperative Research Centre for Catchment Hydrology, Department of Civil and Environmental Engineering, University of Melbourne. 99 pp.

Swales S. & Harris J.H. 1995. The Expert Panel Assessment Method EPAM: a new tool for determining environmental flows in regulated rivers. *In* D.M. Harper & A.J.D. Ferguson eds., *The Ecological Basis for River Management.* Chichester, UK, John Wile & Sons. pp. 125-134.

Tharme R.E. 1996. *Review of international methodologies for the quantification of the instream flow requirements of rivers. Water law review final report for policy development, for the Department of Water Affairs and Forestry.* Pretoria, SA, Freshwater Research Unit, University of Cape Town. 116 pp.

Tharme R.E. 2003. A global perspective on environmental flow assessment: Emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications*, 19: 397-442.

Tharme R.E. & King J.M. 1998. *Development of the building block methodology for instream flow assessments and supporting research on the effects of different magnitude flows on riverine ecosystems*. Pretoria, SA, Water Research Commission Report No. 576/1/98. 452 pp.

Thoms M.C., Sheldon F., Roberts J., Harris J., Hillman T.J. 1996. *Scientific panel assessment of environmental flows for the Barwon-Darling River.* Sydney, Australia, New South Wales Department of Land and Water Conservation. 161 pp.

Tockner K. & Stanford J.A. 2002. Riverine flood plains: Present state and future trends. *Environmental Conservation*, 29: 308-330.

Walker K.F., Sheldon F. & Puckridge J.T. 1995. An ecological perspective on dryland rivers. *Regulated Rivers: Research & Management*, 11: 85-104.

Walter A.C., Burgess G.K. & Johnston P.J. 1994. Assessment of a process for determining environmental flows. *In* Environmental Flows Seminar Proceedings. Artarmon, Victoria: AWWA Inc., pp. 195-201.

Walters C. 1997. Challenges in adaptive management of riparian and coastal systems. *Conservation Ecology*. (Available at http://www.consecol.org/vol1/iss2/art1://, 24 October 2003)

Ward J.V., Tockner U., Uehlinger U. & Malard F. 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. *Regulated River: Research and Management*, 117: 311-323.

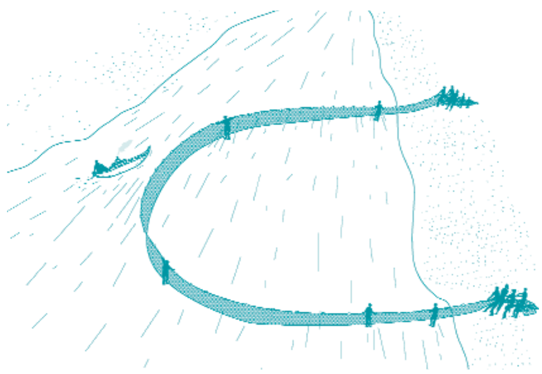
Welcomme R.L. 1985. *River fisheries*. *Fisheries Technical Paper*. Rome, Food and Agriculture Organization of the United Nations. pp. 262 - 330.

Welcomme R.L. & Hagborg D. 1977. Towards a model of a floodplain fish population and its fishery. *Environmental Biology of Fishes*, 2: 7-24

Welcomme R.L. & Halls A.S. 2004. Dependence of tropical river fisheries on river flow. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 2.* Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp. 267-284.

Williamson S.C., Bartholow J.M. & Stalnaker C.B. 1993. Conceptual model for quantifying pre-smolt production from flow-dependent physical habitat and water temperature. *Regulated Rivers: Research & Management*, 8: 15-28.

Winemiller K.O. 2004. Floodplain river food webs: generalizations and implications for fisheries management. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 2.* Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp. 285-310.



CONTRIBUTION OF INLAND FISHERIES TO RURAL LIVELIHOODS IN AFRICA: AN OVERVIEW FROM THE LAKE CHAD BASIN AREAS

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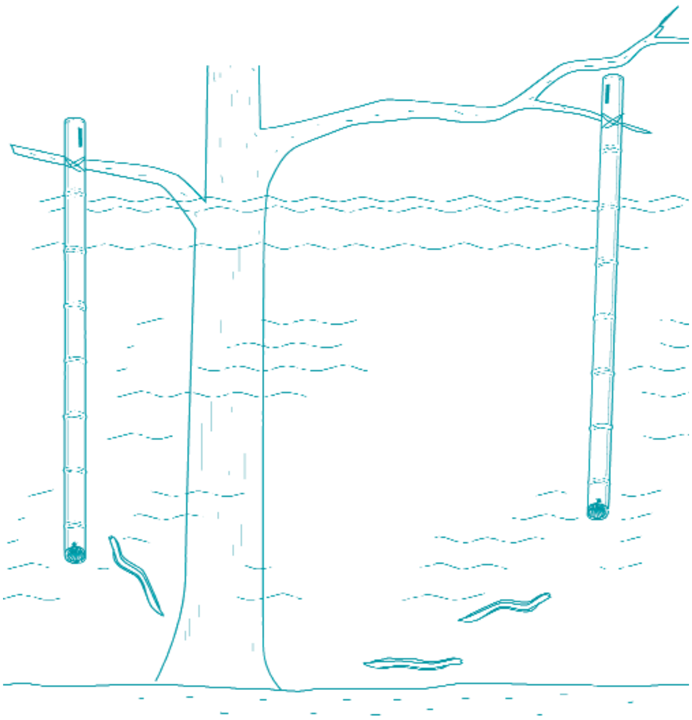


Key-words: Artisanal fisheries; poverty; socio-economics; livelihoods analysis; Africa

ABSTRACT

Within the very arid and difficult environment of the Sahelian region, Lake Chad and its associated riverine system have always played an extremely important role in the livelihoods of the thousands of people living in the Basin. However, due to the remoteness of the region the whole Basin is suffering an important information deficit and it is currently difficult to make accurate and up-to-date assessments of the economic (in particular inland fisheries) activities taking place within the area. The objective of this paper is to improve our knowledge and understanding of the rural livelihoods of the populations of the Basin and in particular, to assess the exact contribution of the fishing activities to the livelihoods of these communities. For this purpose, a detailed socio-economic multi-activity survey was carried out,

including a participatory poverty assessment, in the three major fishing regions of the Basin (the delta of the Chari River, the Yaérés floodplain and the western shore of the Lake). The survey was completed by a series of comparative analyses of the accessibility to fishing grounds and fishing gear ownership across the different socio-economic strata of the populations. Through the detailed description of the seasonal patterns of activities, the survey shows that for the entire area, households, disregarding their wealth level, still rely to a very large extent on subsistence economy where the three major activities (fishing, farming and herding) are closely integrated. With respect to the fishing activity the survey demonstrates the central role of this activity for all wealth groups. The participatory wealth ranking exercise also reveals to what extent the communities themselves perceive ownership of fishing gears as one of the primary signs of wealth. This result is strong evidence that fishing has become a key-element of the wealth differentiation process in the area. This result is corroborated by the analysis of fishing ground accessibility which reveals that in some parts of the Basin, only the wealthiest households have access to the whole range of water-bodies available, while the poorest households are marginalized or even excluded from these water-bodies. In other parts of the Basin, in contrast, fishing activities appear to play a major role as a safety-net for the poorest households. It seems therefore that there is no one-to-one relationship between the contribution of fishing activity and the wealth (or poverty) level of the households and that the well-known adage “fishers are the poorest of the poor” does not reflect the complexity of the empirical situation observed, at least not in the Lake Chad Basin.

INTRODUCTION

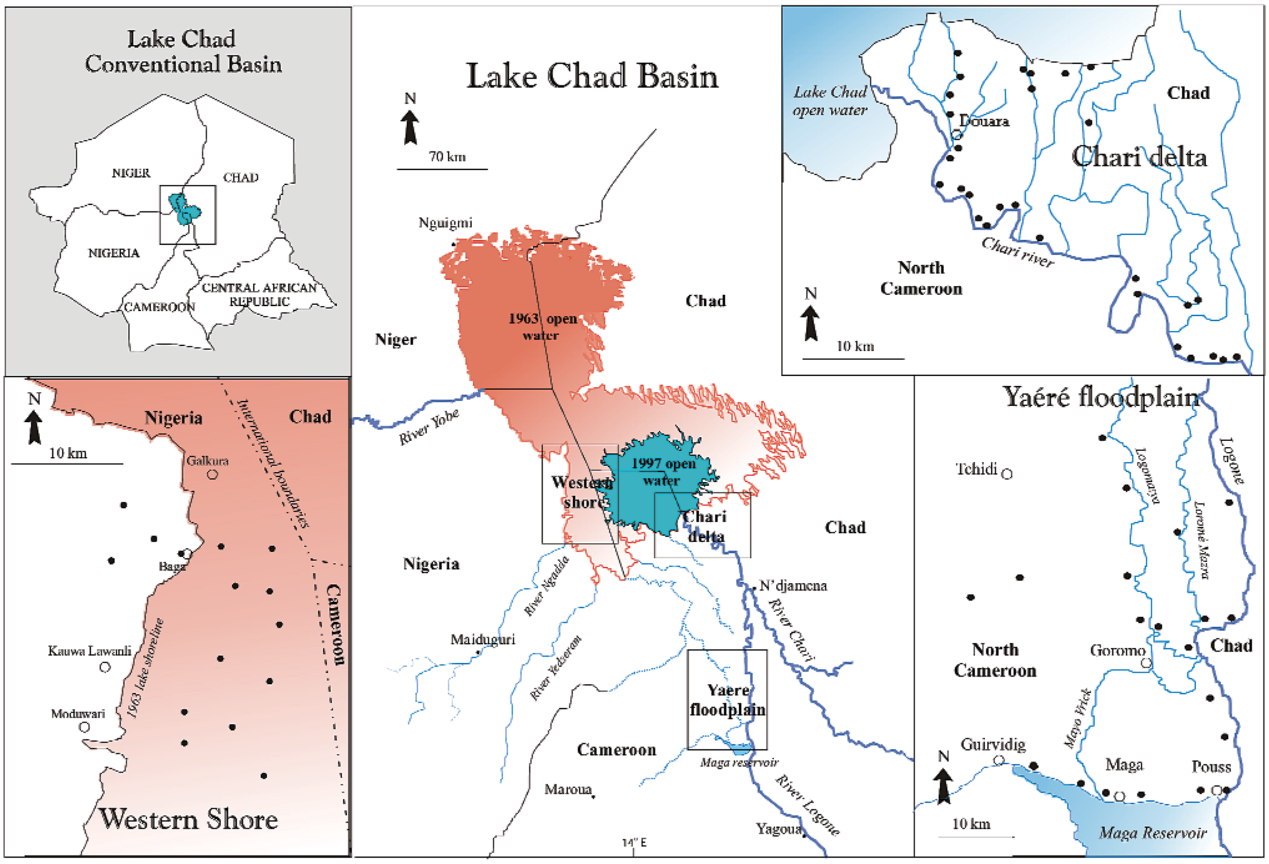
Lake Chad has always played an extremely important role in the livelihoods of the thousands of people living within its vicinities in the very arid and difficult environment of the Sahelian region. However due to the remoteness and recent political instability of the region, the whole Basin is now suffering an important information deficit (FAO for instance considers the national statistics for this region to be unreliable and incomplete - FAO 1995) and it is currently extremely difficult to make any accurate and up-to-date assessment of the economic activities and in particular inland fisheries, taking place within the Basin. Faced with this lack of information, national policy-makers and planners as well as international development agencies are severely constrained in their ability to generate and implement rural development policies appropriate and adapted to this area.

The main objective of the research from which this paper is derived was to expand our knowledge of the livelihoods of the rural communities living in the Lake Chad Basin region and, in particular, to better assess the contribution of fishing activities to the livelihoods of these local populations. For this purpose, a detailed socio-economic survey including a participatory poverty assessment was carried out in the three major fishing regions of the Basin. The survey was completed by a series of comparative analyses of the accessibility to fishing grounds and fishing gear ownership across the different socio-economic strata of the populations. The present paper is a summary of the main findings of this livelihood assessment survey. A more detailed analysis is provided in Béné, Neiland, Jolley *et al*. (2002). This research was part of a more general multi-disciplinary analysis of the Lake Chad Basin fisheries (Neiland and Béné 2002)

RESEARCH METHODOLOGY AND DATA COLLECTION

The data collection was conducted from October 1999 to July 2000 using socio-economic multi-activity survey techniques. The areas included in the survey cover the three major zones of fishing activities within the Lake Chad Basin. These are located (1) along the south-west part of the Lake area (Nigeria), including large zones of the seasonally exposed lake-bed; (2) within the Delta of the Chari River, including the Chari River itself and the south-east part the Lake shore (Chad); and (3) within the Yaéré floodplain located at the border between Cameroon and Chad, along the Logone River (Figure.1). Within these three areas, 64 villages were selected randomly and surveyed: 15 along the Nigerian western shore, 20 in the Yaéré floodplain and 29 in the Chari River delta. In each village, the data was collected through semi-structured group interviews conducted on village key-informants.

The central element of the survey was an activity ranking exercise combined with a participatory wealth ranking exercise. The objective of the participatory wealth ranking exercise was to analyse the nature and degree of the wealth stratification (heterogeneity) within the local populations. An activity ranking exercise was then carried out for each wealth group. Two distinct criteria were used for this: (1) the allocation of households' labour (time-effort) over the whole season in each activity and (2) the contribution of each activity to the households' overall incomes. This distinction was introduced to attempt to embody the high degree of subsistence that characterises household livelihoods in this region. The results were then aggregated across villages of the same area.



■ **Figure 1.** Top left map: general location within the whole Lake Chad Conventional Basin of the region concerned by the study. Central map: detailed location within the study region of the three specific areas included in the survey: the western shores of the Lake, the Chari Delta and the Yaéré floodplain. The black dots on the local maps (bottom left and right hand side maps) indicate the villages surveyed in each area = 64 in total.

The activity ranking exercise was complemented by a comparative analysis of fishing ground accessibility. The objective of this last analysis was to determine whether households of different wealth levels access the same fishing ground. Additional information regarding the villages and their vicinities was also collected through participatory mapping exercises (distance chart) of selected landmarks, including seasonal and permanent ponds, rivers and their tributaries, irrigation channels, grazing and agricultural areas and seasonal calendars of the rain, river-flood cycles and associated activities performed by the villagers.

RESULTS

Table 1 displays the various water-bodies used by the local populations for their fishing activities. In aggregate, 8 different types of fishing grounds are exploited across the Basin. Seasonal ponds and receding channels are the most common type of water-bodies used, followed by rivers (the Logone and Chari), the open waters of the lake and the permanent ponds and oxbows. The comparison between areas shows that the Yaéré floodplain offers the largest diversity of exploitable water-bodies, followed by the Chari Delta and the western shores of the Lake.

The fact that the seasonal ponds and receding channels are, in aggregate, the most common type of water-bodies fished across the basin indicates that a large part of the fishing activity has developed as a temporary activity to adapt to the seasonal dynamics of the environment and, in particular, to make the most of the seasonal flooding. However, the seasonality that characterises the hydrological environment of the Lake area does not affect only fishing activity but the households' activity portfolio as a whole. The analysis reveals indeed that the households' livelihood relies on a strongly seasonal matrix of diversified activities the pattern of which is largely influenced by the local water-flood regime. These multiple activities are closely integrated and all households in the Basin irrespective of their wealth level, are still heavily involved in a subsistence-based economy, where fishing, farming and cattle holding represent the three pillars of the system.

WEALTH STRATIFICATION

In 55 out of the 64 villages (86 percent) surveyed, the respondents identified three wealth groups that they termed 'the poorest' (noted G3 from now on), the 'less poor' -or sometimes called the 'intermediate group'- (noted G2) and the 'rich' (G1). In six villages

Table 1: Types of water-bodies exploited in Lake Chad Basin. Values in brackets are %.

Type of water-body	Number of villages exploiting a particular type of water bodies			
	Yaéré (%)	Chari Delta (%)	Western shores (%)	Aggregate
Number of different water-bodies	7	4	3	8
Seas. ponds and receding channels	9 (45)	15 (52)	15 (100)	39
Main river [(a)]	8 (40)	22 (76)	-	30
Lake Chad's open waters	-	8 (27)	14 (93)	22
Perm. ponds and oxbows	1 (05)	13 (45)	1 (06)	15
Tributaries [(b)]	9 (45)	-	-	9
Artificial reservoirs [(c)]	6 (30)	-	-	6
Irrigation channels	4 (20)	-	-	4
Floodplain	3 (15)	-	-	3
Number of villages	20 (100)	29 (100)	15 (100)	

Notes: [(a)] Main river = Chari and/or Logone; [(b)] Tributaries of the Logone = Logomatya, Loromé Mazé ra, Mayo Vrick and Petit Goroma; [(c)] Maga reservoir (see Fig.1 for location).

(9 percent), the respondents emphasised the absence of rich households and distinguished only two groups: ‘the poorest’ and the ‘less poor’. Further analyses showed that these two groups are relatively comparable in terms of livelihood strategy with the G2 and G3 groups of the 55 other villages. Finally, in three villages (5 percent), respondents identified only ‘rich’ (G1) and ‘less rich’ (G2) households. Over the whole region, the survey indicates that the poorest group (G3) systematically embodies the largest number of households, disregarding the area. In the Yaéré floodplain and along the western shores of the Lake this group represents 51 percent of the total number of households surveyed and 40 percent in the Chari Delta.

ACTIVITY RANKING EXERCISE

Analysis of the activity ranking exercise shows that on a global scale the better-off households (G1) always invest a significant part of their labour (time-effort) in fishing-related activities, followed by farming and then trading and herding. Fishing also plays a major role for G2 households since it ranks first in terms of income contribution for this group in the three areas. The labour invested in fishing, however, varies between areas. The comparative summary of these activity rankings is given in Table 2 for the income contribution. In detail, the three areas can be distinguished as follows.

In the Yaéré floodplain, cattle rearing is the only activity for which the labour allocation remains more or less constant across the three groups. Trading (which includes retail and/or small trade of fish, farming and/or other housing-related products) seems to be a dominant activity for better-off households of this area but stays inaccessible to the poorest. As far as farming is concerned, the interviews suggest that G2 households invest approximately the same amount of labour and derive the same proportion of income than G1 households. Comparatively, G3 invest more labour in that activity but derive lower incomes. In contrast, the role of fishing in households increases with poverty: fishing appears to be comparatively more important for G3 households (both in terms of labour and contribution to income) than for G2 and G1 households. This result suggests that the poorer the households in the Yaéré, the more they rely on fishing.

In the Chari Delta, farming, fishing, cattle rearing, trading and woodcutting are the main activities. However, as in the Yaéré, the importance of each activity varies greatly according to wealth level. Fishing is the dominant activity for the better-off households who invest the largest part of their time and effort in this activity and derive the largest proportion of their income from the commercialisation of their catch. Trading is predominantly operated by G1 (and G2 to a much lower extent) but stays out of reach from the

Table 2: Comparative summary of the activity ranking exercises (in terms of contribution to household’s income) for the 3 areas surveyed. The symbols ‘>>’ ‘>’ ‘ª’ hold respectively for: ‘contributes much more’, contributes more’ and ‘contributes equally”.

Wealth Group	Yaéré Activity contribution	Chari Delta Activity contribution	Western Shore Activity contribution
G1	Farm > Fish > Trade (Herd. é 0)	Fish > Farm > Trade >> Herd	Fish > Farm > Trade (Herd é 0)
G2	Fish é Farm >> Herd é Trade	Farm = Fish >> Trade >> Herd	Fish > Farm > Trade (Herd é 0)
G3	Fish > Farm > Herd (Trade é 0)	Wood >> Fish > Farm (Trade é Herd é 0)	Labour >> Fish é Farm (Trade é Herd é 0)
Activity of last resort	The poorer the households, the more they rely on fishing	Woodcutting central element of the livelihood of the poor	Daily wage labour central element of the livelihood of the poor

poorest households. Farming is the dominant activity of G2 households although fishing also contributes to a large part to their incomes. Herding is a source of minor revenues for both G1 and G2. As far as the poorest households are concerned, the survey indicates that they rely mainly on woodcutting activity, which appears to be the central element of their livelihood, both in terms of labour and income contribution.

Along the western shores of the Lake, the livelihood strategies of the G1 and G2 households are relatively comparable to those of the two equivalent groups in Chari Delat. In particular, the data shows that for both G1 and G2 groups, households invest a significant amount of labour in fishing and derive the largest part of their income from the commercialisation of their catch. They are both also highly involved in farming which is their second major activity. The distinction between G1 and G2 is in fact mainly related to the relative contribution of trading activities to their incomes. Like in the two other areas, G1 households derive a substantially higher proportion of revenues from trade than G2 households. In contrast G3 households are not involved in trading at all. They are employed mainly in wage labour through small daily jobs, e.g. farm clearing/weeding, fish processing (descaling and degutting), fish packaging and loading.

FURTHER RESULTS ON FISHING ACTIVITY

A series of specific analyses were carried out to complete the livelihood analysis and to gain a deeper insight into the specific role of fishing activity in the households livelihood and wealth differentiation process.

Comparative analysis of fishing gears

First the type of fishing gears owned by the households was compared between wealth groups in each village. The data shows that apart from the seine (‘*Tauraw*’) which is owned almost exclusively by G1 families but operate collectively, all groups, disregarding the area, use the same set of traditional, individual fishing gears, i.e. essentially gillnets, traps (Mali traps or ‘*goura*’), hook-lines, cane trap (‘*ndurutu*’), cast nets and dip nets (‘*sakama*’).

A large dissimilarity, however, exists in terms of *number* and *size* of gear owned by the households, depending on their wealth level. In particular the comparison for the three most common types of gear (gillnets, *goura* and hook-lines) –Table 3 top part- shows that the richest households (G1) across the whole region hold systematically a larger number of units of

Table 3: Top part: Comparative analysis of the number of gill nets, hook-lines and *goura* per household for the different wealth groups (range estimated by the key-respondents in each village). Bottom part: Number of different types of fishing gear owned by households of each wealth group (average across villages of the same area).

Estimated number per household [Range] (average)						
Area	Fishing gears	G1	G2	G2/G1 (b)	G3	G3/G1 (b)
	Gill nets	[2-6] (4.2)	[1-5] (2.4)	0.57	[0-2] (1.2)	0.29
Yaéré	Hook-lines (a)	[2-15] (6)	[1-10] (4)	0.67	[1-5] (1.6)	0.27
	Goura traps	[15-100] (50)	[2-50] (26)	0.52	[2-30] (12)	0.24
	Gill nets	[3-30] (11)	[3-12] (6)	0.55	[0-2] (0.5)	0.14
Western shores	Hook-lines (a)	[7-40] (24)	7-20 (12)	0.50	[3-6] (4.5)	0.19
	Goura traps	[100-600] (142)	[20-120] (73)	0.51	[0-20] (15)	0.11
	Gill nets	[4-30] (12)	[2-10] (4)	0.33	[0-2] (1.1)	0.09
Chari	Hook-lines (a)	[3-15] (9)	[2-10] (5)	0.56	[1-5] (3)	0.33
Delta	Goura traps	[10-100] (77)	[5-100] (83)	1.08	[0-25] (9)	0.12

Average number of different types of fishing gear owned by households			
Wealth groups	Chari Delta	Western shores	Yaéré floodplain
G1	3.78	3.73	3.31
G2	3.20	3.13	3.25
G3	0.96	0.46	2.80

Notes: (a) standardised 1000-hooks, (b) ratio of average values.

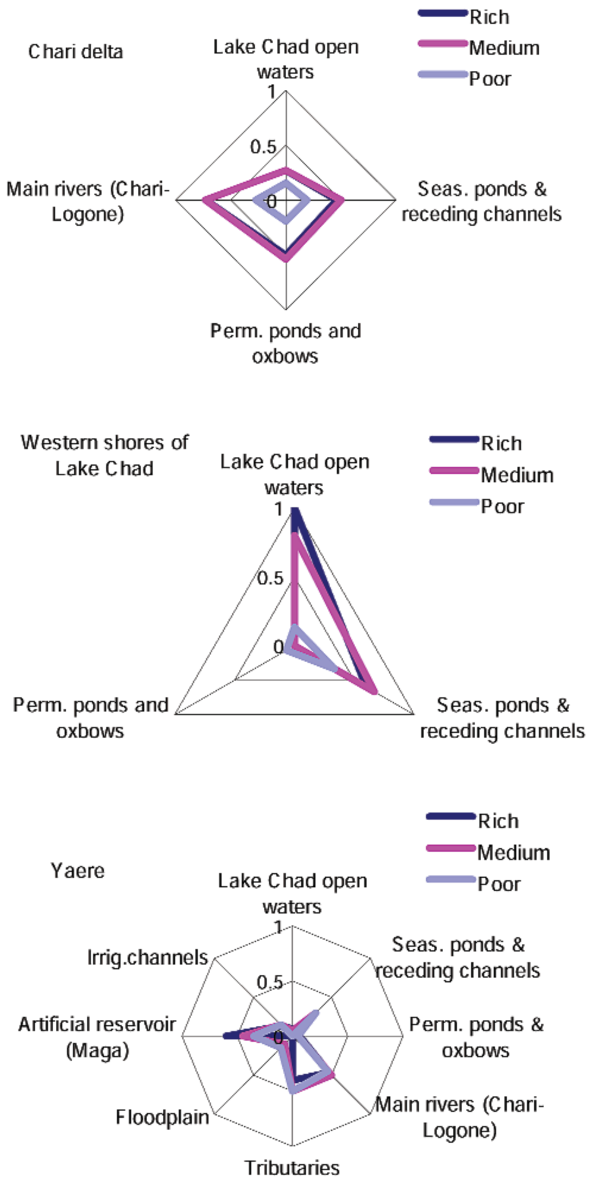
each gear compared to the other wealth groups. For instance, along the Western shores of the Lake, the G1 households own on average 2 times more hook-lines than the G2 households and almost 10 times more *goura* than the G3 households.

The estimate of the number of different types of fishing gears (in other words the 'diversity' of fishing gear) of the households as a function of their wealth level (Table 3 bottom part) is also very informative. The data show that this number declines with poverty, indicating that the poorest have a lower diversity of fishing gears than the better off. The decline is specially marked along the western shores and in the Chari Delta where the number of gear types per household is even smaller than 1 for the G3 group, reflecting the fact that a significant number of the poorest households in these areas own no fishing gear at all.

Fishing grounds access

A large number of social and/or ethnographic studies have emphasised that in Africa (but more generally in a large number of countries around the World), control to and restriction of access to fishing grounds is often a factor of wealth stratification within communities (Davies and Bailey 1996; Kremer 1994; Fay 1989; Kassibo 1994; Neiland, Jaffry and Kudaisi 1997). It was therefore anticipated that some form of access discrimination within the Lake Chad Basin's villages would be observed in favour of the richest/more powerful groups. To evaluate the degree of this potential inequity, a comparative analysis of the access to the water-bodies exploited by the different wealth groups was undertaken within each village. The results are synthesised in Figure 2.

The different polygons reflect the types and proportions of water-bodies accessed by the different wealth groups of the villages (aggregated per area). The comparison highlights some very instructive features, which had been disguised by the (global) typology presented in Table 1. In particular, we observe that while the polygons' shape and size are remarkably similar between the three groups in the Yaéré floodplain, indicating that all households in that area have



■ **Figure 2.** Results of the comparative analysis on accessibility to fishing grounds. The accessibility ranges from 0 to 1. A value of 0 means no access to the water body considered. A value of 1 means the water-body is accessed in 100 percent of the villages surveyed (within the area considered). The analysis was performed separately for each wealth group in each village and then aggregated by area.

access to the same fishing grounds disregarding their wealth level, the situation is radically different in both the Chari Delta and western shores areas. In these areas, the polygons of the poorest households are significant smaller than the polygons of the two other groups, indicating that the poorest households have reduced access to the fishing grounds in these areas.

DISCUSSION

ROLE OF FISHING ACTIVITIES IN RURAL LIVELIHOOD AND WEALTH STRATIFICATION

The comparative analysis of the activity-ranking exercise offers a good starting point to discuss the role of the fishing activities in the rural livelihoods (and wealth stratification) of the Lake Chad Basin populations. The analysis reveals that this contribution varies between wealth groups within the same area but also between areas for the 'same' wealth group. The first major conclusion of this study is therefore that the original question which motivated this study, i.e. 'what is the contribution of fishing activities to rural populations' livelihood?' can not be correctly answered if the different wealth groups that constitute the local populations/communities are not separated and the specific role played by fishing activities analysed within each group separately.

In the present case, wealth stratification highlighted several points. It shows that G1 households across the whole Basin always invest the largest part of their labour (time-effort) in fishing activities. Furthermore, this high labour investment is usually successfully transformed into revenues. For instance, both in Chari Delta and along the western shores, fishing activity contributes to the largest share of the G1 and G2 households' income, while in the Yaéré, fishing is ranked 2nd, after farming, for the better-off households. In fact, in the Yaéré floodplain, a more detailed analysis of the situation (Béné *et al*. in press) shows that the specific land tenure system associated with the relative scarcity of the non-flooding land, plays a major role in the predominance of farming over fishing activities for the better-off households. In contrast, the poorest households of the Yaéré tend to privilege fishing (both in terms of labour and contribution to income). In this respect, the analysis of the accessibility to fishing grounds suggests that the relative intergroup equity of access that characterises the water-tenure system in this part of the Basin is certainly one of the major factors that permits the poorest households of the Yaéré to rely on the fishing activity as the central element of their livelihoods.

The situation is quite different in the Chari Delta and along the western shores of the Lake. In those two areas, fishing remains relatively 'inaccessible' to the poorest who have to find alternative activities as a main source of income (in the Chari Delta, they rely mainly on wood cutting, while along the western shores of the Lake they hire their labour). In this respect, for these two areas (in contrast to the Yaéré floodplain area), it is interesting to notice the significant difference that exists between the poorest households and the rest of the communities in terms of access to the fishing grounds. The poorest only access a marginal part of the water-bodies available to the rest of the community. This difference reflects the 'direct' (financial) and 'indirect' (technical) restrictions that prevent the poorest households from having full access to the fishing grounds. The 'direct' restriction results from the various legitimised (i.e. institutionalised) and illegal taxes and/or fees that are imposed on the households for access to water-bodies. Indeed, the detailed analysis of the local institutional arrangements in these areas (Béné *et al*. 2003a; Bene *et al*. 2003a and b) shows that in 100 percent of the villages surveyed in the Chari Delta and along the western shores of the Lake, acquiring the rights of access to a restricted fishing ground involves systematically some form of fees payment, either in cash or as a proportion of the catch (or both). The local traditional authorities levy a large part of these fees, but the survey also reveals the existence of large-scale illegal taxation systems operated by soldiers of the Joint Patrol Forces or even by central government agents. These different fees (which overlap each other) represent multiple financial barriers that affect more particularly the poorest and prevent them from entering the fisheries. On the other hand, these poorest households also face 'indirect' (or technical) restrictions of access to certain fishing grounds resulting from their lack of adequate fishing gears and in particular lack of boats necessary to fish water bodies such as the open-waters of the Lake. The existence of these 'technical' restrictions was largely illustrated for instance through the analysis of the fishing gear ownership.

These various findings suggest that fishing activities determine household wealth (and represent therefore a key-element of the wealth differentiation), but also that fishing activities are, in turn, strongly determined by wealth. First, fishing determines wealth and participates to wealth differentiation in the sense that the better-off households, who can afford a larger number of fishing gears, and also more efficient and more productive gears such as the seines (*Tauraw*), are actually in a better position to transform their labour investment into a higher income in comparison to the poorer households who fish on marginal and usually less productive grounds with less efficient gears. Furthermore, for these better-off households, the incomes generated by the fishing activity are usually directly re-invested either in more efficient or larger fishing gears (which accentuates further the gap with the poorest) or sometimes in non-fishing activities. In this respect, numerous key-respondents emphasised during the interviews that additional investments in fishing inputs (through new fishing gears or more labour allocated to this activity) can generate instantaneous income surplus, in contrast to farming activities where several months (until the harvest time) would have to pass before eventual benefits might be returned from the investment. Given the very high (environmental and political) uncertainty that characterises these Sahelian regions, this capacity of the fishing activity to generate instantaneous gains represent (according to households' experience) a substantial advantage over farming.

Fishing is therefore a central element of wealth differentiation. But, at the same time fishing is also strongly determined by wealth. As emphasised above through the analysis of the Chari Delta and western shores data, only the wealthiest households have access to the whole range of water-bodies (amongst those available), while the poorest are marginalized or even excluded from these water-bodies. This differential in fishing ground access is mainly determined by the households' wealth as illustrated by the comparative analysis of access to water-bodies.

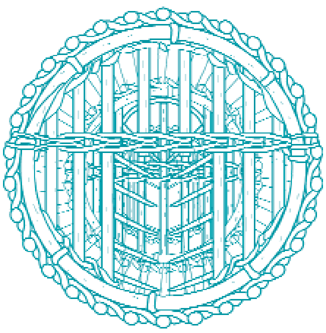
The second major conclusion of this analysis is certainly that, although the access to fishing grounds is strongly related to wealth, there is nothing like a one-to-one relationship between wealth level (or symmetrically poverty level) and the contribution of fishing activities to household livelihood. As the results of this survey have shown, fishing can represent the vital activity on which the poorest and most deprived households of a community rely to generate both income and food in the absence of equitable access to land (as in the Yaéré floodplain) and where, therefore, fishing can be seen as the "last alternative of the poorest" (cf. Table 2). But, as illustrated in the Chari Delta or along the western shores, fishing can also reveal itself a powerful lever for wealth differentiation and a central element in the livelihoods of the better-off households who use it to generate important revenues to be re-invested in various fishing or non-fishing activities. For instance, Neiland *et al*. (2000), using individual household income data show how the better-off households along the western shores of the Lake use a large part of the revenues generated by the fish catch to purchase farming inputs (fertilisers, seeds, etc. but also to hire farming labour).

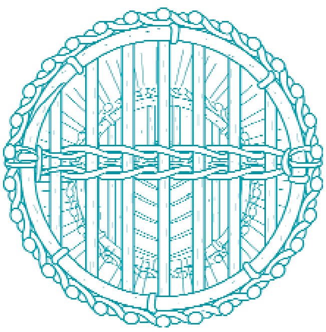
An important lesson from the above discussion is therefore that the way fishing activity contributes to household livelihood is remarkably complex and difficult to assess and that the relation between wealth (or poverty) and fishing activities is more than ambiguous. This last point brings additional support to the few recent field studies (Kremer 1994; Neiland *et al*. 1997; Neiland 2000) that tend to question the long-established view that fishers are the 'poorest of the poor' and that fishing will always remain 'a societal safety valve for surplus labour' (e.g. Bailey and Jentoft 1990, p.341). In fact, as the livelihood analyses carried out in the Chari Delta and along the western shores of the

Lake suggest, one can even observe situations where the poorest are too poor to be fishers! In those circumstances, the widespread perception that "fishery rhymes with poverty" (Béné 2003), still widely spread out amongst experts from international agencies and decision-makers, is far too simplistic to reflect or embody the complexity of the reality. In particular, this perception has prevented the development of adequate frameworks to assess the exact relationship, which exists between fisheries, poverty and wealth, and to identify the conditions which could make this activity a powerful tool for poverty alleviation and rural economic development. There is in that domain an urgent need of further empirical and conceptual research.

ACKNOWLEDGMENTS

The research presented in this paper is part of the INCO-DEV project IC-18-CT98-0331 funded by the European Commission. The authors are grateful to M. Baba, E. Belal, L. Dara, T. Jolley, B. Ladu, K. Mindjimba, S. Ovie, J. Quensière, O. Sule, F. Tiotsop and A. Zakara for their collaboration during the fieldwork and their helpful comments during the data analysis. The opinions presented here are those of the authors and do not necessarily reflect the views of the European Commission.





REFERENCES

Bailey C. & Jentoft S. 1990. Hard choices in fisheries development. *Marine Policy*, July: pp. 333-344.

Béné C. 2003. When fishery rhymes with poverty, a first step beyond the old paradigm on poverty in small-scale fisheries. *World Development*, 316: 949-975.

Béné C., Mindjimba K., Belal, E., Jolley T. & Neiland A. 2003a. Inland fisheries, tenure systems and livelihood diversification in Africa: The case of the Yaéré floodplains in Lake Chad Basin. *African Studies*, 622. (forthcoming)

Béné C., Neiland A., Jolley, T., Ladu B., Ovie S., Sule O., Baba O., Belal E., Mindjimba K., Tiotsop F., Dara L., Zakara A. & Quensiere, J. 2003b. Natural-resource institutions and property rights in Inland African fisheries. The case of the Lake Chad Basin region, *International Journal of Social Economics*, 303: 275-301.

Béné C., Neiland A., Jolley T., Ladu B., Ovie S., Sule O., Baba O., Belal E., Mindjimba K., Tiotsop F., Dara L., Zakara A. & Quensière J. 2002. Inland fisheries, poverty and rural livelihoods in sub-Saharan Africa: Investigation in Lake Chad Basin areas. *In* Neiland and Béné eds. *Sustainable Development of African Continental Fisheries: A Regional Study of Policy Options and Policy Formation Mechanisms for the Lake Chad Basin*. CEMARE University of Portsmouth and European Commission, Final Report EU-INCO Project No.IC18-CT98-9331. pp. 127-152.

Davis A. & Bailey C. 1996. Common in custom, uncommon in advantage: Common property, local elites, and alternative approaches to fisheries management. *Society and Natural Resources*, 9: 251-265.

FAO 1995. Review of the state of the world fishery resources: Inland capture fisheries, *FAO Fisheries Circular 885*. Rome, Food and Agriculture Organization.

Fay C. 1989. Systèmes halieutiques et espaces de pouvoirs: Transformation des droits de pratiques de pêches dans le Delta Central du Niger, *Cahier des Sciences Humaines*, 25, No.1-2: 213-236.

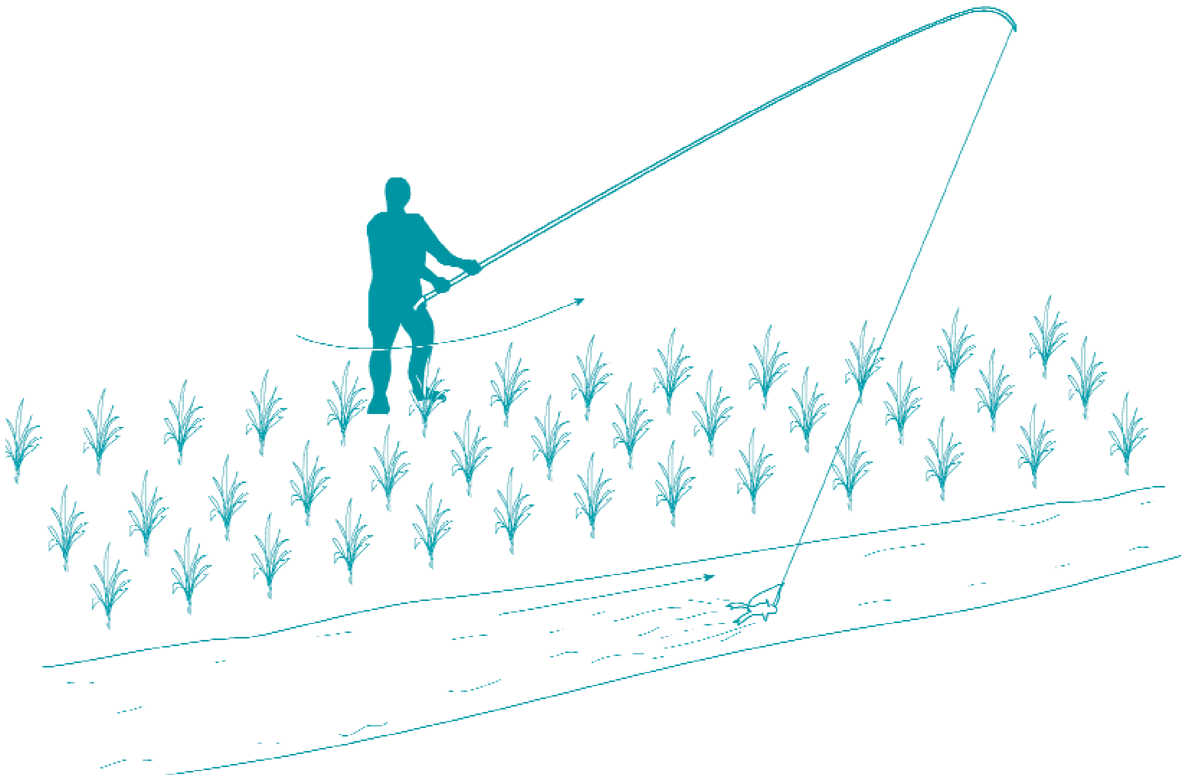
Kassibo B. 1994. Système de production et d'activité: La zone pré-lascutre de Sendégué. *In* Quensière, J. ed., *La Pêche dans le Delta Central du Niger*. Paris, ORSTOM. pp.383-400.

Kremer A. 1994. Equity in the fishery: *A floodplain in N.E. Bangladesh, Research paper R94E.* Bath, UK, Centre for Development Studies, University of Bath.

Neiland A.E. and Béné C. eds. 2002. *Sustainable development of African continental fisheries: A regional study of policy options and policy formation mechanisms for the Lake Chad Basin. Final Report EU-INCO Project No.IC18-CT98-9331CEMARE.* Brussels, University of Portsmouth and European Commission. 289 pp.

Neiland A.E., Jaffry, S., Ladu, B.M., Sarch, M.T. and Madakan, S.P. 2000. Inland fisheries of North East Nigeria including the Upper River Benue, Lake Chad and the Nguru-Gashua wetlands. Characterisation and analysis of planning suppositions. *Fisheries Research,* 48: 229-243.

Neiland A.E., Jaffry S. & Kudaisi K. 1997. Fishing income, poverty and fisheries management in North-East Nigeria. *In* Neiland A.E. ed. *Traditional management of artisanal fisheries in North East Nigeria, Final Report DFID Research project R5471, CEMARE Report No. R43.* 291-319.



STATE OF DEGRADATION AND APPROACHES TO RESTORATION OF FLOODPLAIN RIVERS IN INDIA

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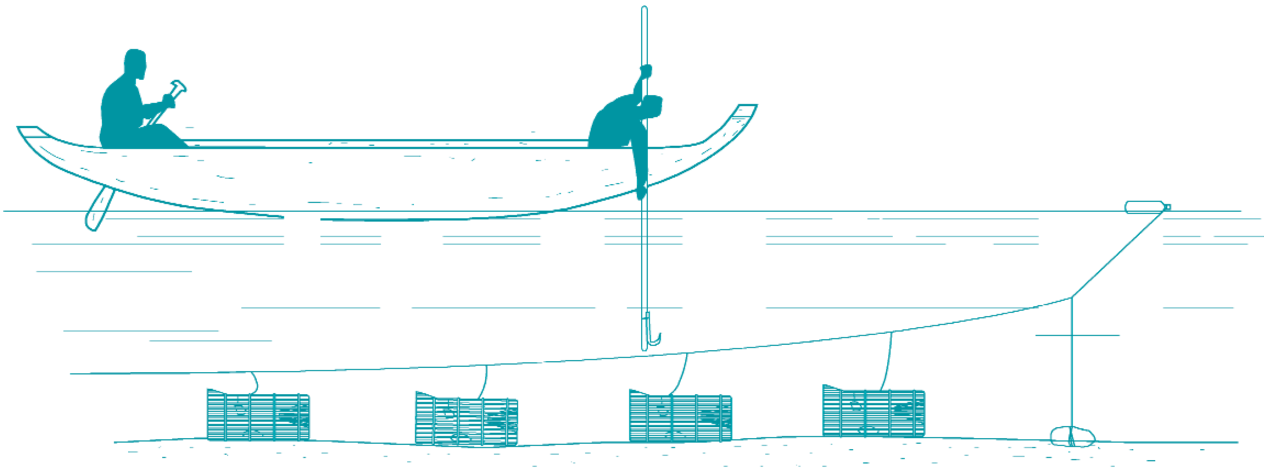


ABSTRACT

India has a large network of river systems of which three major rivers - Indus, Ganga and Brahmaputra - which originate in the Himalaya, drain nearly two-thirds of the land area and account for nearly the same proportion of the country's total water resources. They form extensive floodplains and deltas. At least a part of their basins lies in neighbouring countries (China, Nepal, Pakistan and Bangladesh). The three river basins are also among the most densely populated regions of the world where human activities have influenced the landscape for several millennia. During the past five decades, rivers have become rapidly degraded. They are extensively regulated for water diversion, flood control and hydropower by a series of dams, barrages and embankments. Discharge of domestic and industrial effluents, besides numerous activities in the catchments, floodplains and within the river channels have rendered the water unfit for human use. The biodiversity in general and fisheries in particular have declined very sharply. The Water (Prevention and Control) Act adopted in 1974 to regulate discharge of industrial and other effluents in surface waters and the Ganga Action Plan started in 1985 to provide for treatment of domestic sewage in major cities along the River Ganga have aimed at improving water quality. The National River Conservation Directorate under the Ministry of Environment and

Forests, has until now focussed mainly on the treatment of domestic sewage and industrial effluents, ignoring the importance of environmental flows and habitat diversity (including floodplain) to the conservation and management of river water quality as well as biodiversity, particularly fisheries on which millions of people depend for their livelihoods. The need for improving river flows and habitat restoration has now been recognised and plans are being formulated to initiate action in the Yamuna River basin starting from the uppermost parts of the watershed. While dams and barrages will continue to be in place and the embankments cannot be removed, it is proposed to focus on the restoration of floodplain areas between the two embankments and in unregulated stretches. This paper presents the conceptual framework for the proposed floodplain restoration program.

INTRODUCTION

Rivers play a major role in the economy of a country by sustaining agriculture, industry, energy generation and providing biological resources. However, humans have grossly abused the rivers worldwide by extensive regulation of flows, habitat alteration and disposal of all kinds of wastes into them. The impacts of these activities are already appearing in declining fisheries, increasing incidence of floods, lowered groundwater tables and growing incidence of water-borne diseases. Conservation and restoration of rivers have become vital for the overall sustainable development of a region.

The Indian mainland is drained by 15 major (drainage basin >20 000 km^2), 45 medium (2 000 to 20 000 km^2) and over 120 minor (<2 000 km^2) rivers, besides numerous ephemeral streams in the western arid region (Rao 1975). These river systems are grouped, according to their origin, into Himalayan and Peninsular rivers. Rivers Indus, Ganga and Brahmaputra are three major rivers, which together with their many tributaries, originate in the Himalaya. Their basins cover nearly two-thirds of the Indian subcontinent and are shared by different neighbouring countries (China, India, Nepal, Pakistan, Bangladesh). Rivers Ganga and Brahmaputra form extensive floodplains and a delta that ranks among the largest in the world. The three river basins are also among the most densely populated regions of the world where human activities have influenced the landscape for several millennia.

These rivers have played a major role in shaping the history of human civilzation in the subcontinent. The early agrarian civilizations of Harappa and Mohenjodaro, which flourished in the Indus river basin, were dependent upon intensive irrigation that required diversion of river water through an extensive system of canals. Human settlements on the banks of River Ganga and its tributaries have continued to exist for more than 5000 years. The rivers were extensively used for irrigation, drinking water, recreation, fishing and transport. Interestingly, the rivers were revered as mothers and worshipped as goddesses.

RIVER DEGRADATION IN INDIA

Until recently India remained a primarily agricultural economy with more than 85 percent of the human population living in villages and dependent upon agri-pastoral activities. The climate of the Indian subcontinent is governed primarily by the monsoons which are described as “one of the most dramatic of all weather events, tantalizingly complex, rich in variations from place to place and year to year, day to day and difficult to predict” (Fein and Stephens 1987). It is further influenced greatly by the unique geomorphological features of the region that includes the world’s highest mountain ranges, to produce extremely large spatial and temporal variability in the total annual precipitation. The high variability of unpredictable precipitation necessitated the construction of reservoirs (irrigation tanks) for storing surface runoff and diversion of river water through canals for irrigation since prehistoric times (see Gopal 2000). The water of R. Yamuna was diverted as early as the 13th century and major canals were constructed on Rivers Ganga and Yamuna between 1789 and 1868 to divert their flow soon after their descent onto the plain.

Since independence, the country has witnessed rapid, unplanned urbanization and industrialization and intensification of agriculture. The "green revolution" was achieved with the help of high yielding varieties, intensive application of agrochemicals and irrigation. The natural environment has been the victim of this economic development. Deforestation has reduced the forest cover from more than 23 percent before independence to a present 13 percent; land degradation and soil erosion have increased and both air and water are severely polluted particularly near major urban and industrial centres. The all-round environmental degradation has obviously affected the rivers, which have been over-exploited and even abused for development.

During the past fifty years, river regulation has proceeded at a faster rate. Besides barrages for diverting water; thousands of multipurpose reservoirs have been created by building high dams for water supply, irrigation, hydropower and fisheries. Large stretches of rivers, particularly those passing through the urban areas, have been modified for flood control and urban development on reclaimed land through channelization, the construction of embankments and filling up the floodplain. Besides reservoirs, water harvesting throughout the catchment areas by constructing smaller check dams or tanks for collecting the runoff has also affected flows in the streams and rivers downstream.

Urban and industrial growth has made a major impact on the river water quality through the discharge of untreated domestic sewage and industrial effluents. The impacts have been aggravated by greatly reduced flows and channelization of the rivers. In several stretches, many rivers have virtually turned into sewers. Human settlements, deforestation, mining, quarrying, grazing and other activities right up to the headwaters have extensively degraded the catchments and increased sediment loads of all the rivers (CPCB 1996). The increasing use of fertilizers and pesticides in agriculture has further contributed to the degradation of water quality. Consequently, the river biota have also been seriously affected. Riverine fisheries have declined considerably and many species have nearly disappeared.

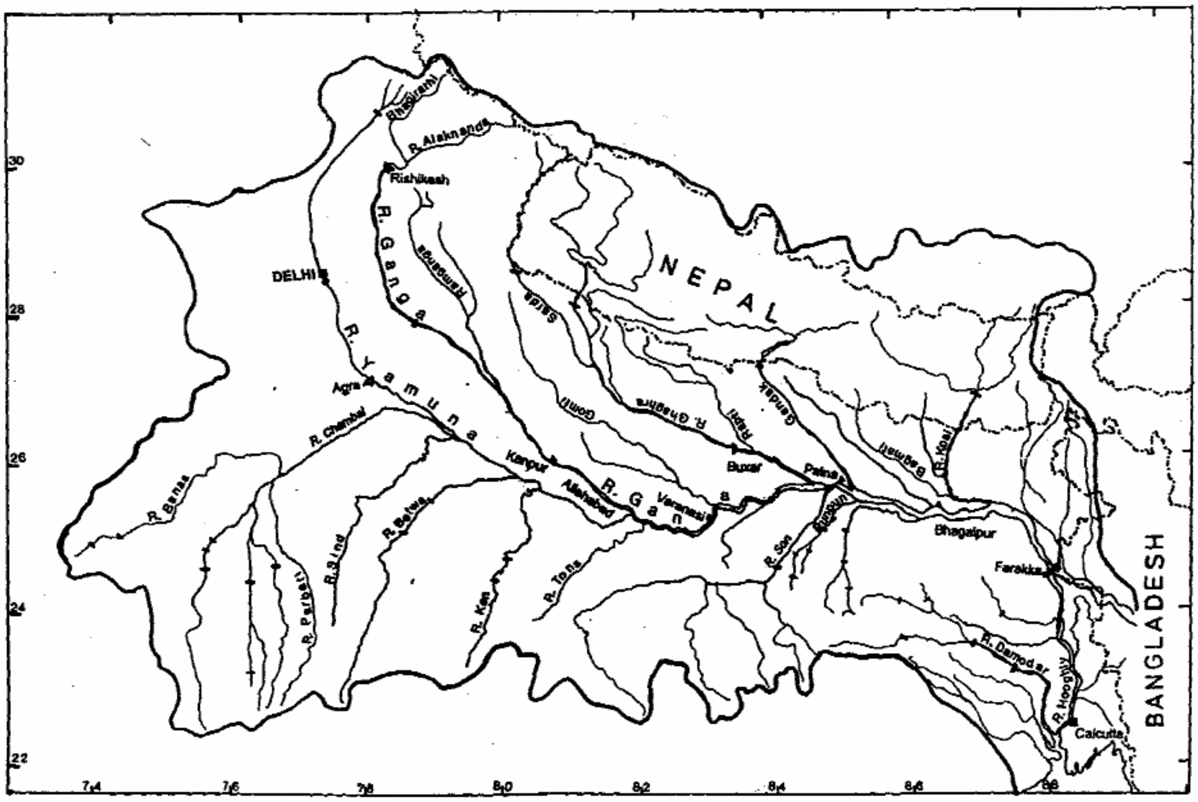
Conservation and management of rivers started receiving some attention only during the 1970s. Considerable emphasis has been laid on the improvement of water quality through interception, diversion and treatment of domestic sewage and industrial effluents. However, water quality continues to deteriorate further largely due to the reduction or total absence of flow and increasing degradation of the watershed. Gopal (2000) discussed earlier the issues, policies and actions required for the conservation and management of rivers.

In this paper, I focus on the state of degradation of River Ganga and its largest tributary River Yamuna and present a conceptual framework of efforts that have recently been initiated to rehabilitate the watershed in the upper reaches and to restore the floodplain. There is considerable published information on the Ganga river system (Anonymous 1980, 1982, 1983; Gopal and Sah 1993; Gopal 2000), a brief overview of which is given below as a background to the proposed restoration.

RIVER GANGA

R. Ganga – the longest river (2 525 km) in India arises from the Gangotri glacier (3 129 masl) in the Himalaya within India, flows southwest before descending in the plains at Rishikesh (350 masl). It then flows south and turns eastward meandering its way through the plain up to Farakka where it turns south and divides into two main channels one of which, the Padma River, flows through Bangladesh and meets R. Brahmaputra. It finally joins R. Meghna in Bangladesh in its last stretch just before forming the extensive delta (Figure 1). River Yamuna, the largest tributary (1 376 km long) of Ganga, also arises in the Himalaya from the Yamunotri glacier (6 320 masl) and flows almost parallel to R. Ganga until its confluence with the latter at Allahabad. The Yamuna River itself is joined by another major tributary R. Chambal, which drains a large area lying on the south and west of R. Yamuna and brings more water than the R. Yamuna at their confluence. The total discharge of R. Yamuna at Allahabad also exceeds that of R. Ganga. Several tributaries of Ganga originate in Nepal (Sharma 1997) and contribute over 40 percent of the annual flow of R. Ganga at Farakka (Khan 1994). A few tributaries that arise in Nepal meet R. Ganga inside Bangladesh, whereas others arising from the hills east of Vindhyan ranges, join from the right in its lower reaches.

break in the slope. For example, R. Son has shifted back and forth during the past few centuries whereas R. Kosi flowing through the plains of north Bihar has moved about 120 km westwards during the past 220 years (Wells and Dorr 1987). Flow regulation has only contributed to greater shifting of river channels.



■ **Figure 1.** The Ganga River system

The R. Ganga and its major tributaries are perennial but exhibit very large seasonal variation in their discharge. The rivers arising in the Himalayas receive snowmelt during the dry summer period, which is followed by the southwest monsoon. The north-flowing tributaries that arise in central India, also receive some runoff during the winter. A manifold increase in the river discharge during the rainy season and an extremely low gradient along most of the river course (10 cm km^{-1} in the middle reaches and less than 5 cm km^{-1} in the lower reaches) results in an extensive floodplain that extends to tens of kilometres on either side of the main channel.

Meandering and braiding are common to all floodplain rivers but the Ganga river system is characterized by shifting of river channels over long distances due to the high sediment load and an abrupt

Notwithstanding the reverence, River Ganga and its tributaries have been the greatest victims of human onslaught. It is one of the most regulated river systems with dams and barrages on practically every tributary and extensive embankments throughout the river basin (see Agrawal and Chak 1991). For example, the small gradient of 36 m on River Ganga between Hardwar and Aligarh (about 200 km) has been exploited for 13 small hydroelectric projects. Recently, a dam has been completed in the hills at Tehri on its major tributary, R. Bhagirathi, to exploit its hydroelectric potential despite the fact that the area lies in a seismic belt. River Yamuna has a series of barrages for hydropower in a 50 km stretch shortly before the water is nearly completely diverted for irrigation at Tajewala.

Excessive water extraction, dams and embankments have rendered the rivers nearly dry in several stretches. The floodplains have been eliminated or greatly reduced and the river channel's water carrying capacity has decreased further due to accumulation of silt that is neither carried downstream nor spread on the floodplain. Further and by far the greatest problem for rivers is caused by the discharge of untreated, or at best partly treated, domestic and industrial effluents. The problem of pollution is further increased by the disposal of solid wastes, religious offerings, idols, dead bodies and caracasses and other in-stream activities. Many studies on water quality, biota, bioindicators of pollution, assessment of heavy metal pollution and microbiology undertaken on River Ganga during 1983-1989 (Krishnamurthy 1991) revealed increasing levels of pollution in the plains. Though the Himalayan stretch had relatively unpolluted water, the middle stretch at Kanpur is heavily polluted with heavy metals from industrial effluents. Biological studies show that the species composition and the total population of various organisms along the river course have changed considerably. Chakraborty and Chattopadhyay (1989) have reported a shift in the species composition and an increase in abundance of the planktonic community in the estuarine section of R. Ganga (known as the R. Hoogly) after the construction of Farakka barrage, due to greater availability of freshwater and lowering of salinity.

Long-term studies on the fishery resources of the river have shown a sharp decline in the fish catch and also a significant change in the species composition. Dams have long been considered to impact upon the fishes (Jhingran 1991). In the Himalayan stretch, habitat alterations including dams have drastically impacted upon the fish communities. The characteristic coldwater schizothoraciine fishes such as mahseer (*Tor putitora*, *Tor tor*) and snowtrout (*Schizothorax richardsonii*, *S. plagiostomus*) have declined because their migration routes have been blocked (Sehgal 1994). In the lower reaches, the Farakka Barrage (which was constructed to ensure flow to the Diamond Harbor seaport) has frequently been blamed for causing the decline in hilsa (*Hilsa* (=*Tenualosa*) *ilisha*) and other fisheries. Hilsa is a typical long-distance anadromous species that used to migrate beyond the middle reaches of R. Ganga. Its catch declined from 19.3 tonnes to 1.04 tonnes at Allahabad and from 32 tonnes to 0.6 tonnes at Buxar after the construction of the Farakka barrage (Chandra 1989). In the plains, carps (*Cirrhinus mrigala*, *Catla catla*, *Labeo* spp) and catfishes (*Mystus* sp., *Wallago attu*, *Ompok* sp., *Pangasius pangasius*) constitute the major fisheries. Freshwater prawns (*Macrobrachium* spp) are also abundant. Fish landings have declined during the past 4-5 decades, from 961 kg per km in 1956-60 to 630 kg per km in 1981-87 (Chandra 1989; De, Ghosh and Unnithan 1989). The loss of feeding and breeding habitats in the floodplain lakes due to embankments, the increased silt load and the growth of macrophytes, which have reduced the deep perennial pools in the river channel, have been identified as major causes for declining fish catches (Jhingran 1991). Other river valley projects on the tributaries such as R. Kosi and R. Gandak have also adversely affected the fisheries in north Bihar.

Among other fauna that have been seriously affected by changes in the river habitat and water quality, the Ganges River dolphin (*Platanista gangetica*) is the most important. This dolphin was once abundant and widely distributed in the Ganga-Brahmaputra river system, with its distribution limited upstream by the lack of water and rocky shores and downstream by the salinity. Pollution, water withdrawal and dams are considered responsible for its population decline to only 152 from about 2000 in 1988-89 (Smith *et al*. 1994; Sinha 1997).

RIVER YAMUNA

The River Yamuna is the most important river after the Ganga and has attracted much attention because Delhi, the capital of India, Agra, the city known for Taj Mahal and Mathura, the birthplace of Lord Krishna, are all located within a stretch of 200 km on its banks. This stretch is the most polluted and degraded in the entire country. Gopal and Sah (1993) have described the characteristics of Yamuna river basin and reviewed the state of knowledge of the river. A barrage 200 km upstream of Delhi, the diversion through the Agra canal of the wastewater from Delhi and extensive channelization has resulted in the nearly complete withdrawal of water from the river. This together with heavy discharge of untreated domestic and industrial effluents has turned the river into a sewer at least between Delhi and Agra. Upstream of Delhi, it remains nearly dry for most of the year except for a few weeks during the short rainy season. It partly regains its riverine characteristics after its confluence with the R. Chambal, which has a larger flow than that of the Yamuna. The water quality and the biota have changed greatly over the past four decades (Gopal and Sah 1993). Turtles and crocodiles, once abundant in the river, have almost disappeared. Even in the River Chambal, the crocodiles have declined, necessitating the establishment of a National Chambal sanctuary for the Gharial.

Various anthropogenic impacts occur in the floodplain and extend to the entire upper watershed. In floodplains excessive grazing and cultivation have completely eliminated the natural riparian vegetation. Tree species such as *Tamarix dioica*, *Anthocephalus kadamba* and *Mitragyna parviflora* and reeds (*Phragmites* and *Arundo*) which once dominated the banks of River Yamuna have disappeared or occur only rarely. The riparian forests, dominated by species of *Barringtonia*, *Syzygium* and *Calamus*, which were common (Champion and Seth 1969), are now extremely rare.

The upper watershed of R. Yamuna (particularly that of its major tributary R. Tons) lying between 1 000 and 4 000 m altitude, is under intense human pressure as most of the local communities are wholly or largely dependent on the natural resources in the region. The area is increasingly threatened by deforestation, forest fires, herb gathering, over-grazing, poaching and construction (personal observations). Tourism is also slowly but steadily picking up. The area is highly prone to landslides and landslips, which are increasing largely due to road construction and various anthropogenic activities. Large areas (~30-40 percent) have become deforested and de-vegetated, resulting in severe erosion and landslides. Over-grazing in the alpine meadows is resulting in heavy erosion and rill and gully formation. The river is heavily loaded with silt that affects water quality and biodiversity as well as the use of water (such as in power generation). Available data suggest that the peak discharges during the monsoon season have increased whereas the lean period discharges have decreased.

RIVER CONSERVATION EFFORTS

The government, the scientific community and also the people have been conscious of the problem of growing water pollution in rivers, declining fish yields, increasing frequency of floods and droughts and the growing scarcity of water resources (e.g. Agrawal and Chak 1991). As early as 1974, the Water Prevention and Control Act was adopted by the Parliament to regulate discharge of effluents into the rivers and other water bodies. An irrigation policy was formulated in 1972 that promoted maximum crop production per unit area of arable land and highest possible use of river water to bring maximum possible area of agriculture under a single irrigation scheme. The National Water Policy (MOWR 1987) emphasises the development, utilisation, management and conservation of water resources, according to water use priorities with supply of drinking water at the top followed by irrigation, hydropower, navigation, industrial and other uses. It has recognized the need for modification of the prevailing pattern of agriculture and introduction of accountability and transparency on use of water and its source. The Ganga Action Plan, launched in 1985, provided for interception, diversion and treatment of sewage in all major towns along the River Ganga. This programme had been extended later to River Yamuna and all other rivers in the country and a National River Conservation Directorate (NRCD) had been set up within the Ministry of Environment and Forests (MOEF) to implement it with the help of the State governments.

However, these policies and programmes follow a sectoral, short-term approach instead of a holistic long-term planning and many policies are contradictory to each other. There is no coordination between different ministries and agencies concerned with water resources, agriculture, industry, environment, urban planning, energy, transport and watershed development. Several ministries deal with water as a commodity and treat it differently according to individual sectors including: drinking water supply, irrigation, hydropower, etc. Rivers are the responsibility of the states under the government federal structure as far as sharing of water resources is concerned. Similarly land is a state responsibility whereas the central government can deal with issues like water pollution and biodiversity.

Thus, while there are many stakeholders in the river systems and their watersheds, no one seems responsible for their conservation. The conservation of rivers has been limited to efforts towards improving water quality by treatment of wastewaters. Unfortunately, there has been no appreciation of the nature of rivers as ecosystems whose ecological integrity depends upon their physical, chemical, biological characteristics and interactions with their landscape (watershed).

PROPOSAL FOR YAMUNA RIVER FLOODPLAIN RESTORATION

During the past few years, serious concern has been voiced at the continued degradation of River Yamuna at Delhi and the inability of the Government to take remedial action. Public Interest Litigation was moved in the Supreme Court, which has directed the Government to ensure improvement in the river to bathing quality of water within a specified time. Among other factors mentioned earlier, the degradation of River Yamuna at Delhi is attributed primarily to the lack of flow and discharge of large volumeS of partly treated sewage. Only about half of the sewage generated in the metropolis of Delhi is treated. Often, the treatment plants function inefficiently and the effluent does not meet the prescribed standard. A large population of slum dwellers residing on the riverbank also contributes to the pollution load. Currently projects are underway to provide for additional STPs for treating most of the sewage and to relocate the slums from the riverbank. However, lack of the freshwater required for dilution of treated effluents discharged into the river remains a serious problem. The river discharge at Tajewala (about 200 km upstream of Delhi) is completely diverted and shared by four states. Delhi receives only a small amount through a canal for drinking water supply to the city. The neighbouring states are unwilling to reduce their share so as to make some water available for the river at Delhi. The problem is further compounded by extensive use of the upstream floodplain and also the riverbed for agriculture by exploiting groundwater and with the application of agrochemicals. Whatever little land is unfit for agriculture is intensively grazed. Natural riparian vegetation is almost non-existent except for annual ruderals.

The problem of in-stream flow is not unique to the R. Yamuna or Indian rivers in general. The in-stream flow requirements are being debated worldwide in terms of “minimum”, “adequate” or “environmental” flow and methods are being developed to estimate these requirements under diverse conditions (Tharme 1996; Richter *et al.* 1997; Richte *et al.* 2002; Richter and Richter 2000). At the same time, several approaches have been suggested and/or employed for restoring flows in different countries (The Nature Conservancy 2002). These approaches include removal of dams, regulated release of water from the reservoirs, reduction in water use and various nonstructural methods of floodplain management including restoration of the original conditions (FISRWG 1998; Rutherford, Jerie and Marsh 2000; Phillips, Bennett and Moulton 2001).

In India, while the rivers will continue to be threatened by ever-increasing withdrawal of water, there is also no possibility in the near future of dismantling dams and removal of embankments. The mitigation of the problem requires strategies for minimizing the wasteful use of water in agriculture, efficient wastewater treatment systems and recycling of water. These options have often been discussed at several forums but there has hardly been an attempt made to reduce water consumption. The policies of state governments to provide free electricity for irrigation have only increased water consumption. Floodplain restoration, therefore, remains the only viable alternative though it also requires great political will to support the change in land use back to that in the past.

It is encouraging that the importance of floodplains as an integral part of the river ecosystem has now been realized. The NRCD has recognized the hydrological role of floodplains in storing huge amounts of water derived from peak flow and storm runoff during the rainy season and later releasing it gradually, as well as in recharging the groundwater and improving its quality. Storage of the monsoon season runoff for augmenting flows in critical reaches had been suggested earlier also (e.g. Anonymous 1982; Bhargava 1985). Therefore, it is proposed to restore considerably large areas of floodplain, a 60-70 km stretch upstream of Delhi, with the primary goal of improving flow downstream.

The Proposal

The Survey of India's topo sheets (1:25 000) based on the last survey made in 1969-70, show that during the past thirty years, the river-floodplain system between the embankments has undergone many changes. Only few additional embankments have been built on the left of the river, mostly near Delhi. The main river channel has shifted its course, generally towards the east and the meandering has decreased considerably. Sediments brought by the river have raised the floodplain level and filled up all side channels and water bodies. However, this area is still submerged for a short period (several days) during the peak flood period in the rainy season.

It is proposed to restore wetlands and lost channels that existed during late 1960s. Additional water bodies will be created for storing peak floodwater. Some river meanders will be restored and recreated. Habitat diversity of the main river channel will be enhanced by various structural and non-structural measures. Another major component of the restoration project will be the extensive plantation of native trees, shrubs, reeds and grasses along the natural levee for checking erosion and bank cutting. Appropriate vegetal cover will be promoted on the floodplain in between the water bodies and the area will be suitably landscaped. Fisheries and freshwater prawn culture will be introduced in the water bodies created on the floodplain.

These measures will help retain most of the peak floodwater in the river-floodplain system. Given the loamy to clayey loam texture of the sediments, the ground water recharge will certainly occur. The large volume of water proposed to be stored on the floodplain is also expected to help maintain some flow downstream for a few months after the rainy season. With a gradual rise in water table, more water is likely to be available for flow in the river.

An increase in habitat diversity and the vegetation is expected to revive the natural fisheries as well as other riverine biodiversity (birds, amphibia, reptiles, molluscs and macro-invertebrates) that once occurred in the area. The loss of agricultural production will be more than compensated by the potential for fisheries and the production of forage and fuel. Additional benefits will accrue in terms of improvement in water quality due to a reduction in the application of agrochemicals and through nutrient transformation in the restored floodplain wetlands.

Only incorporating the socio-economic aspects and community participation can ensure the implementation and success of any such project. A programme of rehabilitation by providing alternate opportunities for livelihoods to people who own or cultivate the land in the floodplain has yet to be developed. Efforts will be made to involve these people in the restoration and follow-up management activities and motivate them to take up fisheries and prawn culture that are economically more profitable.

Rehabilitation of the Upper Watershed

Simultaneously with the floodplain restoration, the NRCD has initiated the preparation of another project for the rehabilitation of the upper watershed of the River Yamuna in the Himalayan ranges (>1 000 m altitude). The proposed rehabilitation measures include construction of a number of check dams on all drains and rivulets in a series to reduce the runoff and its velocity and re-vegetation of barren and open areas. In order to ensure that the environment is not degraded again due to continued impacts from local communities, the availability of natural resources has to be enhanced and their socio-economic condition and health has to be improved. Besides involving the local people in the rehabilitation work, an education and awareness programme is also planned.

It is hoped that these projects will be implemented soon with funding support from international agencies and the cooperation of the concerned departments and agencies of the state governments and the NRCD.

REFERENCES

Agarwal A. & Chak A. 1991. *Floods, flood plains and environmental myths. State of India's environment, a citizens' report 3*. New Delhi, Centre for Science and Environment. 167 pp.

Anonymous 1980. The Ganga Basin. Assessment *and development study of river basin series adsorbs/2/198081*. New Delhi, Central Board for the Prevention and Control of Water Pollution.

Anonymous 1982. *The Ganga Basin part I: The Yamuna subbasin. Assessment and development study of river basin series ADSORBS/2/198081*. New Delhi, Central Board for the Prevention and Control of Water Pollution. 114 pp.

Anonymous 1983. *Quality and trend of River Yamuna 197782. Assessment and development study of river basin series ADSORBS/10/198283*. New Delhi, Central Board for the Prevention and Control of Water Pollution. 114 pp.

Bhargava D.S. 1985. Water quality variations and control technology of Yamuna river. *Environmental Pollution*, A 37: 355376.

Chakraborty P.K. & Chattopadhyay G.N. 1989. Impact of Farakka barrage on the estuarine ecology of the Hooghly-Matlah system. pp. 189-196, *In* A.G. Jhingran & V.V. Sugunan eds. *Conservation and management of inland capture fisheries resources of Indi*a. Barrackpore, Inland Fisheries Sopciety of India.

Champio, H.G. & Seth S.K. 1968. *Revised forest types of India*. New Delhi, Manager of Publications.

Chandra R. 1989. Riverine fishery resources of the Ganga & the Brahmaputra. pp. 52-60, *In* A.G. Jhingran & V.V. Sugunan eds. *Conservation and management of inland capture fisheries resources of India*. Inland Barrackpore, Fisheries Sopciety of India.

CPCB Central Pollution Control Board. 1996. *Water quality status and statistics 1993 & 1994. Monitoring of Indian aquatic resources MINARS/10/1995-96*. New Delhi, Central Pollution Control Board. 459 pp.

De D.K., Ghosh A. & Unnithan V.K. 1989. Biology and migration of Hooghly hilsa in the context of Farakka barrage. pp. 197-202, *In* A.G. Jhingran & V.V. Sugunan eds. *Conservation and management of Inland Capture Fisheries Resour*ces of India. Barrackpore, Inland Fisheries Society of India.

Fein J.S. & Stephens P.L. eds. 1987. *Monsoon*. New York, John Wiley. 631 pp.

FISRWG 1998. *Stream corridor restoration: Principles, processes, and practices.* Federal Interagency Stream Restoration Working Group FISRWG. GPO Item No. 0120-A; SuDocs No. A 57.6/2: EN3/PT.653. (Available at http://www.usda.gov/stream_restoration/)

Gopal B. 2000. River conservation in the Indian subcontinent with contributions from Bose, B. & Goswami, A.B., *In* P.J. Boon, B.R. Davies, & G.E. Petts eds. *Global perspectives on river conservation: science, policy and practice.* Chichester, UK, John Wiley & Sons. pp. 233-261

Gopal B. & Sah, M. 1993. Conservation and management of rivers in India: Case study of the River Yamuna. *Environmental Conservation*, 20: 243-254.

Jhingran V.G. 1991. *Fish and fisheries of India, Third Edition*. New Delhi, Hindustan Publishing Corporation.

Khan T.A. 1994. *Challenges facing the management and sharing of the Ganges. Transboundary Research Report 81*. Albuquerque, NM, Transboundary Research Centre, University of New Mexico.

Krishnamurthi C.R., Bilgrami K.S., Das T.M. & Mathur R.P. eds. 1991. The Ganga: A scientific study. New Delhi, Northern Book Center. 246 pp.

MOWR Ministry of Water Resources, 1987. *National water policy.* New Delhi, Ministry of Water Resources, Government of India. 17 pp.

Phillips N., Bennett J. & Moulton D. 2001. Principles and tools for protecting Australian Rivers. Canberra, ACT, Land and Water Australia. 60 pp.

Rao K.L. 1975. India's water wealth: Its assessment, uses and projections. New Delhi, Orient Longman. 255 pp.

Richter B.D., Baumgartner J.V., Wigington R. & Braun D.P. 1997. How much water does a river need? *Freshwater Biology*, 37: 231-249.

Richter B.D., Mathews R., Harrison D.L. & Wigington R. 2002. Ecologically sustainable water management: Managing river flows for ecological integrity. *Ecological Applications*. (forthcoming)

Richter B.D. & Richter H.E. 2000. Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. *Conservation Biology*, 14: 1467-1478.

Rutherford I.D., Jerie K. & Marsh N. 2000. A rehabilitation manual for australian streams, vol. 1 & 2. Canberra, ACT & CRC for Catchment Hydrology Land and Water Resources Research Development Corporation.

Sehgal K.L. 1994. State-of-art of endangered, vulnerable and rare coldwater fishes of India. *In* P.V. Dehadrai, P. Das & L.R. Verma eds. *Threatened fishes of India*. pp. 127-135. Muzaffarnagar, India, Society of Nature Conservators.

Sharma C.K. 1997. A Treatise on water resources of Nepal. Kathmandu, Nepal, Sangeeta Sharma. 493 pp.

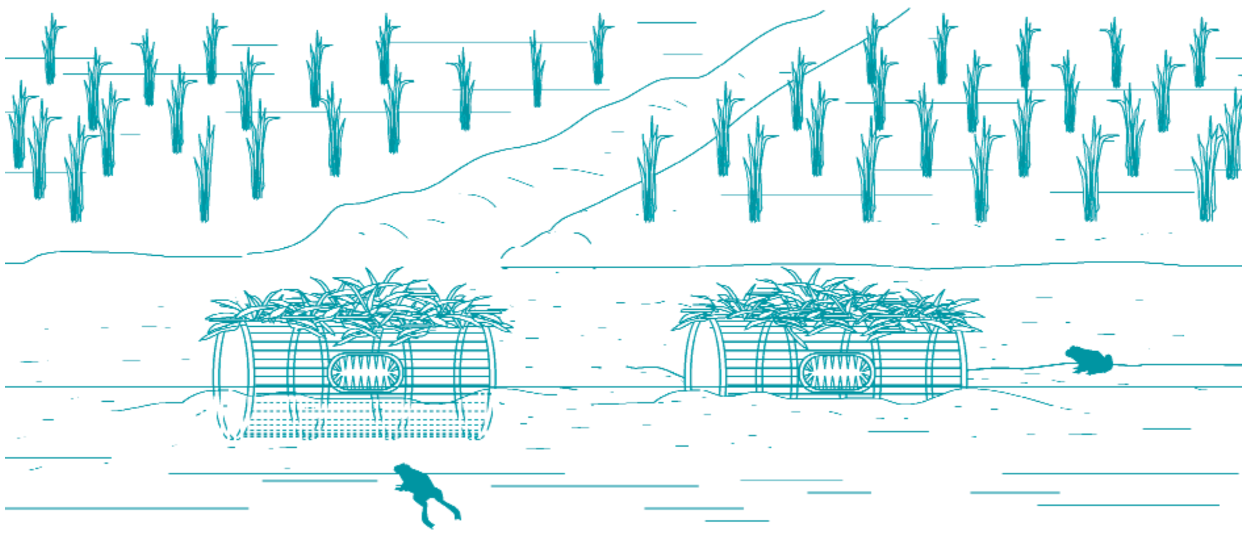
Sinha R.K. 1997. Status and conservation of Ganges River dolphin in Bhagirathi-Hooghly river system in India. *Int. J. Ecol. Environ. Sci*., 23: 343-355.

Smith B.D., Sinha R.K., Regmi U. & Sapkota K. 1994. Status of Ganges River Dolphins *Platanista gangetica* in the Mahakali, Karnali, Narayani and Saptakosi rivers in Nepal and India. *Marine Mammal Science*, 10: 368-375.

Tharme R. 1996. Review of *International Methodologies for the Quantification of the Instream Flow Requirement of Rivers. Water law review final report for policy development for the Department of Water Affairs and Forestry*. Pretoria, SA.

The Nature Conservancy, 2002. *Flow restoration database*.(Available at http://www.freshwaters.org/info/eswm/)

Wells N.A. & Dorr J.A. 1987. Shifting of the Kosi River, Northern India. *Geology*, 15: 204-207.



THE POLITICS OF FISHERIES KNOWLEDGE IN THE MEKONG RIVER BASIN

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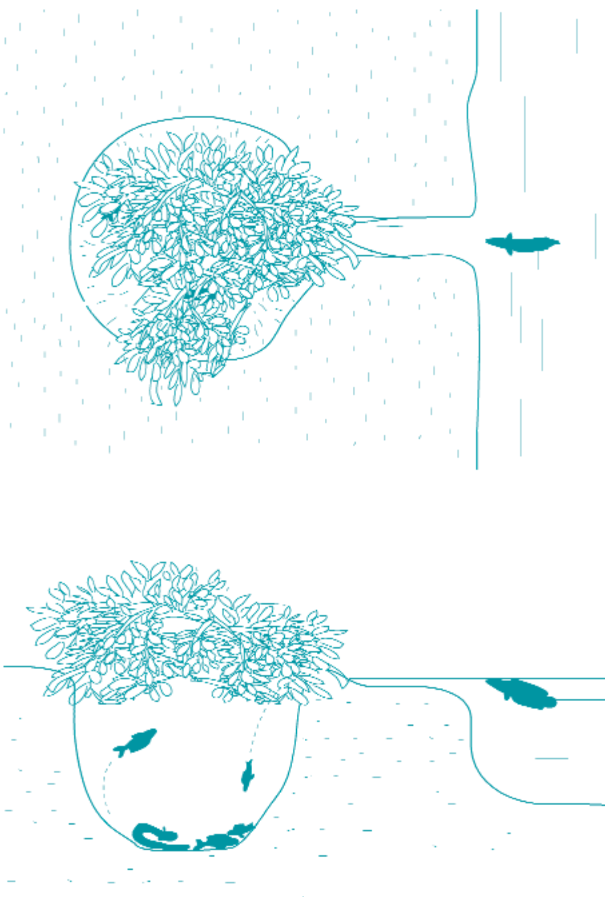


ABSTRACT

The Mekong River Basin is a highly diverse ichthyofaunal resource and a highly productive fishery in both subsistence and commercial terms, which has come under increasing stress. About this there is general agreement, but beyond these generalities the level of agreement rapidly dissipates. The politics of fisheries knowledge in the Mekong River Basin involves tensions along a number of lines: scientific and indigenous knowledge of fisheries; basic science and EIA-driven fisheries studies; culture and capture fisheries knowledge; taxonomic and livelihood-oriented fisheries research; NGO and governmental articulations of the causes of fisheries decline; and fisheries consumption and production statistics used by riparian countries and those produced by the Mekong River Commission.

In this paper, I examine fisheries knowledge in the Mekong River Basin in the context of the politics of its production and ownership. The paper examines the tensions over fisheries knowledge in an attempt to direct attention to the circumstances of its production. The purpose of this approach is to highlight for fisheries managers and river basin managers more generally, the significance of understanding the politics of knowledge as a pre-requisite for using such knowledge as a management input. I argue that it is not sufficient to come up with expert knowledge that is privileged as "best estimate", particularly in the highly complex and politicised power/knowledge milieu that is prevalent in the Mekong River Basin. Rather we need to explore and develop approaches to knowledge that accommodate and go some way to resolving different epistemologies, through an inclusive and more culturally grounded research agenda.

INTRODUCTION

Few doubt the significance of the fisheries of the Mekong River, its tributaries and its delta. The vastness and diversity of the fishery are well known, as is the fact that it is important for the livelihood of many, if not most, of the more than sixty million people who live in the Mekong River Basin. Most recognise that there are extractive and environmental pressures on the resource. Yet beyond these basic points of agreement, there is a lot of uncertainty, debate and tension over fisheries knowledge. Informed policy needs to be cognisant of the intricacies of knowledge production. While many of the tensions and points of disagreement are familiar to researchers and others who have worked in the area of Mekong fisheries, there has been relatively little structured investigation or discussion about the circumstances of knowledge production, appropriation and its significance for policy.

The politics of knowledge are significant in many circumstances and are certainly not the preserve of Mekong fisheries. Knowledge and power are intricately bound up and there is a continuing tension between positivist, objectified knowledge in the guise of science and a relativist, contextual epistemology in the guise of indigenous knowledge. Intermediate positions include the concept of situated knowledge, which does not negate the existence or significance of real-world facts, but at the same time points us to the circumstances of knowledge production and its "embodiment" in the sense of existing through the scientist or other producer of such knowledge (Haraway 1996).

In this paper, I briefly discuss the politics of environmental knowledge in the Mekong Basin and the significance of such politics for fisheries management, before identifying key lines of tension in fisheries knowledge production. The paper is not encyclopaedic about types of knowledge or forms of knowledge production, but it does try to cover key areas in which understanding the epistemology of fisheries is important for those working at policy and practical levels in the Mekong River Basin.

THE POLITICS OF ENVIRONMENTAL KNOWLEDGE IN THE MEKONG

Rapid economic development in the Mekong Region and more specifically in the Mekong River Basin has generated increasing environmental concern. The environment has become an arena of critique and debate over the most appropriate path of development for the countries and peoples of the Mekong, but sustainable development discourses have also allowed all to make claims to environmental concern. As different players have taken on the environmental mantle, environmental knowledge has become central to tensions between different interests.

The politics of environmental knowledge reflects the variegated interests within the Basin, delimited geographically, sectorally and socio-politically (Hirsch and Cheong 1996). Geographically, the division of the basin into six sovereign states means those different countries' respective interests shape the way in which environmental knowledge is produced and treated. The division between China and the lower Mekong countries is sharpest here. A recent Chinese perspective on fisheries and other environmental implications of the development agenda in Yunnan (He Daming 2002) reflects the ways in which scientists' rationale can be shaped by their country's specific interest.

Sectoral tensions reflect the different charges that fisheries, hydropower, environmental and other agencies may have, showing that the politics of a shared river basin are not delineated only along national lines. Within government as well, there can be quite different perspectives between local and national government, with local authorities sometimes – but not always – better aware of and more responsive to local realities and concerns. Socio-politically, the power divides between small-scale farmers and fishers, government agencies, corporate interests in the resource base and the scientific community are reflected quite openly in some countries (notably Thailand) and remain well below the surface in others (notably Laos and Viet Nam). Nevertheless, the politics of knowledge remain relevant in all cases, perhaps nowhere more so than in fisheries.

KEY LINES OF TENSION IN FISHERIES KNOWLEDGE PRODUCTION

Key lines of tension mark out the current state of knowledge of fisheries in the Mekong River Basin and the ways in which this knowledge affects policy formulation and implementation. A summary with illustrative examples is presented for each of several "axes of tension" below. Two caveats are in order. First, there are many shades of grey and these "axes" are drawn to illustrate lines of tension rather than to suggest absolute polarisation or dichotomies. Second, there is a good deal of overlap and resonance between the axes, for example between scientific and local knowledge on the one hand and government and NGO tensions on the other.

SCIENTIFIC AND INDIGENOUS KNOWLEDGE: WHOSE KNOWLEDGE COUNTS?

Research on fisheries in the Mekong and its tributaries has focused on taxonomy, migrations, trends in fish stocks, fish ecology and fishing-based livelihoods. Direct sampling has been difficult for logistical reasons, for reasons of access by scientists until recently (including the years of conflict) and due to the very limited or non-existent local scientific research infrastructure in Laos and Cambodia. The very diversity and highly migratory nature of the Mekong fishery also pose challenges to sampling-based research.

Of course, there is an enormous repository of knowledge about the Mekong fishery in the communities who have long been dependent on the resource and who daily observe the spawning, migratory and feeding habits of different fish species. There has been increasing recognition over the past two decades that local knowledge "counts" (Chambers 1983). International symposia and publications on the significance of indigenous knowledge have moved well beyond the anthropological and ethno-ecological arena in which the subject has been developed since the 1950s (Conklin 1954). Yet, indigenous knowledge has continued to be ignored or treated by many resource managers and developers as unscientific, hence of little interest or value. The low status of indigenous knowledge and the pejorative connotation of what is sometimes termed "anecdotal evidence" continue to devalue such knowledge in a research context. This has immediate implications where, for example, the only evidence in decline of a fishery is based on such knowledge, such as in the case of the Se San River where local reports of fisheries impacts of upstream hydropower development at Yali Falls in Viet Nam are not accepted because there is no scientific data to back them up, compounded in this case by the lack of baseline information in the EIA.

There have been recent accommodations between scientific research and indigenous knowledge. In particular, the Assessment of Mekong Fisheries Component (AMFC) of the Mekong River Commission's (MRC) Fisheries Program has employed and developed techniques for using local ecological knowledge (LEK) to develop an understanding of fish migrations on the Mekong mainstream and tributaries (Poulsen and Valbo-Jorgensen 2001). This is a breakthrough in the application of fishers' own knowledge for large-scale fisheries management at a basin level. Nevertheless, while natural and social scientists have come to recognise the significance and value of indigenous knowledge, there remain deeper epistemological questions of ownership. Research that "mines" LEK for publication in scientific papers or for development of national or basin-wide policy formulation is inherently different to a participatory research framework that works with local fishers and their knowledge as the basis for local management (Baird 1999; WWF 2002). Adaptive management is a promising research/management approach that incorporates this type of participation and local iteration between research and practice (Garaway *et al.* 2002). Another mode in which fishers' knowledge is used is for articulation of those fishers' interests vis-a-vis developments that actually or potentially threaten the fishery (Searin 2002).

Earlier tensions between measurement based on catch per unit effort (CPUE), on the one hand (Warren, Chapman and Singhanouvong 1998) and understandings of the local fishery through intimate knowledge of community practices and familiarity with villagers on the other (Baird 1996), have prompted a syncretic approach whereby methods such as hydro-acoustic sampling of deep pools is being combined with CPUE measurements to assess the effectiveness of management through establishment of fish sanctuaries that are based on local knowledge and community-based processes.

Studies recently undertaken to monitor the fisheries benefits against the costs (in foregone revenue from electricity production) of keeping open the gates of Pak Mun Dam provide another interesting example of tensions between academic science and research based on local knowledge. The Thai government commissioned a team led by Dr Kanokwan Phankasem of Ubonratchathani University to carry out a range of studies, notably fisheries research, in order to monitor the benefits of keeping the dam gates open. The researchers came up with four options based on this research, which found that there were indeed significant livelihood and biodiversity impacts of closing the dam gates and they recommended adoption of the fourth of these – keeping the dam gates open for five years to further monitor the impacts while power demand in Thailand remained well below the country's combined generating capacity. However, the government opted for a "compromise" option, closing the dam for 8 months and opening the gates for 4 months during the wet season. In contrast, villagers along the Mun River organised their own research program under the title Tai Baan Research (Settrachau 2002). As Poh Dam, one of the villagers involved in this program stated:

> If we have researchers here, we fear that they cannot get the information straight, or they cannot do it entirely correctly. Since they only live in the town, how can they know where the fish live, or where they get together in a large number or what they eat? They will end up having to ask the villagers. We think we ought to collate the information ourselves, as outsiders will not understand our way of life. We are the ones affected by the project and our resources have been destroyed (Assembly of the Poor 2002).

The politics of science versus indigenous research is thus based not only on the quality or reliability of information, but also on questions of ownership and the uses to which different types of fisheries knowledge are put. In the accommodation of the two types of knowledge we see a bi-directional process: on the one hand, recognition by the science community of the value and significance of local knowledge and interest in developing tools to make better and systematic use of that knowledge and on the other hand local communities' empowerment by putting their own knowledge base to use in a more systematic and legible way:

> The significance of the Tai Baan Research lies in empowering communities, equipping them with the tools to turn their local wisdom into the form of written documents, collectively produced and owned by the communities producing them (Traisawasdichai 2002).

SCIENCE AND CONSULTANCY: HYDROPOWER AS A KNOWLEDGE DRIVER

The politics of funding are an important element of knowledge production in any setting. Studies of fisheries in the Mekong are funded from four main sources, each with quite specific implications for the type of knowledge produced, its ownership and its input into the policy process. First, scientific research is funded by project grants such as the work of Tyson Roberts supported by the Smithsonian Institution, or the work of eminent fish taxonomists such as Walter Rainboth and Maurice Kottelat with North American and European science grants – although some of this work was also supported by FAO. Second, development and management-oriented research initiatives are funded largely through the MRC, most notably the fisheries program supported by DANIDA. Other, much smaller sources of funding in this category come from development research agencies such as IDRC (Canada) and ACIAR (Australia) and involve collaborations between foreign and local researchers, usually on a specific applied management problem but also, in the early phase of IDRC in quite basic research, for example, involvement in migration studies at Khone Falls. Third, smaller scale fish studies have been supported by non-governmental organizations such as Searin (Southeast Asian Rivers Network), involving local communities documenting their own fisheries practices, knowledge and livelihood dependence in the context of threats to the fishery from projects such as hydropower and blasting of rapids for navigation (SEARIN 2002). Finally and in many cases dominating the knowledge production process, is the swathe of consultancies associated with large scale resource projects (notably dams and mines) that require environmental impact assessments (EIAs) including fisheries impact studies.

A major problem in determining the impacts of a number of recently and not so recently completed dams on Mekong tributaries has been the paucity of baseline studies. Yali Falls, Nam Song and Theun-Hinboun dams, all of which appear to have had major fisheries impacts, were built with quite minimal fisheries research as part of their EIAs (Hirsch 2001). Where fisheries studies are carried out, for example in the case of the Sepon gold and copper project, the EIA is based on data collected over a very short period, almost always during a single season. Yet the natural seasonal and annual variability demands much longer research for a baseline against which impacts can be measured reliably.

Perhaps the most significant political aspect of consultant-generated knowledge is its ownership by the client who commissions it. This lends such knowledge to direct or indirect manipulation – direct in the selective use or delayed release of consultancy reports by project holders when there are potentially embarrassing or costly findings, indirect in the holding back by consultants themselves of findings, or recommendations based on such findings, that might prejudice future contracts. Only in some cases (e.g. Warren 1999) do consultants have the courage to publish findings in a wider forum and more often than not they are contractually bound to keep findings confidential. Consultant-generated research is not normally subject to peer review, although recent moves at MRC have been a positive step in this direction. In some cases, post-impoundment studies of fisheries and other livelihood impacts of hydropower projects have been carried out. For example, ADB commissioned a post-impoundment impact study of Nam Song Dam after it became apparent that the earlier EIA work had not done a proper fish study and that certain recommendations (e.g. for aquaculture ponds) had not been acted upon. The consultants' report found uncompensated losses valued at approximately US$2 million - largely due to impacts on fish catches - among 13 affected communities, but this report has yet to be released publicly more than 24 months after its completion and more than seven years after the dam was finished.

Publicly funded research at MRC presents an interesting intermediate case between consultancy and academic science modes of knowledge production. The non-riparian scientists employed through the fisheries program are on consultancy contracts, but there has been a healthy increase in level of research involvement by riparian nationals seconded from their respective ministries and departments. The sense of ownership of MRC knowledge and data and the level of independence of the research carried out has moved in a positive direction since 1995. The Fisheries

Program newsletter, Catch and Culture, produces articles that demonstrate a considerable degree of openness and independence in an institution whose riparian member states tend to give fisheries quite a low priority in development planning – with the relative exception of Cambodia. As a number of publications quoted in this paper attest and indeed in the holding of the LARS2 conference for which an earlier version of this paper was presented, there are positive moves toward a more accountable and open fisheries knowledge production process. Nevertheless, there remains room for further "indigenization" of research – not a single one of the papers presented over three days at LARS2 was delivered by a riparian national.

CULTURE AND CAPTURE FISHERIES: DEVELOPMENTALISM AND ITS IMPLICATIONS FOR KNOWLEDGE BIAS

Approximately 90 percent of the fish caught and consumed from the Mekong River and its tributaries are wild. Yet the significance of the capture fishery is not matched in relative terms by the resources that Departments of Fisheries put into enhancing knowledge. Aquaculture receives much greater attention as a development program and most of the traditional "research" effort has been at fisheries stations and on-farm ponds where exotic species (notably Chinese and Indian carp and *Tilapia* spp), but more recently indigenous pangasids in cage culture in the Mekong Delta (Trong, Hao and Griffiths 2002), are raised. The MRCS Fisheries Program component Aquaculture of Indigenous Mekong Species (AIMS) aims at domesticating other Mekong species. Meanwhile, significant research effort is now in the private sector, notably CP's sex-reversed Tilapia and with privatisation of knowledge production the aquaculture bias can be expected to intensify given that corporate profits can only be made in this sector.

Part of the explanation for the neglect of capture fisheries relative to their significance is the developmentalist notion that wild fisheries are essentially an undeveloped use of nature in a hunting and gathering mode, whereas modernity demands cultivation, sedentarisation, capitalisation, improved species and so on. A more fundamental reason is that most aquaculture work increases production, while most capture fisheries work is aimed at maintaining, or halting the decline, in natural fisheries. The former is seen as development, the latter is given less priority because it is not measurably making something better. The relative sizes of the capture and culture fisheries in the Mekong (estimated at approximately ten to one, respectively) is lost on most decision-makers. Seemingly dramatic – and, more importantly, readily measurable – increases in aquacultural production achieve a higher profile than the much larger, but less dramatic and less verifiable arresting of capture fisheries decline. These perceptions affect national governments and donor agencies alike, both of which have a hard time understanding the relativities between maintenance of a hugely important resource versus cultivation, sedentarisation, capitalisation, improved species and so on of a much smaller resource.

In part, also, there is an established idea of fisheries research as a technical, natural science issue, whereas livelihood-relevant researches into capture fisheries necessarily involves social aspects of fisheries management. Another, somewhat speculative reason that government fisheries agencies have stayed clear of wild capture fishery research is that findings on the significance of the fishery could quickly enter sensitive territory when such findings highlight the destructive aspects of projects in politically powerful areas of government, notably ministries of energy and industry. Indeed, aquaculture and reservoir fisheries are commonly put forward as mitigation for such projects.

More recent awareness of the size of the capture fishery, combined with interest in aquaculture using indigenous species, has somewhat blurred the lines between capture and culture fisheries research. Additionally, areas of overlap such as rice-field and enhanced back-swamp fisheries also provide examples of "greyer" areas between aquaculture and wild fish stocks. There has been less attention to more critical issues of incompatibility or competition between the two, for example where aquaculture is supported by the feeding of domesticated fish with fishmeal made from wild fish, or where the capture of wild juveniles and fry for aquaculture represents a threat to wild fish populations and hence to capture fisheries (van Zalinge 2002).

TAXONOMY, HABITATS AND ECONOMY: BIODIVERSITY AND LIVELIHOOD ORIENTED ENVIRONMENTALISM

The ichthyofaunal biodiversity of the Mekong River system is second only to that of the Amazon. More than 1 200 species are known and informed estimates suggest there may be up to 1 700 species in total. Not surprisingly, species identification has been a significant part of building fisheries knowledge in the Mekong (e.g. Kottelat 1998). A number of well-known fish experts have produced useful directories (Rainboth 1996; Kottelat and Whitten 1996). Most of the species that await discovery are likely to be endemic to remote montane tributary reaches in Laos, in relative terms having more scientific than livelihood importance. Furthermore, useful research on specific types of habitat (Poulsen *et al.* 2002) and on key wetlands (Daconto 2001) are starting to build up an increasingly sophisticated understanding of the ecosystem functions relevant to fisheries and their vulnerability to hydrological changes.

In a highly biodiverse, until recently little studied, scientifically important yet income-poor river basin whose fishery faces a range of extractive and environmental pressures, there is in principle an allocation of resources in fisheries research between taxonomy and scientific ecology, on the one hand, versus livelihood-oriented questions, on the other. This reflects a wider tension in global environmental concern between biodiversity as a “good” in itself, versus environment as livelihood. The different environmental concerns that prompt research interest in these alternative areas arise from quite different aesthetics and value sets, as suggested by Guha and Martinez-Alier (1997) in their book “Varieties of Environmentalism”. In the Mekong, far greater resources go into livelihood studies, for the good reason that donor agencies and national governments alike prioritise people’s livelihoods over pure research for knowledge sake alone. In this sense, there is not so much a tension as a point of difference in conservation objectives that lie behind the research carried out in each case. On occasion, however, the biodiversity and livelihood knowledge can come into conflict, for example in the case of *Probarbus jullieni* (Sauvage 1880): as a CITES endangered species, research on this valuable table fish is partly hampered by the ban on taking specimens from the wild, even though it is in fact part of an established fishery in southern Laos.

On the other hand, concern with particular species can also have, through political means, a fisheries livelihood benefit. This is where spectacular species, particularly of larger fish species such as the giant catfish, serve as “flagship species” in support of greater attention to ecosystem preservation (Mattson *et al.* 2002).

NGOS AND GOVERNMENT: ENVIRONMENTAL AND EXTRACTIVE CAUSES OF FISHERIES DECLINE

One of the sharpest lines of tension in debates over development futures for the Mekong has emerged between advocacy-oriented and rural livelihood-focused non-governmental organizations, on the one hand and state agencies concerned with infrastructure development on the other. Fisheries have rapidly risen to prominence as a cause taken up by NGOs, primarily because of their importance to livelihoods of millions of people, in part because of their significance as environmental indicators of river health and in part due to their vulnerability as a livelihood resource to many destructive aspects of development occurring in or planned for the region.

Among the debates between NGOs and other actors is the cause of actual or perceived fisheries decline. That there is a perceived decline in fisheries is clear. The nature of this decline is more ambiguous, with both local actors (including fishers) and wider players often failing to distinguish between decline in the overall fish stock and decline in catches (Coates 2002). It is quite conceivable overall and in more specific local circumstances that there may be declines in stocks and associated CPUE, while the level of catch may be stable or increasing (through more "effort"), possibly but not necessarily to unsustainable levels. Even less clear are the reasons for fish decline, but it is here that "knowledge" tends to be declared with greatest certainty. Thus, small fishers tend to be blamed – through destructive practices, lack of management and so on – by state actors and by those with vested interests. Dams and other development-induced impacts tend to get the blame from affected fishers themselves and NGOs who help articulate their concerns and interests. This tension between environmental and extractive causes of fishery "decline" does not always follow the NGO-state actor axis, but it tends to serve the wider discursive interests of those with quite different interests in the river's resources. Pak Mun is, again, a case in point, where EGAT has blamed fishers directly below the dam for extractive destruction of the fishery, while the blasting of rapids and blockage of the Mun River is the main point of contention by local fishers and NGOs working with them.

The International Rivers Network has been one of the more active international NGOs documenting fisheries impacts of dams. Seminal in this process was a study of the Theun-Hinboun Dam carried out by Bruce Shoemaker (Shoemaker 1998), which ADB tried to refute by sending in its own consultants. Since this time, a rather more measured approach has been taken and the Theun-Hinboun Power Company has accepted a considerable proportion of the responsibility for disrupted livelihoods (Theun-Hinboun Power Company 2000). Without the politicisation engendered by the NGO study, slammed at the time by the company and by the public agency that helped fund the dam, the knowledge of impacts would have remained firmly in the minds and communities of the impoverished fishers.

More recently, the series of studies supported through the MRC Fisheries Program has come out more firmly in identifying the anthropogenic environmental threats to fish abundance and diversity in the Mekong system. For example, a recent status review states quite firmly that the palliative notion of "mitigation" or "amelioration" of migratory impacts of dams by constructing fishways is simply not valid for larger projects (Sverdup-Jensen 2002). A political challenge will be to incorporate such conclusions into the basin development planning process.

RIPARIAN LINE DEPARTMENTS AND MEKONG RIVER COMMISSION: HOW MANY FISH ARE EATEN?

One of the most dramatic but also controversial "bits" of fisheries knowledge pertaining to the Mekong is the size of the fishery. The MRC Annual Report for 1996 stated that while the official statistics reported that only 360 000 tonnes of fish were caught in the Mekong Basin, data from MRC executed projects indicated that production may be as high as one million tonnes (MRC Annual Report 1996). In 2001, this was revised upward to a yield of two million tonnes as a "conservative estimate" (Sverdup-Jensen 2002). Further upward revisions are likely. These volumes make the Mekong by far the largest freshwater fishery of any river basin in the world and suggest a raw value of approximately US$1.4 billion (i.e. not taking into account the value generated through processing, transport and other multipliers, retailing and so on).

The figures for the total catch (production) are based on a surrogate measure, fish consumption. The bases for the MRC figures are 15 consumption surveys, five of which were conducted by MRC and ten by other agencies (Sverdrup-Jensen 2002). These were extrapolated to cover the entire LMB using population data from provinces whose characteristics most closely matched those of the survey sites. The basin-wide estimates are based on extrapolations from findings in aqua-ecologically representative areas.

A difficulty with the MRC figures is that they meet with considerable scepticism by the line agencies in each riparian country (although Coates (2002) reports that, since 1999, the Cambodian government has been using figures very similar to the MRC estimates for the country). The skepticism is based on a number of factors related to politics of fisheries knowledge. In part, there is an issue of sense of ownership.

In part it is an issue of lack of consensus over methodology, with perceived biases in sampling and in interpretation of the data. In part it is due to the challenge to historically collected statistics that, if the MRCS studies are to be believed, grossly and systematically under-enumerated the fishery. It is perhaps in this context that most attention needs to be paid to the circumstances of knowledge production.

CONCLUSION: KNOWLEDGE, POLICY AND RELEVANCE

If knowledge is power, then knowledge is political and knowledge about fisheries is no exception. The multi-dimensional politicisation of fisheries knowledge in the Mekong along the lines of tension indicated above suggests some fundamental rifts, which need to be understood – if not necessarily bridged – if understanding of the circumstances of knowledge production is to better inform policy that seeks equitable and sustainable management of the fishery.

Ultimately, policy is concerned with relevance. Yet, what is relevant knowledge to the policy maker may seem different to that which is relevant to the scientist or the fisher, as indicated for example in the tension between biodiversity- and livelihood-oriented fisheries knowledge. Here there is an important distinction to be made between science and scientism, the latter being a mindset – a particular culture of knowledge – that rejects that which has been produced other than under very specific circumstances. Yet, becoming less ‘scientistic’ does not necessarily mean becoming less scientific, so long as caveats are drawn. In many circumstances, the best available knowledge of the fishery on which to base policy is that of the fishers themselves.

The tension between science and other means of knowledge production is further complicated by questions of ownership. The *realpolitik* of connections between knowledge and policy determines that decision makers are most likely to act on understandings in which they have some stake. Externally produced knowledge, if paid insufficient attention to the circumstances, agencies and actors involved in its production, will carry much less weight than data generated by a more inclusive, participatory and almost certainly slower and more patient means.

Knowledge is power also through the pecuniary incentives to apply particular types of knowledge to decision making. The relationship between fisheries knowledge and large-scale resource development remains a fragile one and it is probably no coincidence that the consultancy-generated EIA knowledge remains the least open and accountable, particularly in the context of privatisation of large projects that puts significant areas of information under “commercial in confidence” wraps.

For policy makers, scientists and those who depend on the fishery, the public good is likely to best be served by transparent, inclusive and accountable knowledge production. This includes access by fishers and those working with them to scientific resources, as well as further development of syncretic methods to bring local knowledge into science.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the helpful comments of an anonymous referee.

REFERENCES

Assembly of the Poor, 2002. *The return of pladaek: The struggle and changes after the opening of Pak Moon Dam*, Villagers at Mae Moon Manyuen village, Assembly of the Poor.

Baird I.G., 1999. *Towards Sustainable co-management of Mekong River inland aquatic resources, including fisheries, in southern Lao PDR*. Pakse, Lao PDR, CESVI Cooperazione e Sviluppo, Agriculture and Forestry Division of Champassak Province.

Baird I.G, 1996. Inland community fisheries in southern Laos, *Naga, The ICLARM Quarterly*, January 1996: 13-15

Chambers R. 1983. *Rural development: Putting the last first*. London, Longman.

Coates D. 2002. Inland capture fishery statistics of Southeast Asia: Current status and information needs. Bangkok, Asia-Pacific Fishery Commission, Food and Agriculture Organisation of the United Nations, Regional Office for Asia and the Pacific.

Conklin H.C. 1954. An ethnoecological approach to shifting agriculture. *Transactions of the New York Academy of Sciences*, 172: 133-142.

Daconto G. ed. 2001. *Siphandone wetlands*. Bergamo, CESVI.

Garaway C.J., Arthur R. & Lorenzen K. 2002. Adaptive learning approaches to fisheries enhancements. final report to the DFID fisheries management science programme. London, MRAG. 54 pp

Guha R. &. Martinez-Alierin J. 1997. Varieties of environmentalism: Essays north and south. London, Earthscan.

Haraway D.J. 1989. *Primate visions: Gender, race and nature in the world of modern science*. New York, Routledge.

He Daming & Chen Linhui. 2002, The impact of hydropower cascade development in the Lancang-Mekong Basin, Yunnan. *Mekong Update and Dialogue*, 53: 2-4.

Hirsch P. 2001. Globalisation, regionalisation and local voices: The Asian Development Bank and rescaled politics of environment in the Mekong region. *Singapore Journal of Tropical Geography*, 223: 237-251.

Hirsch P. & Gerard Cheong. 1996. *Natural resource management in the Mekong River Basin: Perspectives for Australian Development Cooperation*. Canberra, AusAID.

Johnston R.J., Gregory D., Pratt G. & Watts M. 2000. *The dictionary of human geography*. Oxford, UK, Blackwell.

Kottelat M. 1998. Fishes of the Nam Theun & Xe Bang Fai basins, Laos, with diagnoses of twenty-two new species *Teleostei: Cyprinidae, Balitoridae, Cobitidae, Coiidae and Odontobutidae, Ichthyological Exploration of Freshwaters*, 91: 1-128.

Kottelat M. & Whitten A.J. 1996. *Freshwater biodiversity in Asia with special reference to fish*. Washington, DC, World Bank Technical Paper No. 343.

Mattson N.S., Buakhamvongsa K., Sukamasavin N., Nguyen Tuan & Ouk Vibol. 2002. *Mekong giant fish species: On their management and biology*. Phnom Penh, Cambodia, Mekong River Commission.

MRC Secretariat. 1997. *MRC Program for fisheries management and development cooperation*. Phnom Penh, Cambodia, Mekong River Commission.

Poulsen A. & Valbo-Jorgensen J. 2001. Local knowledge in the study of river fish biology: Experiences from the Mekong, MRC.

Poulsen A., Ouch Poeu, Viravong S., Suntornratana U. & Nguyen Thanh Tung. 2002. *Deep pools as dry season fish habitats in the Mekong River Basin.* Phnom Penh, Cambodia, Mekong River Commission.

Rainboth W.J., 1996. *Field guide to the fishes of the Cambodian Mekong*. Rome, Food and Agricultural Organisation of the United Nations.

SEARIN. 2002. *Mekong rapids under fire*. Bangkok Project For Rivers And Communities and Love Chiang Khong Group, Southeast Asia Rivers International Network & OXFAM America.

Settrachau C. ed. 2002. *Mae Mun: Kaan klab maa khong khon haa plaa Mun River: The return of fishers*. Bangkok, Southeast Asia Rivers International Network.

Shoemaker B. 1998. Trouble on the Theun-Hinboun: A field report on the socio-economic and environmental effects of the Nam Theun-Hinboun hydropower project in Laos. Berkeley, CA, USA, International Rivers Network. (Available at www.irn.org)

Sverdup-Jensen S. 2002. Fisheries in the Lower Mekong Basin: Status and perspectives. Phnom Penh, Cambodia, Mekong River Commission.

Theun-Hinboun Power Company. 2000. The Theun-Hinboun Power Company's mitigation and compensation program. Vientiane, Theun-Hinboun Power Company. (Available at www.adb.org)

Traisawasdichai M. 2002. *The politics of research*. Bangkok Post, 12 November 2002, p. 3.

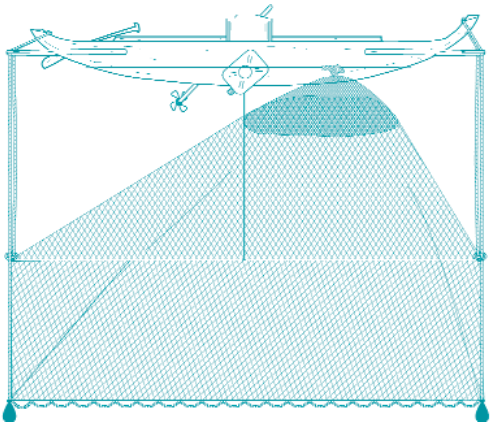
Trong T.Q., Hao N.H. & Griffiths D. 2002. Status of Pangasiid aquaculture in Viet Nam. Phnom Penh, Cambodia, Mekong River Commission.

Van Zalinge N., Sopha L., Ngoe Peng Dun, Heng Kong & Valbo-Jorgensen J. 2002. Status of the Mekong *Pangasianodon hypophthalamus* resources, with special reference to the stock shared between Cambodia and Viet Nam. Phnom Penh, Cambodia, Mekong River Commission.

Warren T.J. 1999. A monitoring study to assess the localized impacts created by the Theun-Hinboun Hydro-Scheme on fisheries and fish populations: Final report to Theun-Hinboun Power Company, (Available at www.irn.org)

Warren T.J., Chapman G.C. & Singhanouvong D. 1998. The upstream dry-season migrations of some important fish species in the Lower Mekong River in Laos. *Asian Fisheries Science*, 11: 239-251.

Worldwide Fund for Nature WWF. 2002. Community based indicators for sustainable fisheries management in the Lower Mekong Basin of Lao PDR. Vientiane, WWF Lao Program.



FISHERIES DYNAMICS IN THE YAZOO RIVER BASIN

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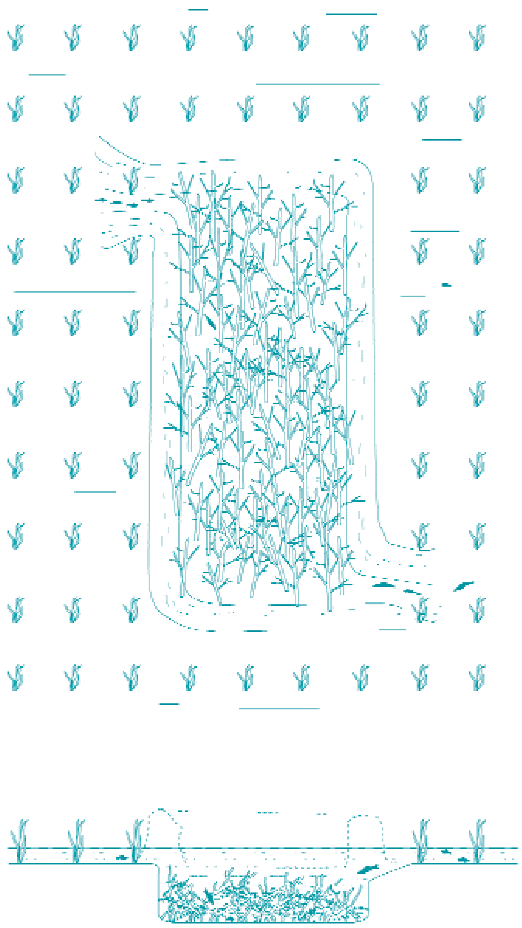


Key words: floodplain river, fisheries, Mississippi, conservation

ABSTRACT

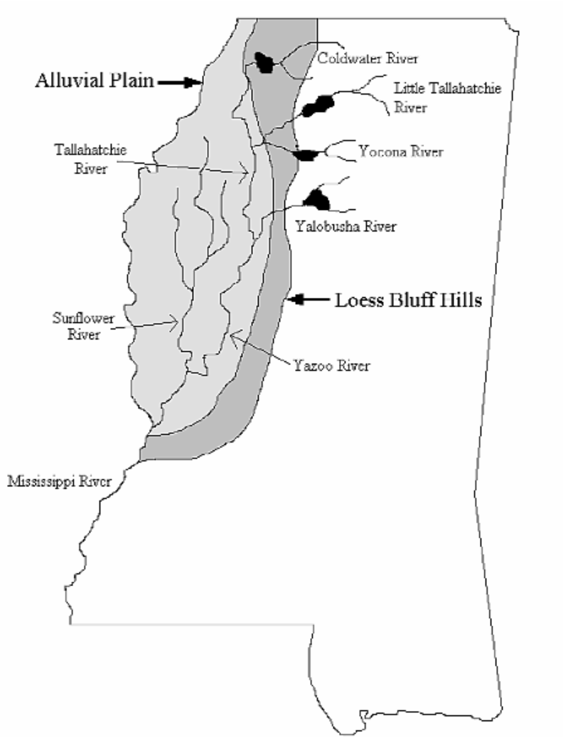
The Yazoo River Basin (Mississippi, United States) is a floodplain river ecosystem integrating six tributary rivers that course through the interior alluvial plain of the Mississippi River. Historically the basin was covered by temperate bottomland hardwood forest, swamps and perennial backwaters subject to seasonal flood pulses. European settlement during the 1800s and early 1900s resulted in extensive deforestation of the floodplain for agricultural purposes. To protect agriculture, federally-sponsored flood control programs during the middle decades of the twentieth century incorporated construction of dams in upstream reaches of tributary rivers, clearing of forests along riparian corridors, dredging and straightening of river channels and removal of large woody debris from channels.

The principal riverine fisheries resources throughout the basin (buffaloes: Catostomidae; catfishes: Ictaluridae) are enhanced by the presence of mature riparian forests, large woody debris in river channels and flood pulses. The fisheries are negatively impacted by activities that alter stream hydrology, convert riparian zones to early successional vegetative stages and disconnect the rivers from their respective floodplains. Recovery of the rivers and their fisheries following these impacts takes approximately 20-30 years.

The rivers serve as cultural icons for a distinct sub-culture of river people extant within communities throughout the Yazoo River Basin. Cultural connections to the rivers are strongest with respect to fishing in rivers (or sections of rivers) that are in advanced stages of recovery from historical flood control activities. Most fishing is recreational, but artisanal fisheries still exist. Partitioning of the fisheries within the rural sub-culture of river people renders main river channels as the domain of fishers in higher economic strata while floodplain backwaters are generally the domain of fishers in lower economic strata. Degradation of rivers erodes the cultural identity of both groups and can result in loss of social status within their respective communities. Proposed periodic maintenance of the region's flood control projects is increasingly controversial as a result of greater public insight into functional dynamics of floodplain river ecosystems, coupled with changes in human value systems associated with these rivers and the living natural resources they support.

INTRODUCTION

The Upper Yazoo River Basin (UYRB; Figure 1), in Mississippi, has experienced profound evolutionary processes in terms of human values systems as well as expectations from land and water resources during the last 300 years, with cultural shifts from a stone-age civilization to a post-modern technological/informational civilization. The first known inhabitants in the region were Native American mound builders who arrived in the UYRB around 1500 B.C. (Smith 1954). Their name stems from the practice of constructing large earthen mounds for religions purposes. During periods of flooding, the mounds also served as refuges for their communities. These people maintained a semi-settled culture, integrating agriculture with exploitation of wildlife and fisheries resources associated with the regions rivers and vast expanses of bottomland hardwood forests and wetlands. They maintained their civilization in the region until a Spanish exploration led by Hernando DeSoto in 1541 brought diseases to the region that decimated the mound builders by the late seventeenth century. Choctaw and Chickasaw tribes then moved into the area and used the rivers for fishing and transportation.



■ Figure 1. The Yazoo River integrated floodplain river ecosystem, Mississippi. Map modified after Jackson and Ye (2000).

With the onset of European settlement, the Native Americans were systematically removed from the UYRB [Choctaws: Treaty at Doaks' Stand (1820), Treaty of Dancing Rabbit Creek (1830); Chickasaws: Treaty of Pontotoc (1832)] (Cloutman 1997).

During the first 50 years of European settlement in the region (early 1800s), high water covered nearly half of the surface area of the UYRB for four or five months of each year (Smith 1954). This interfered with agriculture (primarily cotton production) and as a result, early planters built private levees that generally exacerbated flooding problems for downstream landowners. To help coordinate flood control, local flood control districts were formed in the early years of the twentieth century, but poor engineering typically resulted in problems similar to those associated with the earlier private levees.

Devastating flooding occurred throughout the region in 1927 and stimulated the United States Congress to intervene with authorization for construction of massive flood control projects, primarily to protect agriculture. These federally-sponsored flood control projects in the UYRB resulted in the construction of four flood control reservoirs on principal tributary streams of the Yazoo River: Sardis (1937-40, Little Tallahatchie River), Arkabutla (1940-43, Coldwater River), Enid (1947-52, Yocona River) and Grenada (1947-54, Yalobusha and Skuna rivers) (Jackson, Brown-Peterson and Rhine 1993). No dam was constructed on the Sunflower River. Additionally, stream reaches downstream from the dams and portions of the Sunflower River were channelized and levees were built. Collectively, the design discharge for the system at the confluence of the principal tributary streams near Greenwood, Mississippi is 566 $m^3 s^{-1}$, but this discharge must be reduced during the crop season to 312 $m^3 s^{-1}$ in order to prevent flooding of farmland (U.S. Army Corps of Engineers 1991).

Flood control coupled with the development of cotton defoliant and mechanical cotton pickers encouraged clearing of additional land in the UYRB for agriculture during the 1950s and 1960s. In the 1970s, high prices for soybeans resulted in the clearing of yet more land, typically characterized by heavy soils considered unsuitable for cotton but that could sustain soybean crops. By the late 1980s as much as 60-80 percent of the watersheds/floodplains of the Yazoo River's principal tributary streams had been cleared (Insaurralde 1992). Currently some agricultural lands in the region are being converted back to forests, with economic enterprise in some areas shifting from row crop production to timber as well as concessions, leases and commercial operations focused on recreational hunting and fishing (Jones *al.* 2000).

ECOSYSTEM CHARACTERISTICS

The UYRB covers 34 700 km^2 of which 18 400 km^2 is in the interior alluvial plain of the Mississippi River (a.k.a. The Delta) (U.S. Army Corps of Engineers 1991). It is located within North America's humid subtropical climate region with temperate, wet winters and long hot summers (Jackson and Ye 2000). Drought is a common feature of the climate (Pote and Wax 1986).

Within the UYRB the principal tributary streams coalesce near the city of Greenwood, Mississippi to form the main stem of the Yazoo River. The Sunflower River joins the Yazoo River downstream, approximately 20 miles northeast of the city of Vicksburg, Mississippi. Collectively these streams are an integrated floodplain river ecosystem with most flooding occurring during winter (December-March) and spring (March-June). Ultimately the Yazoo River discharges into the Mississippi River just north of Vicksburg.

Jackson *et al.* (1993) and Brown *et al.* (in press) described physical characteristics of the principal streams in the UYRB. Waters are typically turbid with Secchi disk readings generally < 10 cm. Substrates are highly erodeable aggregates of clay, silt, sand and small gravel. During bankfull stages, channel widths typically exceed 50 m and depths > 10 m can occur. However, during minimum flow periods (seasonally, August-October), sand and mud bars are revealed on the inside of channel meanders and it is sometimes possible to wade across the stream channels. Large woody debris originating from the riparian zones is common in channels as isolated snags or as stationary aggregates (log jams).

Terrestrial, aquatic and ephemeral transitional elements throughout the UYRB are integrated into a dynamic, spatial-temporal mosaic functioning through interactive processes along the river courses, upstream to downstream and laterally along channels (Jackson in press). In accordance with the river continuum concept (Vannote *et al.* 1980) and the flood pulse concept (Junk, Bayley and Sparks 1989) these processes dictate conditions, events and life forms at a given location within the ecosystem and in concert with temperature, depth, current velocity, substrate type and scour and fill (Brown and Matthews 1995), set the stage for biological events.

Heterotrophic processes associated with inputs of allochthonous organic materials drive biological production in these rivers energetically. These inputs can be direct via litterfall into the stream channels or indirect via overbank flooding and inundation of the materials. There is typically marked seasonality to these inputs in the UYRB, with maximum direct input associated with autumnal litterfall from deciduous vegetation and indirect input associated with winter and spring flooding.

Winter and early spring floodwaters quickly drop their non-colloidal sediment loads as they lose hydraulic energy moving across the floodplain. This enhances water clarity on the floodplain and, in conjunction with shallow depths, promotes early seasonal warming via solar radiation. The shallow, relatively clear, warm (relative to water in main channels), nutrient-rich waters on the floodplain encourage more efficient foraging for fishes as poikilotherms and early spawning that subsequently provides young-of-the-year fishes with competitive advantage and enhanced survival potentials through growth as well as storage of lipids in body tissues (*sensu* Goodgame and Miranda 1993; Miranda and Hubbard 1994).

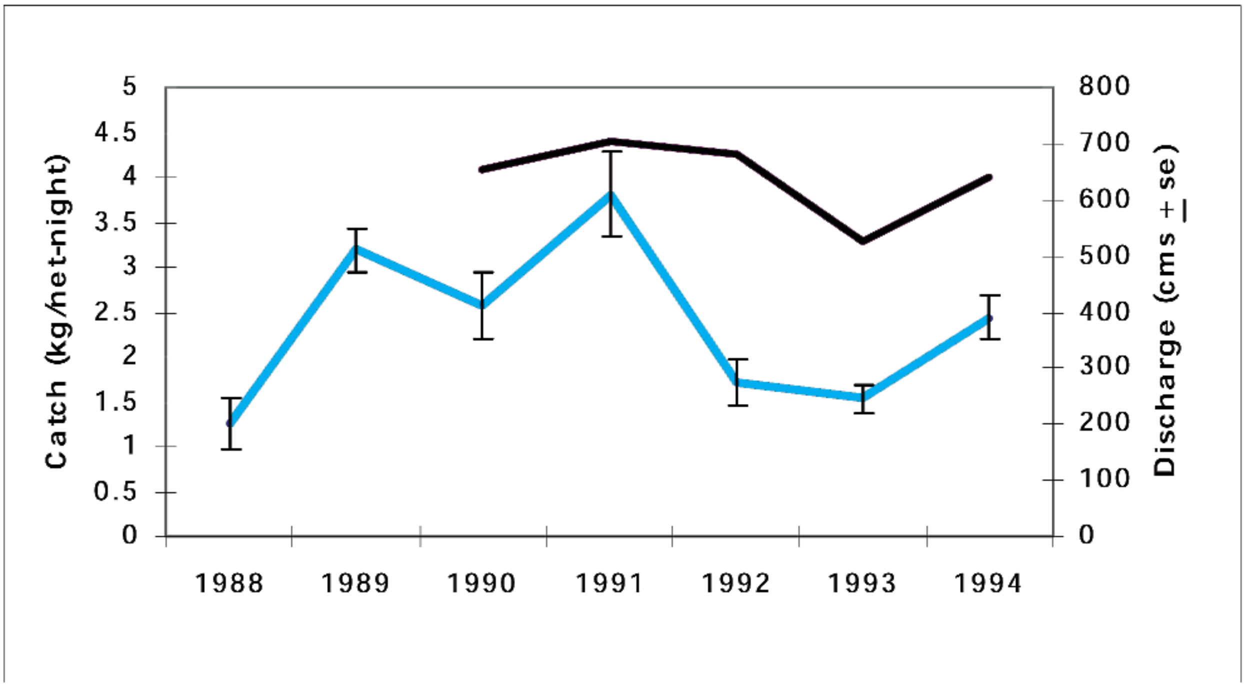
FISH STOCK DYNAMICS

Fishes throughout the UYRB can be classified functionally as euryceous, fluvial generalists (Cloutman 1997). Such species are wide-ranging, adapted to widely fluctuating flow regimes, high turbidity and extreme summer temperatures (Cross, Mayden and Stewart 1986).

Fish production from floodplain river ecosystems like the UYRB typically is associated with the extent and duration of flooding (Welcomme 1976, 1985, 1986) because inundated floodplains provide fish not only with food, but also refuge and spawning grounds (Risotto and Turner 1985; Bayley 1989; Ward and Stanford 1989; Rutherford *et al.* 1995). Recruitment potentials into the fishery are established by flood characteristics but manifestation of the potentials is determined by carrying capacity of the river during minimal flow periods.

With respect to the above orientations, Jackson and Ye (2000) and Jackson (in press) addressed relationships between riverine stocks of buffalofishes (Catostomidae) and catfishes (Ictaluridae) and regional hydrological characteristics in the UYRB. These fishes are the principal exploitable fishery resources in the UYRB. At a species-specific level of resolution, it was difficult to discern relationships describing individual catostomid and ictalurid species relative abundances, but collectively (all species combined) mean annual catch rates tracked overall annual discharge/flood regimes of the integrated Yazoo River system (Figure 2).

Flooding also introduces large woody debris into main river channels of the UYRB. Large woody debris in lowland rivers of the southeastern United States provides important attachment sites for aquatic macroinvertebrates that in turn are utilized as forage items by riverine fishes (Gorman and Karr 1978; Hesse *et al.* 1982; Benke *et al.* 1985; Insaurralde 1992). This instream structure is particularly important when other large substrate (e.g. boulders, rock outcrops, cobble) is lacking in the river channel (Brown and Matthews 1995).



■ Figure 2. Catch rates (kg/net) of catfishes (Ictaluridae) and buffalofishes (Catostomidae) and respective Yazoo River discharge (Mississippi). Catch rates (1990-1994) are depicted on the top line. River discharges (1988-1994) with respective standard errors are depicted on the bottom line. From Jackson and Ye (2000) and Jackson (in press).

Large woody debris is also important as cover and refuge for fishes. Insaurralde (1992) found this to be the case for flathead catfish *Pylodictus olivaris* (Rafinesque), a large predator species and an important sport and commercial fishery resource in the UYRB (Jackson 1999). Insaurralde (1992) found that the presence of large woody debris in the river channel was directly related to the size structure of the stream's flathead catfish stock (i.e. proportionally more large fish when there is more large woody debris).

Jackson (2000) conducted studies of channel catfish *Ictalurus punctatus* (Rafinesque) in the UYRB. Channel catfish are more omnivorous in their diet than are the other two principal catfish species: flathead catfish and blue catfish *Ictalurus furcatus* (Lesueur) (Hubert 1999). Jackson (2000) reported that stream channels subject to clearing of riparian vegetation, removal of large woody debris and dredging had relative abundances of channel catfish approximately 50 percent the relative abundances in stream reaches not so impacted.

Hand and Jackson (in press) studied blue sucker [Catostomidae: *Cycleptus elongatus* (Lesueur)] in the UYRB. Once an important commercial fishery resource throughout the Mississippi River system (including the UYRB) (Coker 1930), blue sucker abundance has declined throughout its range to the extent that it is a candidate species for listing as threatened or endangered. Hand and Jackson (in press) found that in the UYRB, blue sucker abundance was significantly less in stream channels that had been dredged relative to those of channels that had not been recently dredged. The exotic common carp (Cyprinidae: *Cyprinus carpio* Linnaeus) replaced blue sucker in dredged channels.

FISHERIES

The UYRB fisheries consist of two principal types: river channel (lotic) fisheries and backwater (lentic) fisheries. River channel fisheries focus on buffalos (Catostomidae): smallmouth buffalo *Ictiobus bubalus* (Rafinesque), bigmouth buffalo *Ictiobus cyprenellus* (Valenciennes) and black buffalo *Ictiobus niger* (Rafinesque); and catfishes (Ictaluridae): blue catfish, channel catfish and flathead catfish.

Backwaters (oxbow lakes, sloughs, perennial wetlands) support more diverse fish assemblages and fisheries but emphasis and preference typically is focused on fishes in the family Centrarchidae (crappies *Pomoxis* spp., sunfishes *Lepomis* spp.) as well as the above-mentioned catfishes.

Cloutman (1997) addressed both types of fisheries in the UYRB and determined that the river channel fishery was primarily the domain of European-Americans, whereas backwater fisheries were primarily the domains of African-Americans. Brown, Toth and Jackson (1996) investigated this partitioning and concluded that it was the result primarily of economics and tradition. Fishers exploiting the river channels typically utilized boats and multi-hook longlines in recreational fisheries (primarily for catfishes) and nets in commercial/artisanal fisheries (primarily for buffalofishes; secondarily for catfishes). Fishers exploiting backwaters typically fished from shorelines using long poles and single hooks. The two fisheries and their respective fishers rarely overlapped.

River channel fishers were predominately young to middle-age males fishing alone or with a companion. Backwater fishers were more heterogeneous in age and gender composition and more gregarious. River channel fishers sought solitude, quiet and an element of adventure. Backwater fishers viewed fishing as a social event and considered backwaters safer environments than rivers.

In addition to the above-mentioned fisheries, there is recreational hand fishing (referred to by participants as grabbling or noodling) throughout the UYRB. In this fishery, fishers enter the water and probe with their hands along streambanks and in structures (e.g. hollow logs, debris), until encountering a cavity containing a fish (usually catfish), (Jackson, Francis and Ye 1997). The fish are then grabbed, wrestled to the surface and placed into a boat or on the stream bank. The fishery is regulated by open and closed seasons and by size restrictions for fish harvested. Large adult catfishes are the focus of this fishery. In this regard, flathead catfish > 40 kg are occasionally captured and 10-20 kg fish are common (Jackson 1999). Subsequently, concerns have been voiced that removing these fish from the rivers impacts fish recruitment as well as system integrity from loss of large piscivores. However, Francis (1993) studied hand fishing in the Tallahatchie River, a principal tributary of the Yazoo River and concluded that it had minimal potential impact to the stock. Catch efficiencies were low and stocks were resilient, with rapid recruitment replacing fish harvested.

Commercial fisheries in the UYRB are small-scale, typically integrated into a suite of economic activities (e.g. agriculture, timber, small business, local industrial enterprise) rather than providing sole support for participants and thus are most appropriately categorized as artisanal fisheries. Development of aquaculture throughout the region, primarily for channel catfish, relegates wild-caught fish from the rivers as speciality items, sometimes centered on ethnic markets in regional cities but more often peddled on established (local) routes (Brown *et al.* 1996). Although some still persist, most stationary fish markets in the UYRB have closed as viable businesses.

Persons who persist in UYRB artisanal fisheries are generally known in their respective communities as highly skilled specialists and thus have status/social currency (Brown *et al.* 1996). This is oftentimes more valuable than monetary currency. By providing fish to their respective communities when needed, these fishers build a network of contacts throughout local government offices, schools, churches and civic groups.

■ Figure 3. Hoop net deployed for exploitation of catfishes (Ictaluridae) and buffalofishes (Catostomidae) in the Yazoo River integrated floodplain river ecosystem, Mississippi. Photo by J. Olive, Mississippi State University.

Most small-scale commercial/artisanal fishers exploiting UYRB fish stocks utilize hoopnets (Figure 3). Stopha (1994) and Stopha and Jackson (1999) determined catch characteristics from deployment of commercial hoopnets in three UYRB rivers, with emphasis on catches of buffalofishes and catfishes. The nets had circular fiberglass hoops (frames), two throats and were fished on the bottom with codends positioned upstream. The minimum legal bar mesh for these nets in the commercial fishery is 7.6 cm. Fishers primarily use this size mesh with 1.5 m hoops and secondarily with 1.1 m diameter hoops. The minimum legal total length for commercially caught buffalofish is 410 mm. The minimum legal total length for commercially caught catfishes is 305 m. When deployed systematically in stream channels (100 m intervals, alternating banks) and fished overnight (N = 180 nets per configuration, distributed evenly throughout the period January-August 1993), catch rates for legal size buffalofish were approximately 2.0 kg net^{-1} for the larger net and 0.6 kg net^{-1} for the smaller net. In contrast, catch rates for legal size catfishes were approximately 0.4 kg net^{-1} for the larger net and 0.6 kg net-set^{-1} for the smaller net. This suggests that fishers could be more precise in selection of net set locations with the smaller net, a factor particularly important during seasonal low flow conditions (e.g. summer) when catfish movement and subsequently vulnerability to capture is greatest. Buffalofish, on the other hand, typically exhibit more movement along river channels, particularly during winter and spring high water periods, are not oriented specifically to sites/habitats and thus are more vulnerable to the larger diameter nets.

Stopha (1994) noted that the legal size mesh tended to be selective for buffalofish and catfish at or exceeding the minimum legal size, with the notable exception of channel catfish. Channel catfish were for the most part not vulnerable to capture by either net configuration, regardless of fish size. Persons purchasing or receiving fish from UYRB artisanal fishers rarely accept fish that are dressed, frozen or partitioned into steaks or fillets, preferring to obtain these processed products from larger grocery markets. Rather, fish purchased from UYRB fisheries are typically whole and fresh, either alive or on ice. Unless social events demand larger quantities of fish, customers usually buy only enough fish for immediate consumption in the home.

This customer preference encourages UYRB artisanal fishers to exploit smaller fish (ca. 1-2 kg) and in fact larger fish often are returned to the water where captured. When asked about this activity fishers often state that doing so is a conservation practice to sustain the fishery resource, but when pressed on the issue, the reality of economics emerge.

Current (2002) prices paid to fishers in local Mississippi markets range from US$0.80 kg^{-1} to US$1.10 kg^{-1} for buffalofish and US$1.00 kg^{-1} to US$1.80 kg^{-1} for catfishes. Hoop nets (primary commercial/artisanal gear) cost between US$100 and US$200 each, depending on size. A fishing rig consisting of a boat, outboard motor and trailer (not to mention a vehicle to transport the rig) will cost between US$2 000 and US$4 000. Rigs have a life expectancy of approximately 10 years.

Using catch rates reported by Stopha (1994), applying the median value for the above-mentioned prices (US$0.95 kg^{-1} for buffalofish; US$1.40 kg^{-1} for catfishes) and assuming that on average a fisher can maintain a set of 10 nets, gross income from deployment of large hoop nets is US$24.60 day^{-1} and for small hoop nets US$14.10 day^{-1}. If the fisher works five days per week (260 days year^{-1}) annual gross income is $6 396. Poverty in the region is defined at ca. US$8 000/year. However and assuming average expenses of US$25.09 day^{-1} as recorded by Cloutman (1997), commercial/artisanal fishers exploiting riverine fish stocks in the UYRB actually lose money in their activity (US$0.49 day^{-1}). Rather than a viable economic enterprise, the commercial/artisanal fisheries of the UYRB are actually recreational activities that address social/cultural connections to the rivers and their resources.

During the late 1990s, fish traps constructed of wood slats (locally called slat baskets) were legalized

(Figure 4). In Mississippi, slat baskets may not be longer than 1.8 m nor exceed 38 cm in width, height or diameter and may have no more than two throats. There must be at least four slot openings of a minimum of 3.5 cm by 61 cm, evenly spaced around the sides of the trap area (slots beginning at the rear of the trap). Studies conducted elsewhere stated that slat baskets were very effective in capturing channel catfish (Carter 1955; Posey and Schaefer 1967; Perry 1979; Perry and Williams 1987). Recreational fishers targeting channel catfish expressed concern that this new commercial gear would harm channel catfish stocks in Mississippi streams. Subsequently, Shephard and Jackson (2002) conducted a study to determine slat basket catch characteristics under controlled as well as field conditions. They found that the legal gear was selective for channel catfish beyond the length at first maturity. They also found that multi-hook baited longlines (trotlines), typically deployed by recreational fishers, were more effective than slat baskets in capturing channel catfish and also that trotlines were indiscriminate regarding size of fish captured. Cloutman (1997) conducted test fishing with trotlines in the UYRB. Catfishes dominated his catches (Table 1).

■ Figure 4. Fish trap (also known as a slat basket), used for capturing catfishes (Ictaluridae) in Mississippi, Photo by J. Olive, Mississippi State University.

HUMAN DIMENSIONS

The UYRB is an area with a wealth of natural resources, either privately owned or publicly managed, that local residents access extensively and intensively in some cases. Throughout the region, communities are strongly linked to natural cycles of the resource base. It is, however, a region of paradox in that it is rich in fertile land and natural resources but economic and

Table 1: Longline catches (April-August 1995; 1996) from undredged channels of the Yalobusha River, a principal tributary of the Yazoo River (adapted from Cloutman 1997).

		Composition of Catch (%)	
	Species[1]	**1995**	**1996**
Longnose gar	*Lepisosteus osseus (Linnaeus)*	0	6.3
Shortnose gar	*Lepisosteus platostomus (Rafinesque)*	0	6.3
Smallmouth buffalo	*Ictiobus bubalus (Rafinesque)*	0	6.3
Blue catfish	*Ictalurus furcatus (Lesueur)*	45.2	6.3
Channel catfish	*Ictalurus punctatus (Rafinesque)*	42.9	56.3
Flathead catfish	*Pylodictis olivaris (Rafinesque)*	11.9	18.5

[1]Common names in accordance with the American Fisheries Society (Robins, Bailey, Bond, Brooker, Lachner, Lea and Scott 1991).

social inequalities remain entrenched (Gray 1991; Marcum, Holley and Williams 1988). There is a prevailing resistance to social and economic change and persistence of a strong regional identity (Brown *et al.* 1996). Cowdrey (1983) noted that this regional identity was strongly linked to natural resources. Consequently, outdoor recreation (e.g. fishing) provides an outlet for maintenance of local social networks and development (Cowdrey 1983) and it offers participants a sense of control over their lives and circumstances (*sensu* Marks 1991).

Participation in these activities instils a sense of dignity in a socio-economic-political environment that often denies this dignity to the participants and promotes characteristics of political and economic independence (Brown *et al.* 1996). By providing content and meaning to their lives, interactions with the region's natural resources unites participants in a subculture of hunting and fishing through which they have a shared history, ideology, symbolic universe and system of meaning. The subculture that has developed around river fisheries in the UYRB is identifiable through values, ways of life, beliefs, etc. and is passed from member to member and generation to generation (Brown *et al.* 1996). It also contains explicit knowledge and practices that are not common to people outside of the group (*sensu* Waxman 1983; Hollingshead 1939).

Because the natural resources of the UYRB (e.g. the rivers) are not mobile and are in part unique to the area itself, the economies and subcultures that have developed around the utilization of the rivers' resources also are not mobile; they will be just as much tied to the place as are the physical conditions of the area with which they interact (Brown *et al.* 1996). Subsequently, if the rivers and their associated fishery resources are negatively impacted through anthropogenic activities (e.g. channelization, siltation, disconnection of floodplains; non-point source pollution), the non-mobile subculture of river fisheries also is negatively impacted. If the identity that defines the people of the subculture is threatened or destroyed, they are left with few if any alternatives. Such social degradation strikes at the very heart of a region that is rapidly losing population, relevancy and voice in the post-modern world. It is, in this sense, one of the more natural resources - dependent regions of the United States and much of this connection rests within the realm of proper, natural, functioning of the region's floodplain river ecosystems.

CONSERVATION

A mixture of agriculture, poverty and politics has challenged river conservation in Mississippi. There is also a fierce clinging to a culture of independence and autonomy. People want to be left alone to pursue their individual dreams and goals. A willingness to accept, much less work for, the public domain typically comes to life slowly and painfully here. But come it does and come it has in the realms of conservation and management of natural resources, particularly wildlife and fisheries resources and certainly with respect to rivers.

River conservation in Mississippi has had a sad history but its slow evolution has not been the result of malicious intent. People, agencies and institutions did and continue to do what they believe protects and enhances the human experience. In the past this meant massive public works to control rivers, to make them less prone to flooding, to make them better highways for commerce. In the process, through time, rivers as cultural icons, precious treasures in a conceptual sense, were safeguarded (Jackson 1991). But the physical and environmental reality differed from the images of the mind and much that was treasured was damaged.

It was not until the late 1980s that a collective voice arose to challenge the continued destruction of streams throughout the region and especially with regard to the rivers in the UYRB (Jackson and Jackson 1989). At state, regional, national and even international levels, professional organizations and conservation groups confronted projects in the UYRB that proposed river dredging, channelization, clearing of riparian forests and removal of large woody debris from channels. Advocates of river conservation met stiff resistance in the political arena and in the courts but with persistence prevailed.

Federal agency laboratories began studies and programs of stream restoration (*e.g.* Shields, Knight and Cooper 1998). State agencies, conservation groups, academic institutions, private industry and legislative bodies proposed and ultimately were successful in establishing a state-wide program for conservation and management of natural and scenic streams (Mareska and Jackson 2002). Through public media coverage and special events featuring rivers throughout the state, citizens were reminded of their rich heritage and cultural connections to the rivers.

Challenges continue, however and constant vigilance is required lest advances begin to erode. Dredging and other flood control projects are still proposed for streams across the state and especially in the Yazoo River floodplain river ecosystem. But the tide has turned. People have rediscovered rivers and have returned to their waters. Lands bordering the rivers are being purchased, leased and managed for forests and wildlife. Entrepreneurs have begun to establish businesses featuring river trips and river fishing.

People throughout the region, through education and through time, have begun to understand the interconnectedness of rivers with the landscape (Bayley 1995). The message is relayed through the public school systems, through religious institutions, through civic groups, through the halls of legislative bodies and in social gatherings. People are also beginning to understand the interconnectedness of rivers with themselves and through this process are learning how to live with the UYRB rivers and to treasure the natural resources they afford.

REFERENCES

Bayley P.B. 1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production and yield. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 399-408

Bayley P.B. 1995. Understanding large river-floodplain ecosystems. *Bioscience*, 45: 153-158.

Benke A.C., Henry R.L. III, Gillispie D.M. & Hunter R.J. 1985. Importance of snag habitat for animal production in southeastern streams. *Fisheries*, 105: 8-13.

Brown A.V. & Matthews W.J. 1995. Stream ecosystems of the central United States. *In* C.E. Cushing, K.W. Cummins & G.W. Minshall eds. *Ecosystems of the World 22: River and Stream Ecosystems*. Amsterdam, Elsevier Science. pp. 89-116.

Brown A.V., Brown K.B., Jackson D.C. & Pierson W.K. The lower Mississippi River and its tributaries. *In* A.C. Benke & C.E. Cushing eds. *Rivers of North America*. New York, Academic Press. (forthcoming)

Brown R.B., Toth J.F. Jr. & Jackson D.C. 1996. *Sociological aspects of river fisheries in the delta region of western Mississippi. Completion Report*. Federal Aid to Sport Fish Restoration Project F-108. Jackson, Mississippi, Mississippi Department of Wildlife, Fisheries and Parks. 98 pp.

Carter E.R. 1955. Evaluation of nine types of commercial fishing gear in Kentucky Lake. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 81954: 44-53.

Cloutman D.G. 1997. Biological and socio-economic assessment of stocking channel catfish in the Yalobusha River, Mississippi. Mississippi State University. 184 pp. (Doctoral dissertation)

Coker R.E. 1930. *Studies of common fishes of the Mississippi River at Keokok, Iowa*. United States Bureau of Fisheries Document 1072. pp. 141-225.

Cowdrey A.E. 1983. *This land, the South: An environmental history*. Lexington, Kentucky, U.S.A The University Press of Kentucky.

Cross F.B., Mayden, R.L. & Stewart, J.D. 1986. Fishes in the western Mississippi Basin Missouri, Arkansas and Red Rivers. *In* C.H. Hocutt & E.O. Wiley eds. *The Zoogeography of North American Freshwater Fishes*. New York, John Wiley & Sons, pp. 363-412.

Francis J.M. 1993. *Recreational handgrabbing as a factor influencing flathead catfish stock characteristics in two Mississippi streams*. Mississippi, USA, Mississippi State University. 90 pp. (Master's thesis)

Goodgame L.S. & Miranda L.E. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. *Transactions of the American Fisheries Society*, 122: 131-138.

Gorman G.T. & Karr J.R. 1978. Habitat structure and stream fish communities. *Ecology*, 59: 507-515.

Gray P.A. 1991. Economic development and African Americans in the Mississippi Delta. *Rural Sociology*, 562: 238-246.

Hand G.R. & Jackson D.C. Blue sucker stock characteristics in the upper Yazoo River basin, Mississippi, U.S.A. *Fisheries Management and Ecology.* (forthcoming)

Hess L.W., Schlesinger A.B., Herganrader G.L., Reetz S.D. & Lewis H.S. 1982. The Missouri River study - ecological perspectives. *In* L.W. Hesse, G.L. Hergenrader, H.S. Lewis, S.D. Reetz & A.B. Schlesinger eds. *The Middle Missouri River*. The Missouri River Study Group. Lincoln, NE, Nebraska Game and Parks Commission. pp. 287-301.

Hollingshead A.B. 1939. Behavior systems as a field of research. *American Sociological Review*, 4: 816-822.

Hubert W.A. 1999. Biology and management of channel catfish. *In* E.R. Irwin, W.A. Hubert, C.F. Rabeni, H.L. Schramm, Jr. & T. Coon eds. *Proceedings of the International Ictalurid Symposium. American Fisheries Society Symposium 24*, Bethesda, MD, USA. pp. 3-22.

Insaurralde M.S. 1992. Environmental characteristics associated with flathead catfish in four Mississippi streams. Mississippi, USA, Mississippi State University. (Doctoral dissertation)

Jackson D.C. 1991. Social and cultural values of turbid, warmwater streams and their fisheries in the southeastern United States. *In* J.L. Cooper & R.H. Hamre eds. *Warmwater Fisheries Symposium I*. General Technical Report RM-207. pp. 169-174. Fort Collins, CO, USA, USDA Forest Service Rocky Mountain Forest and Range Experiment Station.

Jackson D.C. 1999. Flathead catfish: Biology, fisheries and management. *In* E.R. Irwin, W.A. Hubert, C.F. Rabeni, H.L. Schramm, Jr., & T. Coon eds. *Proceedings of the International Ictalurid Symposium*. American Fisheries Society Symposium 24, Bethesda, MD, USA. pp. 23-36.

Jackson D.C. 2000. Distribution patterns of channel catfish Ictaluridae: *Ictalurus punctatus* in the Yalobusha river floodplain river ecosytem. Seventh International Symposium on the Ecology of Fluvial Fishes. *Polish Archives of Hydrobiology*, 471: 63-72.

Jackson D.C. Fisheries dynamics in temperate floodplain rivers. *In* L.H. Fredrickson, R.M. Kaminski & S.L. King eds. *Ecology and management of bottomland hardwood systems: The state of our understanding*. Columbia, MO, Bottomland Hardwood System Symposium Steering Committee and University of Missouri-Columbia. (forthcoming)

Jackson D.C. & Jackson J.R. 1989. A glimmer of hope for stream fisheries in Mississippi. *Fisheries*, 143: 4-9.

Jackson D.C. & Ye Q. 2000. Riverine fish stock and regional agronomic responses to hydrological and climatic regimes in the upper Yazoo River basin. *In* I.G.Cowx ed. *Management and ecology of river fisheries*. Fishing News Books. Blackwell Science, London, UK. pp. 242-257.

Jackson D.C., Brown-Peterson N. J. & Rhine T.D. 1993. Perspectives for rivers and their fisheries resources in the upper Yazoo River Basin, Mississippi. *In* L.W. Hesse, C.B. Stalnaker, N.G. Benson & J.R. Zuboy eds. *Proceedings of the Symposium on Restoration Planning for Rivers of the Mississippi River Ecosystem*. *Biological Report 19*. Washington, DC, USA, U.S. Department of the Interior. National Biological Survey. pp. 255-265.

Jackson D.C. Francis J.M. & Ye Q. 1997. Hand grabbling blue catfish in the main channel of a Mississippi river. *North American Journal of Fisheries Management*, 17: 1019-1024.

Jones W.D., Munn I.A., Jones J.C. & Grado S.C. 2000. A survey to determine fee hunting and wildlife management activities by private non-industrial landowners in Mississippi. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 521998: 421-429.

Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 110-127.

Marcum J.P., Holley C. & Williams M.W. 1988. Residential segregation by race in Mississippi, 1980. *Sociological Spectrum*, 8: 117-131.

Mareska J.F. & Jackson D.C. 2002. Use of shadow bass stock characteristics to evaluate natural and scenic waterways in Mississippi. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies*, 542000: 167-178.

Marks S.A. 1991. *Southern hunting in black and white*. Princeton, NJ, USA, Princeton University Press.

Miranda L.E. & Hubbard W.D. 1994. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. *Transactions of the American Fisheries Society*, 123: 80-87.

Perry W.G. 1979. Slat trap efficiency as affected by design. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies*, 32(1978): 666-671.

Perry W.G. & Williams A. 1987. Comparison of slat traps, wire cages, and various baits for commercial harvest of catfish. *North American Journal of Fisheries Management*, 7: 283-287.

Posey L. & Schaefer H. 1967. Evaluation of slat traps as commercial fishing gear in Louisiana. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners*, 18(1964): 517-522.

Pote J.W. & Wax C.L. 1986. Climatological aspects of irrigation design criteria in Mississippi. *Mississippi Agricultural and Forestry Experiment Station Technical Bulletin* 138. Mississippi State University, USA. 16 pp.

Risotto S.P. & Turner R.E. 1985. Annual fluctuations in abundance of the commercial fisheries of the Mississippi River and tributaries. *North American Journal of Fisheries Management,* 5: 557-574.

Rutherford D.A., Kelso W.E., Bryan C.F. & Constant G.C. 1995. Influence of physico-chemical characteristics on annual growth increments of four fishes from the lower Mississippi River. *Transactions of the American Fisheries Society,* 124: 687-697.

Shephard S. & Jackson D.C. 2002. *Lengths and ages at maturity for channel catfish in Mississippi, relationships to stream ecosystem characteristics, and susceptibility to capture in passive gear. Freshwater Fisheries Report 210. Federal Aid to Sport Fish Restoration Project F-133*. Jackson, MS, USA. Mississippi Department of Wildlife, Fisheries and Parks. 38 pp.

Shields F.D. Jr. Knight S.S. & Cooper C.M. 1998. Rehabilitation of aquatic habitats in warmwater streams damaged by channel incision in Mississippi. *Hydrobiological*, 382: 63-86.

Smith F.E. 1954. *The Yazoo River*. New York, Rinehart and Company, Inc. 362 pp.

Stopha M.E. 1994. *Hoop and mesh size influences on hoop net catches of buffalofishes Catostomidae and catfishes Ictaluridae in the upper Yazoo River Basin of northcentral Mississippi*. MS, USA, Mississippi State University. 62 pp. (Masters thesis)

Stopha M.E. & Jackson D.C. 1999. Influences of 3 different mesh and hoop size configurations on hoop net catches of buffalofishes in the upper Yazoo River Basin. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies*, 51(1997):79-87.

U.S. Army Corps of Engineers. 1991. *Supplement I to the final environmental impact statement on the operation and maintenance of Arkabutla Lake, Enid Lake, Grenada Lake, and Sardis Lake, Mississippi.* Vicksburg, MS, USA, U.S. Army Corps of Engineers. 123 pp.

Vannote R. L., Minshall G. M., Cummins K. W., Sedell J.R. & Cushing C.E. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences, 37: 130-137.

Ward J.V. & Stanford J.A. 1989. Riverine ecosystems: The influence of man on catchment dynamics and fish ecology. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.,* 106: 56-64.

Waxman C.F. 1983. *The stigma of poverty: A critique of poverty theories and policies.* Second edition. New York, Pergamon Press. 159 pp.

Welcomme R.L. 1976. Some general and theoretical considerations on the fish yield of African rivers. *Journal of Fish Biology,* 8: 351-364.

Welcomme R.L. 1985. River fisheries. *FAO Fisheries Technical Paper 262*. Rome, Food and Agricultural Organization of the United Nations. 330 pp.

Welcomme R.L. 1986. The effects of the Sahelian drought on the fishery of the central delta of the Niger River. *Aquaculture and Fisheries Management*, 17: 47-154.

THE FLOOD PULSE CONCEPT: NEW ASPECTS, APPROACHES AND APPLICATIONS - AN UPDATE

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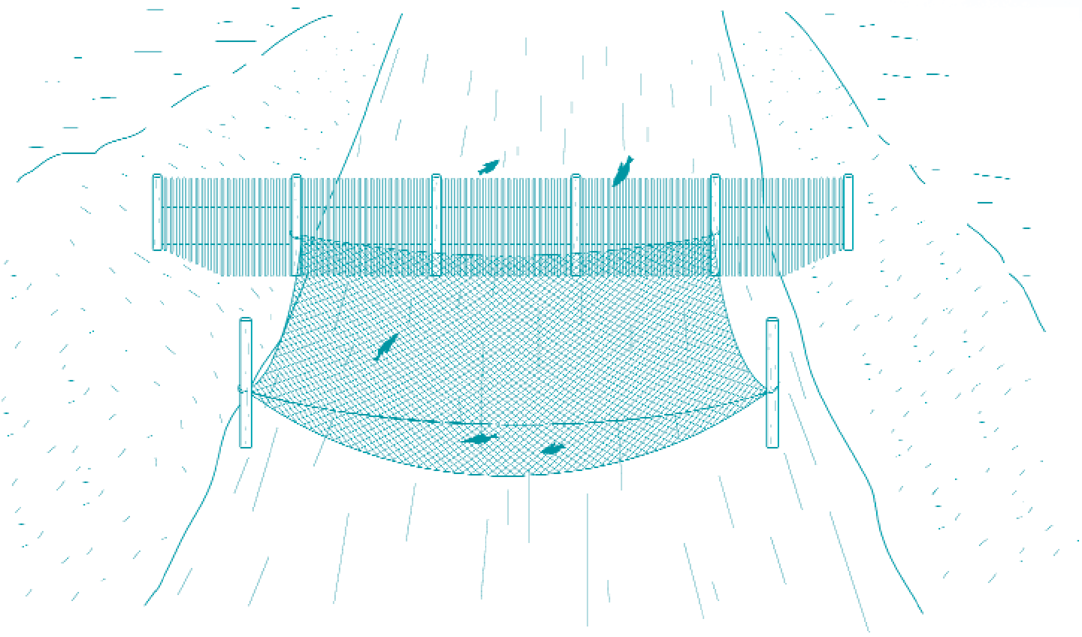


ABSTRACT

The flood pulse concept (FPC), published in 1989, was based on the scientific experience of the authors and published data worldwide. Since then, knowledge on floodplains has increased considerably, creating a large database for testing the predictions of the concept. The FPC has proved to be an integrative approach for studying highly diverse and complex ecological processes in river-floodplain systems; however, the concept has been modified, extended and restricted by several authors. Major advances have been achieved through detailed studies on the effects of hydrology and hydrochemistry, climate, paleoclimate, biogeography, biodiversity and landscape ecology and also through wetland restoration and sustainable management of floodplains in different latitudes and continents. Discussions on floodplain ecology and management are greatly influenced by data obtained on flow pulses and connectivity, the Riverine Productivity Model and the Multiple Use Concept. This paper summarizes the predictions of the FPC, evaluates their value in the light of recent data and new concepts and discusses further developments in floodplain theory.

INTRODUCTION

Rivers and floodplain wetlands are among the most threatened ecosystems. For example, 77 percent of the water discharge of the 139 largest river systems in North America and Europe is affected by fragmentation of the river channels by dams and river regulation (Dynesius and Nilsson 1994). In recent reviews on wetlands, demographic trends, economic and political development, demand for hydroelectric energy and water, agriculture and animal ranching, eutrophication and pollution, fisheries, logging, recreation and ecotourism and invasion by exotic species have been identified as the most important current determinants for the development of rivers and floodplain wetlands (Tockner and Stanford 2002; Junk 2002). The global water crisis and the threat to aquatic organisms, especially riverine biota (Dudgeon 2000; Pringle 2001), increase the necessity to develop models that serve both science and policy. The flood pulse concept (FPC) (Junk, Bayley and Sparks 1989) was primarily designed as a scientific concept, but it also outlined some strategies for use, recently specified in Junk *et al.* (2000). Here, the impact of advances in river ecology on this and other contemporary concepts is critically analyzed.

THEORETICAL BACKGROUND

Historical development

Limnologists classify inland waters as standing waters (lakes, ponds) and running waters (streams and rivers). Both system types receive allochthonous substances and produce autochthonous organic matter, both of which are metabolized and recycled. Standing waters, however, are closed systems that store inorganic and organic matter, circulate organic matter and dissolved inorganic substances in characteristic internal cycles in the lake basin and eventually deposit them in the sediments. These systems are characterized mainly by thermal and/or chemical stratification. Running waters are open systems that transport water and dissolved and suspended matter from the continents to the sea or to endorheic basins. This transport includes intermediate deposition and re-suspension of sediments in the river channel or in the connected floodplain, where production and degradation of organic matter also takes place.

These characteristics are reflected for lakes in the “Seentypenlehre” (Lake typology), elaborated by Thienemann and Naumann between 1915 and 1935 (e.g. Thienemann 1925; Naumann 1932) and for streams and rivers in articles by Illies (1961a) and Illies and Botosaneanu (1963) on the differentiation into different zones. These zones, described in these early studies as *rhithron* and *potamon* with epi-, meta- and hypo-subzones, were mainly characterized by abiotic patterns (current, temperature) and by the occurrence of distinct animal and plant communities that depend on a given set of these abiotic patterns. For example, epirithral communities are those typical of glacier outflows and that depend on low temperatures, high oxygen concentrations and fast current. In latitudinal comparisons, Illies (1961b) found evidence for a generality of this zonation in mountain streams worldwide - high-elevation streams in the tropics have communities similar to those of low-latitude coldwater streams.

Later, Vannote *et al.* (1980) substituted this rather static view of river classification with the River Continuum Concept (RCC), which introduced a dynamic concept of continuously changing physical conditions and biological components along the river channel, especially regarding the allochthonous and autochthonous inputs and the processing of organic matter in the flowing water along the river continuum. The RCC predicts major changes in the load and quality of organic matter and the biota in the stream/river channel from the headwaters to the lower river courses. The high allochthonous input from riparian vegetation in the headwaters decreases with increasing channel width (increasing stream order). Autochthonous primary production in the headwaters is low because of shading by trees (P/R <1), increases in the middle reaches because of low water depth and high irradiation (P/R >1) and decreases again in the lower reaches because of high water depth and increased turbidity and turbulence (P/R <1). In contrast to the zonation concept, the RCC claims that occurring species are replaced continuously rather than in discrete stages. The percentage of shredders decreases and the number of collectors increases with increasing stream order because of decreasing input of coarse particulate organic material and an increasing amount of fine particles owing to the increasing level of processing. Headwater communities tend to optimize their use of allochthonous matter, whereas an organism living in the lower river reaches largely depend on the inefficiency of organisms living in the upper reaches to process organic material. The interplay of processing, storage and leakage is predicted to reduce the diversity of organic matter types and the maximization of energy utilization (i.e. adaptation to poorly degradable organic matter) along the river continuum.

The RCC further predicts that biodiversity of aquatic organisms is lower in the headwater regions and in the lower parts of the rivers and that highest diversity is found in the middle reaches of the streams, where the variability of temperature, riparian influence and flow are highest and allow numerous different taxa to find their thermal optima.

One of the major constraints of the RCC is that it was originally based mostly on results from northern, temperate, low-order streams with dense tree canopies and steep gradients that flowed towards more-or-less-regulated rivers in long-term-managed areas. The hydrology of small streams is strongly influenced by local rainfall and is rather erratic. Flooding of small streams occurs only for short periods and is often altered by management of rivers in intensively used areas. Therefore, flooding events and floodplains received little or no attention in the first version of the concept, but were considered later (Minshall 1985; Sedell, Richey and Swanson 1989).

Floodplains fall into the wetland category, which includes ecosystems at the interface of aquatic and terrestrial ecosystems and are therefore often called ecotones. However, large wetlands have to be considered as specific ecosystems with unique properties not adequately covered by present ecological paradigms and by limnology, estuarine ecology and terrestrial ecology (Mitsch and Gosselink 2000). Floodplains are areas that are periodically inundated by the lateral overflow of rivers or lakes and/or by rainfall or groundwater; the biota responds to the flooding by morphological, anatomical, physiological, phenological and/or ethological adaptations and characteristic community structures are formed (Junk *et al.* 1989).

Until the 1970s, floodplains were studied separately by different disciplines: limnologists studied floodplain lakes treating them as classical lakes, ecologists dealt with the terrestrial fauna and flora and hydrologists investigated water and sediment transport. An integrated approach was used by Welcomme (1979), who summarized data on floodplain fishery, limnology and hydrology and coupled fish production with the nutrient status of the parent rivers and the extent of flooding. The consequences of the fluctuating water level on fish have also been summarized by Lowe-McConnell (1975, 1987). Bayley (1980) pointed to limits in limnological theory with respect to fish production in river floodplains. Junk (1980) described the multiple land-water interactions of the Central Amazon River floodplain, analysed limnological concepts of rivers and lakes, pointed out a gap in limnological theory and described floodplains as specific ecosystems.

During the first Large River Symposium in Toronto in 1986, the discussion on the applicability of the RCC to large river-floodplain systems led to the formulation of the Flood Pulse Concept (FPC) (Junk *et al.* 1989). This concept focuses on the lateral exchange of water, nutrients and organisms between the river channel (or a lake) and the connected floodplain. It considers the importance of the hydrology and hydrochemistry of the parent river, but focuses on their impact on the organisms and the specific processes in the floodplain. Periodic inundation and drought (flood pulse) is the driving force in the river-floodplain system. The floodplain is considered as an integral part of the system that is periodically coupled and decoupled from the parent river by the aquatic/terrestrial transition zone (ATTZ). The flood pulse can be monomodal or polymodal, predictable or unpredictable and with a high or low amplitude. Predictable pulsing favors the adaptation of organisms and increases primary production and efficiency of nutrient use.

The FPC predicts that the nutrient status of the floodplain depends on the amount and quality of dissolved and suspended solids of the parent river; however, it includes the premise that internal processes of the floodplain and nutrient transfer mechanisms between the terrestrial and the aquatic phase strongly influence nutrient cycles, primary and secondary production and decomposition. At the same time, flooding is considered as a disturbance factor that leads to a regular setback of community development and maintains the system in an immature, but highly productive stage.

Another tenet of the FPC is that in the river-floodplain system, a large part of the primary and secondary production occurs in the floodplain, whereas the river is mainly the transport vehicle for water and dissolved and suspended matter. The river is also the refuge for aquatic organisms during low-water periods and serves as a route for active and passive dispersal. The “highway analogy” describing the river channel as a transport and migration corridor was used to visualize the different functions of the main river channel and its floodplain (Junk *et al.* 1989). The FPC was based on the personal experiences of the authors on the Amazon and Mississippi rivers but also on a vast literature about other river systems. Therefore, the concept was not restricted to large tropical rivers, as is sometimes cited (e.g. Benke *et al.* 2000), but was conceived as a general concept for large river-floodplain systems.

Mostly limnologists, ichthyologists and fisheries biologists study the ecology of floodplains and their organisms. They test the predictions of the FPC only for the aquatic phases of the system. However, it has to be stressed that the FPC covers the river-floodplain-system during the entire year and that its predictions are also valid for the terrestrial phases that are an integral part of the river-floodplain system.

Further concepts in running-water ecology

Various conceptual approaches independent of (or complementary to) the RCC and FPC were developed in the 1980s and 1990s on lotic ecosystem structure and functioning. Many early seminal papers dealt with the distribution of organisms within the lotic systems. A key aspect was the description of hyporheic zones in which important ecosystem processes occur. Early work by Schwoerbel (1961) on the distribution of benthic and stygal fauna in bed sediments was extended by the description of aquatic organisms far from the river channel area (Stanford and Ward 1988) and factors contributing to vertical distribution of the organisms (Bretschko and Leichtfried 1988) and by the understanding of organic matter dynamics in this zone (e.g. Williams 1989; Triska, Duff and Avanzino 1993). Ward (1989) included the function and occurrence of hyporheic zones in general stream theory by describing streams as four-dimensional systems.

The importance of stream hydraulics (Statzner and Higler 1986) and of disturbance (Resh *et al.* 1988) for the distribution for benthic organisms has shown that variation in water flow caused by climate and geomorphology can set limits to the generalizations of the RCC since flow conditions typical of upstream and downstream areas can change several times along the river course (“discontinuum”, Poole 2002). Consequently, the template provided by the habitat conditions (Southwood 1977) and its alignment with species traits (Townsend and Hildrew 1994; Resh *et al.* 1994) might be more important for the occurrence of a species than the position of the given site along the continuum. Since geomorphology is subject to non-continuous local variations, the distribution of stream habitats appears as a mosaic (Pringle *et al.* 1988) of hierarchically ordinated and dynamic patches (Townsend 1989; Poole 2002). Various hierarchical concepts have been developed for riverine landscape patterns and their scale-dependent processes (e.g. Frissell *et al.* 1986; Townsend 1996; Petts and Amoros 1996; Poff 1997; Montgomery 1999; Ward, Malard and Tockner. 2001; Poole 2002).

Further conceptual approaches have dealt with the production and processing of organic matter, such as the nutrient spiraling concept (Elwood *et al.* 1983; Pinay *et al.* 1999), or with human impacts, e.g. the interruption of natural flow pathways by dams [the Serial Discontinuity Concept (Ward and Stanford 1983a; Ward and Stanford 1995)]. As an alternative to the RCC, Montgomery (1999) proposed a multi-scale hypothesis in which spatial variability in geomorphic processes governs temporal patterns of disturbances that influence ecosystem structure and dynamics (Concept of Process Domains). Channel networks can be divided into discrete regions in which community structure and dynamics respond to distinctly different disturbance regimes.

EXTENSIONS OF THE FPC

HYDROLOGY AND FLOW CHARACTERISTICS

The FPC was developed based upon data and long-term observations of neotropical (Amazon) and temperate zone (Mississippi) rivers. It provided a general outline and strengthened the premise that rivers and their floodplains have to be considered as one unit and therefore cannot be treated separately in ecological studies. The FPC has stimulated various studies on river-floodplain ecosystems in, e.g. Lower Rhine floodplain lakes (van den Brink *et al.* 1994), Missouri floodplain lakes (Knowlton and Jones 1997), the Danube (Tockner, Malard and Ward. 2000), the Murray-Darling (Humphries, King and Koehn 1999) and the Mississippi River (Sparks, Bayley and Kohlert 1990). Various studies in which the FPC has been applied and its tenets tested have lead to proposals for supplementation to the original conceptual framework.

Increasing knowledge on the hydrological characteristics of rivers has contributed much towards the understanding of their ecological processes. The hydrographs of individual rivers are influenced by a series of partly interacting factors, such as climate, gradients, landscape morphology, floodplain buffering and human impacts, which together cause very complex patterns. Several authors have identified different measures for identifying the hydrological variability of rivers and have provided tools for classifying rivers according to their hydrological signature (Richter, Baumgartener, Powell *et al.* 1996; Puckridge *et al.* 1998). Providing more detail on the type of flow variation, Puckridge *et al.* (1998) have stressed the general importance of water level variations even below the bankfull stage (flow pulses), which might have significant influence on the habitat size and characteristics. Irregular flood events, especially in streams (e.g. Winterbourn, Rounik and Cowie 1981) and arid zone rivers, have selected for resilient strategies of organisms to survive these events (Poff and Ward 1989; Lytle 2001) rather than to adaptations to profit from them (Junk *et al.* 1989). However, this view has recently been modified because in seasonal climates, the period of flash flood events can be predicted and because flash-flood events mobilize organic matter resources from stream wetlands (Wantzen and Junk 2000).

Tockner *et al.* (2000) extended the FPC by considering that flooding resets temperature diversity in isolated aquatic floodplain habitats. Thus, aquatic habitats within floodplains might have a much broader temperature range than the river itself, especially in rivers with wide and diversified beds, such as the alpine Fiume Tagliamento, where flow pulses occur frequently.

Unpredictable flooding and decoupling of the flood pulse from the temperature pulse leads to low temperatures during floods and high temperatures that trigger spawning of some fish species during low water level in some parts of the Murray Darling River system in Australia (Humphries *et al*. 1999, Low Flow Recruitment Hypothesis).

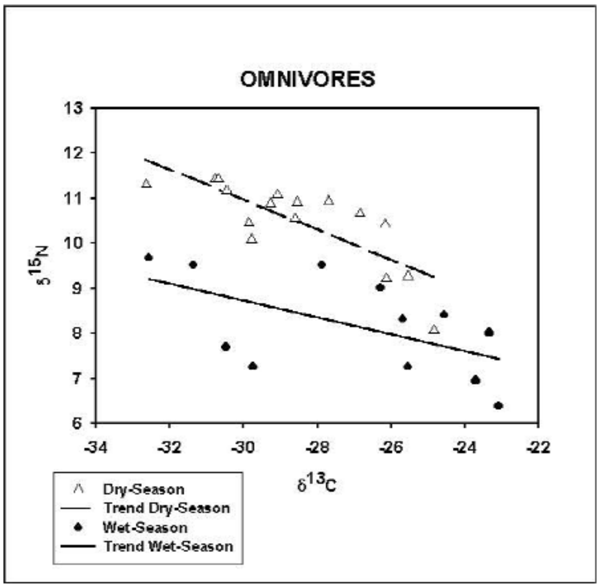
The fact that water level changes influence riverine systems four-dimensionally in space and time (Ward 1989) is important. Rising water levels not only increase the wetted surface of the channel and eventually of the floodplain, but at the same time influence the exchange between groundwater and surface water either by allowing an up-welling of groundwater or by forcing a down-welling of the surface water into the aquifer vertically and laterally. The hyporheic zone serves as an interface between groundwater and surface water (Schwoerbel 1961). Similarly, floodplains act as interfaces for the interchange between the river mainstreams and their tributaries or surface runoff from rainwater. The flow direction of the interfaces is influenced by the fourth dimension, time, such that the recent and the past hydrological situations become decisive: elevated water levels can cause blocking or even backflow of the tributaries and groundwater outflows. In the northern Pantanal wetland, frequent changes in the flow direction occur in floodplain channels that connect water bodies that receive rain and river water, depending on the respective water level (Wantzen and Da Silva, unpublished data). In the southern areas of the Pantanal, high levels of river water block the tributaries after the rainy season; therefore, a large part of the inundation occurs after cessation of the rainfall (Hamilton, Sippel and Melack 1996).

ALLOCHTHONOUS AND AUTOCHTHONOUS PRODUCTION AND NUTRIENTS

The FPC has focused on the productivity within the floodplain areas, in contrast to the RCC, which has focused on the import of more-or-less processed allochthonous matter from the upriver sections. Both concepts have been criticized by Thorp and Delong (1994) in the Riverine Productivity Model (RPM), which predicts that autochthonous production in the river channel and allochthonous inputs in the lower reaches provide a substantial portion of the organic carbon used by river animals. While analyzing the potential influence of the floodplain on the carbon budget in a channel site and a floodplain region of the Ohio River, Thorp *et al.* (1998) did not find significant differences in the isotopic C and N signatures, which indicated a low floodplain contribution during a short-termed, unpredictable flood event at low water temperatures in wintertime. This, however, does not necessarily contradict the predictions of the FPC.

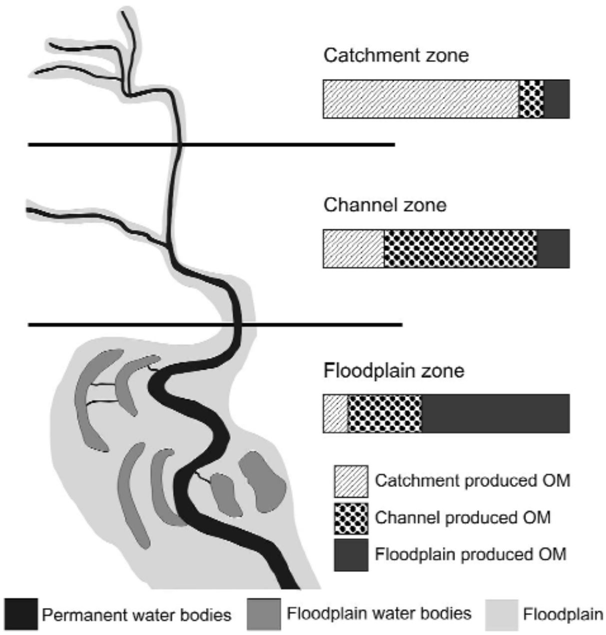
Depending on temperature, light, nutrients and substrate conditions, river channels can show a considerable autochthonous primary production, which fuels the riverine food web as shown for Rhine River (Friedrich and Mueller 1984). Especially in those rivers where these conditions are beneficial for algal growth and where conditions for production in the floodplain are restricted by turbidity, timing of inundation during the winter and river regulation (e.g. of the Ohio River), the in-channel primary production can be substantially higher than floodplain production. River channels can support diverse and productive fish communities under these conditions (Galat and Zweimuller 2001; Dettmers *et al.* 2001); however, this is not the case in very large and turbid lowland rivers with a sandy, permanently moving bed load.

In those rivers that show a predictable, sufficiently long and timely inundation, such as the Mississippi River, the exploitation of floodplain resources provides a “flood pulse advantage” Gutreuter *et al.* (1999) for floodplain fishes compared to pure riverine species (Bayley 1991). Stable isotope ratios of many floodplain fish species of the Pantanal wetland show seasonal variation, which indicates a large variability in carbon sources and the trophic level between seasons (Wantzen *et al.* 2002) (Figure. 1).



■ **Figure 1.** Seasonal isotopic shifts in small omnivore floodplain fish species in the Pantanal wetland, Brazil. Filled circles: rainy season values; open triangles: dry season values. There is a general increase in d15N values from the wet to the dry season, which indicates more omnivorous feeding when the wetland is flooded and elevated carnivory during the dry season when the lake becomes confined to its basin (Modified after Wantzen *et al.* 2002, with permission).

In regulated rivers, where connected lakes represent remains of a floodplain, e.g. in the lower Rhine River in the Netherlands, the seepage and overflow of nutrient-rich river water determines the productivity and composition of the phytoplankton such that lakes with higher connectivity have a higher productivity (van den Brink *et al.* 1993). In most river-floodplain systems, primary production in the floodplain is much higher than in the channel, (e.g. Australia, review by Robertson *et al.* 1999). We agree with Dettmers *et al.* (2001) that organic matter input and production derive from the upstream sites (RCC), from the floodplains (FPC) and from the river channel (RPM). The relative contribution of these sites to the organic matter budget of a river depends on the production and transport conditions in these three units (Figure 2).



■ **Figure 2.** Schematic interplay of variable carbon sources in different segments of a river. Owing to the topographical variation in the landscape, the sequence of the segments can vary along the river course. Top: in catchment areas with strong aquatic-terrestrial interfaces, the floodplain extension is relatively small and inputs of terrestrially produced organic matter are high. Middle: in natural (mountainous, steep-bordered) or human-made (channelized) segments, the extension of the floodplains is restricted and carbon fixation occurs largely by riverine plankton and aquatic macrophytes. Below: in floodplain areas, carbon can contribute to river carbon budget via water flow from the floodplain to the mainstream or via feeding migration of fish and other aquatic animals between the floodplain and the main channel.

When considering the contribution of floodplain carbon to the entire river carbon budget, two aspects have to be stressed:

Flow conditions vary considerably between different river-floodplain systems. If geomorphology limits the exchange between river and floodplain, the contribution of the floodplain carbon to the mainstream carbon budget can be lower than expected. Lewis (1988) found that in the Orinoco and some tributaries, non-floodplain sources, including within-channel and near-channel stagnant or slow-flowing areas, accounted for 63 percent of the annual transport of phytoplankton carbon, while the floodplain accounted for only 37 percent.

Mobile organisms such as fish actively seek floodplain carbon in mass migrations as soon as flooding begins in order to feed in the floodplain (Welcomme 1985; Lowe-McConnell 1987; Winemiller 1989; Junk *et al.* 1997; Wantzen *et al.* 2002). When small floodplain fish migrate back into the main channel during the falling limb of the hydrograph, they are preyed upon in large quantities by riverine predators (Wantzen *et al.* 2002). Therefore, floodplain carbon can contribute significantly to river food webs without strong hydrological connectivity.

THE MULTIPLE USE CONCEPT

Floodplain management should be based on conceptional considerations in order to avoid negative side effects as much as possible (e.g. Nienhuis, Leuven and Ragas 1998). The FPC predicts exchange of nutrients and energy between the aquatic and terrestrial phases. Human use of terrestrial resources will affect aquatic resources and vice versa. These impacts have to be considered when developing management concepts.

The economic and ecological analysis of the different utilization forms led to the formulation of an integrated multiple-use concept for the central Amazon River floodplain (Junk 2000). It favours the optimization of the use of different resources instead of the maximization of the economic return of a single resource. Priority is given to the sustainable use of fishery resources because of low environmental impact, large requirement of labour force and high economic importance. Subsistence fisheries can be combined with smallholder agriculture and dairy farming on the highest levees and floodplain-adapted sustainable forest management by selective logging. Large-scale cattle and water buffalo ranching for beef production and agro-industries are considered destructive for the ecosystem because of the destruction of floodplain forests and socially unacceptable because of low labor force requirements (Junk *et al.* 2000). Decentralized administration of floodplain resources by local communities is considered essential to stimulate the participation of the local population in the complex management processes (Isaac *et al.* 1998; McGrath *et al.* 1999). Multiple use concepts will vary considerably for different floodplains because of the large variety of floodplain types and related socio-economic parameters.

OPEN QUESTIONS IN FLOODPLAIN RESEARCH

When river or lake water inundates the floodplain via overspill or via floodplain channels, various key processes occur simultaneously: (1) pre-flood thermal and chemical heterogeneity between main channel and floodplain water bodies temporarily resets (Sabo *et al.* 1999a; Tockner *et al.* 2000); (2) considerable inputs of mainstream (or lake) water-bound substances (dissolved and suspended, organic and inorganic) flush into the floodplain (Fisher and Parsley 1979; Lewis *et al.* 2000); (3) terrestrial habitats are flooded, large amounts of biomass decays and large amounts of inorganic and organic matter deposited during the terrestrial phase are mobilized by the overlaying water (Hamilton *et al.* 1997; Sabo *et al.* 1999b); (4) terrestrial organisms migrate into non-flooded habitats or show adaptations to flooding (Adis 1984; Adis, Marques and Wantzen 2001); (5) aquatic organisms are flushed or migrate into the floodplain or eclode from resting stages (Welcomme 1985; Irmler 1981) and (6) terrestrial carbon and floodplain products from the canopy of the floodplain forest, such as terrestrial invertebrates, fruits and seeds, are incorporated in the aquatic food webs (Junk *et al.* 1989; Wantzen *et al.* 2002).

When the water level falls the following key processes occur simultaneously: (1) water stored in the floodplain with any dissolved and suspended matter enters the parent river or lake (Benke *et al.* 2000), (2) the ATTZ falls dry and becomes colonized by terrestrial organisms (Junk and Piedade 1997; Adis and Junk 2002), (3) large amounts of water-borne organic carbon becomes stranded and incorporated in the terrestrial food webs (Junk and Weber 1996), (4) aquatic organisms move to permanent water bodies or show adaptations to periodic drought (Irmler 1981), (5) permanent water bodies become increasingly isolated from the parent river or lake and develop specific physical and chemical characteristics and specific species assemblages (Furch 1984; Tockner *et al.* 1999).

These changes either have a direct influence on aquatic and terrestrial flora and fauna in the floodplains and related rivers and lakes, for example through changes in the community composition and population density (e.g. Heckman 1998; De-Lamônica-Freire and Heckman 1996; Sabo *et al.* 1999b; de Oliveira and Calheiros 2000), or indirectly trigger various behavioral traits, such as spawning and migration of fish (Welcomme 1985; Junk *et al.* 1997), breeding of waterfowls (Petermann 1999; Magrath 1992) and reproduction and migration of terrestrial invertebrates (Adis and Junk 2002).

The complexity and the interdependence of these processes are yet not fully understood. Currently, questions arise about recent, past and future climatic impacts, the importance of landscape connectivity and dynamics of the flooding on biodiversity and biogeochemical cycles and how to include the results of floodplain research into sustainable management strategies.

THE IMPACT OF FLOOD PULSE ON WETLANDS IN DIFFERENT CLIMATIC ZONES

The FPC states that the flood pulse is the main driving force in river-wetland systems. This is true for the humid tropics, but in lower latitudes, there are other driving forces that also affect the biota and processes in the floodplains and that can overlap with the flood pulse. The FPC mentions these forces, but their impacts require more attention in comparative studies. In semiarid and arid regions, drought and fire affect the floodplains during the terrestrial phase, with consequences for the aquatic phase. In temperate regions, biota react to day length and/or temperature (light/temperature pulse) and this cycle is superimposed on the flood pulse (Junk 1999). Some effects (on fish fauna), because of the decoupling of the flood pulse from the temperature pulse, are discussed by Humphries *et al.* (1999) for the Murray-Darling River basin. In high latitudes, prolonged ice cover and low temperatures strongly affect the biota; and the biota might require as many adaptations to these events as to the flood pulse.

PALEOCLIMATOLOGICAL HISTORY OF FLOODPLAINS

The predictions of the FPC also have to be interpreted in the light of the paleo-ecological conditions that have influenced evolutionary processes and rates of speciation and extinction. For instance, the FPC states that predictable pulsing favors the development of adaptations of fauna and flora and increases species diversity. This statement holds true for some river floodplains, but not for others. The Amazon River floodplain is very rich in plant and animal species that are highly adapted to the predictable monomodal flood pulse. Approximately 1 000 flood-adapted tree species are found in the floodplains of the Amazon basin. In the floodplain of the Mamirauá Reserve near Tefé, about 800 km upstream of Manaus, which covers an area of about 11 240 km^2, until today approximately 500 tree species have been recorded, about 80 percent of which are floodplain-specific (Wittmann 2002 and unpublished data). In comparison, the large majority of the about 250 tree species of the Pantanal of Mato Grosso, a wetland of approximately 140 000 km^2, have broad ecological amplitude; only about 5 percent are restricted to regularly flooded areas (Nunes da Cunha and Junk 2001 and unpublished data). The number of flood-resistant tree species in bottomland hardwood forests of the USA approaches about 100 species, many of which also occur in the uplands (Clark and Benforado 1981). In northern European floodplains, only about a dozen flood-resistant tree species occur.

Many Amazonian soil arthropods are floodplain-specific and have complex survival strategies (Adis and Junk 2002). First observations indicate that flood-adapted soil arthropods in the Pantanal are less common than in Amazonia (Adis *et al.* 2001). Terrestrial soil invertebrates in Europe are poorly adapted to the flood pulse. Most are immigrants from the non-flooded uplands and suffer high losses during floods (Adis and Junk 2002).

Paleoclimatological history analysis of Amazonia shows that during the last ice age the temperature was probably about 5^{o}C cooler, the precipitation about 50 percent lower (Haffer and Prance 2001), the declivity greater (Müller *et al.* 1995) and the floodplain area considerably smaller than today (Irion pers. comm.). However, the flood pulse continued to be monomodal and predictable with respect to dry and rainy seasons and there was sufficient floodplain area left to guarantee survival of flood-adapted plant and animal species. Despite the change in environmental conditions in the Amazon basin, basic structures and functions of the large river floodplains situated north and south of the equator were comparatively little affected and extinction rates were low. In comparison, during the ice ages, the Pantanal of Mato Grosso, about 2 500 km south of the equator, suffered from extremely dry periods that eliminated most of the flood-adapted plant and animal species.

Today's wetland conditions became reestablished in the Pantanal only about 7 000 years ago and wetland organisms of the lower Paraguay River, the surrounding Cerrado and Amazonia colonized the area (Ab'Saber 1988). Mobile animals, such as birds, which are very diverse in the Pantanal, were most efficient at colonization. However, pronounced annual and pluriannual droughts in combination with frequent wildfires led to additional stress for plants and animals. A broad ecological amplitude was a better survival strategy for the organisms than adaptation to specific wetland conditions, as shown by trees that occur over a large range of habitats. The number of total species and the level of adaptation are comparatively low and endemic species are rare because the time span after the dry glacial period was too short for genetic diversification (da Silva *et al.* 2001). This holds true even with respect to genera that show high diversification rates, as for instance, the tree genus *Inga*. Most of the 300 species have developed in the last 2 million years (Richardson *et al.* 2001).

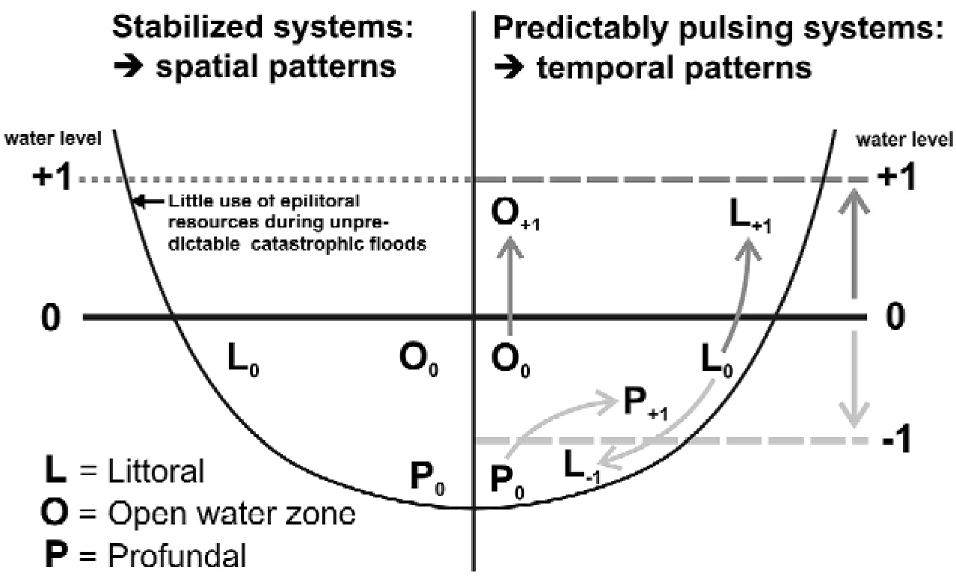
During the ice ages, European and North American river floodplains suffered even larger climatic changes. The temperature was lower and glaciers covered most of Northern Europe and North America. The discharge regime of the large rivers was determined by snow and ice melt. The light-temperature pulse strongly superimposed on the impact of the flood pulse. Today's wetlands of these areas began to develop about 10 000 years ago with deglaciation and there was very little time for organisms to adapt to the new conditions in the floodplains. However, during the ice ages, North American floodplain species could migrate to a certain extent to lower latitudes and later recolonize the newly formed wetlands, an option that was blocked in northern Europe by high mountains (Alps and Pyrenees), which explains the relatively small number and low level of adaptations of organisms to flooding in the European floodplains. These examples also illustrate the influence of the time scale to the degree of specialization and the development of flood-adapted communities.

CONNECTIVITY AND LENTIC-LOTIC LINKAGES

Amoros and Roux (1988) introduced the technical term "connectivity" from landscape ecology to limnology in order to describe the level of connection of the mainstream with floodplain lakes. Connectivity levels vary from permanent connection to short-term connection during extreme floods (Ward, Tockner, and Schiemer 1999; Wantzen and Junk 2000). With decreasing connectivity, the impact of the river on floodplain lakes diminishes and lakes develop their own limnological characteristics. For the Austrian Danube River floodplain near Regelsbrunn, Tockner *et al.* (1999) have shown that species number and community structure of many aquatic organisms change depending on the connectivity level. The quality of connectivity changes when, at very high water levels, floodplain lakes change from water storage to water transport systems, i.e. from a lentic to a lotic system (*limnophase* and *potamophase, sensu* Neiff 1990). Strong flow pulses (Puckridge *et al.* 1998) may lead to dramatic resetting of the limnetic succession by cleaning the lake of accumulated organic debris and profoundly modifying aquatic plant and animal communities (Marchese, Escurra de Drago and Drago 2002). On the other hand, the establishment and the cessation of flow conditions are crucial for the oxygen budget in detritus-rich floodplains. Two processes become important: 1) When terrestrially accumulated organic matter becomes flooded and decays, large amounts of oxygen can be consumed, as shown for tropical floodplains (Braum and Junk 1982; Junk, Soares and Carvalho 1983; Sabo *et al.* 1999b), which eventually cause fish kills (Hamilton *et al.* 1997) and 2) when flow ceases in floodplain water bodies, high-water-level stratification and hypoxia occur (Melack and Fisher 1983; Junk *et al.* 1983; Sabo *et al.* 1999b), which affects aquatic organisms.

Very large floodplains have complex connectivity patterns. For example, lakes can become connected to the mainstream by other lakes. In this case, migrating aquatic organisms have free access to lakes and the river; however, input of dissolved and suspended matter is concentrated in the lake near the river and is low in the remote lake, which maintains lacustrine conditions. Tributaries with different water quality can cause hydro-chemical disconnection of floodplain lakes, as shown in the Ria Lakes formed by clear water and black water tributaries in the Amazon River floodplain. These lakes can be permanently connected to the Amazon River, which transports white water. When the water level falls, the black and clear water of the tributaries advances to the lake mouth; when the water rises, the white water of the mainstream represses the river water and dominates part of the lake. The mobile frontier between river water and the water of the tributaries can become a hydro-chemical barrier for aquatic organisms despite the hydrological connection, as shown by the growth of aquatic macrophytes and the occurrence of water snails and bivalves that concentrate in the whitewater-influenced area because of better nutrient and calcium supply and higher pH values (Junk, unpubl.). Detailed studies on the impact of the hydrological and hydro-chemical connectivity level on flora and fauna in tropical river floodplain systems are still lacking.

Lentic-lotic linkages have so far been considered mainly in interconnected rivers and lakes where lentic and lotic conditions alternate along the continuum of the river course. Similar linkages exist in river-floodplains systems; however, they occur in a temporal dimension (syntopically during different hydrological periods) rather than in a spatial dimension (synchronically at different sites Figure 3). Adopting this perspective, spatially scaled processes in weakly or non-pulsing systems (e.g. regulated rivers) can be considered analogous to temporal scales in pulsing systems. For example, regulated lakes and rivers are stratified into profundal and littoral zones all year round. Processes such as open-water plankton production and shallow-site plankton filtering by benthos are spatially separated, but linked by the water movement. In river-floodplain systems, both processes can occur at the same site, but at different water levels. The moving littoral follows the rising or sinking water level in the ATTZ. In the same way, infralittoral and profundal zones migrate along the flooding gradient, provided that the depth is sufficient. When water levels recede, the functional units of the deep water disappear in floodplain systems (Figure 3).



■ **Figure 3.** Schematic comparison between hydrologically stabilized (left) and pulsing (right) aquatic ecosystems at normal water levels (0), extremely high water levels (+1) and extremely low water levels (-1). Left: in the stabilized system (regulated lake or river or natural water body without floodplain), water level 0 prevails most of the time, allowing the establishment of well defined littoral (L), pelagial (O) and profundal (P) communities that are well adapted to these environmental conditions and are optimized in using the locally occurring resources. Occasional extreme floods are catastrophic events that do not allow the use of the resources of the flooded epilittoral by flora and fauna. Right: in pulsing systems, the organisms are adapted to periodically changing water levels and profit from resources of varying origin. Flora and fauna move along the flooding gradient; therefore, the same place in the ecosystem can harbor littoral and profundal communities at different water levels. Not shown in the graph: Extreme low water levels urge the profundal and pelagial organisms either to migrate into deeper water bodies or to estivate at the sites, whereas terrestrial (epilittoral) species have developed survival strategies during flooding.

TIMING AND SHAPE OF THE FLOOD PULSE

The FPC has drawn attention to the importance of the timing of the flood pulse and the stage of the life cycle of the organisms, but for many floodplains, data are still insufficient for detailed predictions. Many floodplain organisms have a "physiological and phenological window of susceptibility" to the benefits and disturbances of the flooding. The timing decides whether an organism can profit from the flood-borne resources or apply survival strategies or not. Winter flooding does not have such deleterious effects to non-flood-adapted trees as flooding during summer when trees are physiologically fully active. Similarly, unpredicted winter flooding had no significant effect on floodplain-carbon uptake by fish in a river in the USA (Delong *et al.* 2001), whereas predicted timely flooding in the Pantanal did (Wantzen *et al.* 2002). Most fish species of the upper Paraná River have adapted their spawning to the flood pulse and are affected by the many reservoirs that in addition to interrupting connectivity between river reaches, modify timing and shape of the pulse. These changes influence spawning behavior and affect recruitment success of some species but also affect community structure, for instance by increased predator pressure (Agostinho *et al.* 2000; Agostinho, Gomes and Zalewski 2001).

A slowly rising water level of the Amazon River leads to interruption and/or delay of spawning migration of many migrating fish species and in extreme conditions to gonad absorption (Junk pers. obs.). Different flood patterns lead to different macrophyte assemblages, which in turn are important habitats and food sources for many fishes (Petr 2000). The effects of different flood patterns on fish populations have been summarized by Welcomme and Halls (2001).

The impact of human induced hydrological changes has been shown for seedling establishment of poplar (*Populus* spp.) in North American rivers (Rood and Mahoney 1990). Timing of floods for the management of grasses and herbs for ducks and geese is a major tool in polders along the Mississippi River (Fredrickson and Reid 1988; Reid *et al.* 1989). Comparative studies on aquatic macrophytes and water birds in the central Amazon River floodplain and the Pantanal of Mato Grosso point to the importance of the amplitude of the flood pulse for species composition and life forms. In the Amazon River flood plain, a high flood amplitude of up to 15 meters hinders the growth of submersed plants and probably also the food uptake of some wading birds. Both groups occur in large abundance and species numbers in the Pantanal of Mato Grosso, where the flood amplitude is only 1-3 meters (Junk and Petermann, unpubl. data). However, for most plant and animal species and communities such information is still missing. Considering the increasing man-made changes of river discharge, studies are required for a better understanding of the impact of the quality of the flood pulse on the biota.

EXTREME CLIMATIC EVENTS AND GLOBAL CHANGE

The effect of extreme hydrologic and climatic events on river-floodplain systems has been stressed by the FPC, but has been little studied. Long-term and deep flooding affect the ecosystem through profound levels of hydraulic energy and/or by physiological stress. Studies on streams show that 80 percent of the annual transport of particulate organic matter can occur during a single extreme flooding (Cummins *et al.* 1983; Hobbie and Likens 1973). Such an event reshapes the entire channel bed and the floodplain of rivers in mountainous regions, such as the Tagliamento River in the Alps (Arscott, Tockner and Ward 2000) and also strongly modifies the floodplain of lowland rivers (Sparks, Nelson and Yin 1998).

Pluriannual dry and wet periods can have long-lasting effects on community structure in floodplains. The long flood period of the Amazon River in the beginning of the 1970s led to the dieback of many floodplain trees in low-lying areas. These areas still have not yet been recolonized by trees; a pluriannual dry period is required for successful reestablishment in very low lying areas on the flood gradient (Junk 1989). The spread of *Vochysia divergens*, a flood-tolerant tree species, in the Pantanal of Mato Grosso during the last 30 years has been associated with a long-lasting wet period after a pluriannual dry period in the beginning of the 1960s (Nunes da Cunha and Junk unpublished). Fish catches in the central delta of the Niger River declined from 90 000 tonnes yr^{-1} to 45 000 tonnes yr^{-1} because of little rainfall in the 1980s (Lae 1994).

The study of the impacts of extreme climatic events will be crucial for wetland ecosystem management and protection strategies. The IPCC (2001) indicates that the planet Earth will suffer considerable climate changes during the next century, which will be, to a considerable extent, the result of a man-made increase in greenhouse gases, such as carbon dioxide and methane. A global average temperature increase of 1.4 to 5.8^{o} C is predicted. Nearly all land masses, mainly those at northern high latitudes during the cold season, will warm more rapidly than the global average. Global mean sea level is projected to rise by 0.09 to 0.88 m because of temperature-related expansion of the water and melting of the glaciers of the northern polar regions and high mountains. Changes in precipitation will occur in most regions - rainfall will increase in some regions and drought will increase in others. The strongest impact will be felt in northern sub-polar regions (permafrost regions), high mountains, coastal areas, deserts and savannas, where water is already a limiting factor. In many river floodplains, man-induced changes of hydrology, pollution and wetland destruction will be more important than the effects of climate change (Vörösmarty 2002), but extreme climate change events will overlap with other human-induced modifications and aggravate the situation.

BIODIVERSITY

As stated by the FPC and other authors, floodplains are hot spots of species diversity (Gopal and Junk 2000). They harbour not only many wetland-specific plants and animals, but also many species from adjacent terrestrial and deep-water habitats that can have fundamental impacts on structures and functions of floodplains. For instance, terrestrial plant species substantially contribute to habitat diversity; primary production and nutrient cycles and terrestrial ungulates affect plant community structure and increase secondary production. However, inventories of floodplain species are rare and incomplete because they require interdisciplinary approaches (Gopal, Junk and Davies 2000, 2001).

One aspect of flooding is a variably strong disturbance that can modify or even reset environmental conditions in the system. Therefore, the FPC has integrated the tenets of the intermediate-disturbance hypothesis (Connell 1978; Ward and Stanford 1983b) by predicting that floodplain areas with an intermediate (and predictable) level of flooding are expected to provide the highest diversity. The two extremes for the disturbance-diversity relationship for a given floodplain habitat are, therefore, (1) frequent-to-permanent changes in the physical habitat structure caused by flooding (e.g. rainfall-driven floodplain habitats in low-order streams) and (2) low number or lack of hydrological changes with a continuous ecological succession of species, leading to a climax community (e.g. remote floodplain lakes during terrestrialization). By interrupting ecological succession in some patches, flooding causes the development of a mosaic of different successional stages at the same time on a small spatial scale. The intensity of multi-year wet and dry phases in floodplains, however, can provide additional stressors. In the Pantanal of Mato Grosso, for instance, the occurrence of numerous life forms is limited by the extreme desiccation, combined with fires during the dry phase (Nunes da Cunha and Junk 2001; da Silva *et al.* 2001).

In riverine floodplains, hydrological variation shapes a high diversity of physical habitat structures that might be more heterogeneous across the floodplain than along the main channel (Marchese and Ezcurra de Drago 1992; Arscott *et al.* 2000), thus creating the basis for a diverse flora and fauna. In Amazonia, forest diversity is related to river dynamics (Salo *et al.* 1986). However, flooding and drought can also reduce spatial heterogeneity by linking aquatic populations that were separated in different water bodies during the low-water period (*vice versa*, isolated terrestrial populations during a flooding period can mix genetically during drought). Similarly, the permanent drift of organisms from the catchment or upriver areas inoculates the riverine or near-river populations regularly and thus hinders the development of genetically distinct populations.

Connectivity between the main channel and the floodplain habitat has become a central theme in the biodiversity debate (Ward, Tockner and Schiemer 1999; Wantzen and Junk 2000; Amoros and Bornette 2002). Lateral connectivity has been suggested to determine the diversity patterns of many taxonomic groups directly (Tockner *et al.* 1999). Flood-pulsing systems encounter variable degrees and spatiotemporal patterns of connectivity. Therefore, the diversity of hydrological patterns is a key element for the maintenance of habitat and species diversity in river-floodplain systems.

Biogeochemical cycles

According to the FPC, river floodplains can be considered as biogeochemical reactors that temporarily store and process organic and inorganic matter. The flood pulse exerts hydraulic forces that erode, carry and deposit these substances. Long-term storage favors *in situ* alteration, weathering and liberation of dissolved substances, as shown for an Amazonian Várzea lake (Weber, Furch and Junk 1996; Irion, Junk and de Mello 1997). The water level fluctuations provoke changes in water chemistry by mixing water bodies and resource input during the rising limb of the hydrograph and by increasing stratification, oxygen consumption and concentration of ions in the restricted water bodies during the falling limb. In floodplains that widely dry out periodically, like the Pantanal, a large part of the organic matter is turned over during the change of the hydrological phases.

Periodic flooding and drought of sediments leads to sequential occurrence of different redox processes. For example, organisms like cyanobacteria and legumes fix atmospheric nitrogen, but the change between anoxic and oxic conditions during the water-land transition and the availability of large amounts of organic material favor denitrification (Kern, Darwich, Furch, *et al.* 1996; Kern and Darwich 1997). Wassmann and Martius (1997) estimate the methane production of the Amazon River floodplain at 1-9 Tg CH_4 yr^{-1}, corresponding to 1-8 percent of the global source strength of wetlands. High primary production leads to considerable pulses in carbon dioxide uptake and release, but also to carbon storage in the sediment and carbon export to the oceans. About 10^{14} g of organic carbon is annually transported by the Amazon River to the Atlantic Ocean (Ritchey *et al.* 1980). A considerable part of it may derive from the floodplain (Junk 1985).

Junk (1980) points to an underestimate of the total wetland area in tropical South America because small wetlands are often not considered in inventories, although they might comprise about 50 percent of the total wetland area, most of them floodplains. This might also hold true to some extent for other tropical and subtropical regions. We hypothesize that these small floodplains and temporary wetlands also follow the predictions of the FPC. Mapping of these areas and inclusion of their impact on the budgets of biogeochemical cycles and the hydrological cycle and for maintenance of biodiversity are challenges for the future.

Sustainable management and restoration of river floodplains

River floodplains have provided multiple benefits since early human settlement. Predictable floods favored the management of floodplain resources and the development of ancient cultures, for example, on the Euphrates and Tigris Rivers and the Nile River several thousand years ago. Pre-Columbian human density in the floodplain of the Amazon River was several times higher than that in the adjacent upland. Rice cultivation started in China about 7000 years ago (Boulé 1994) and continues to be the nutritional basis for much of the human population worldwide.

The economic value of floodplains for buffering extreme hydrological events has been underestimated for a long time. A dramatically increasing human population during the last two centuries led to large-scale floodplain destruction and deterioration worldwide (Junk 2002, Tockner and Stanford 2002). In the past, large flood events led to heavy losses of goods and humans in Europe and brought about major flood control measures, such as the "correction" of the Rhine River by Tulla in the nineteenth century (Friedrich and Mueller 1984). The 500-year-old European tradition in river regulation (Nienhuis *et al.* 1998) was first transferred to North America and later applied worldwide. Only some decades ago did the negative ecological, economic and social side effects of floodplain destruction become apparent, as recently shown by the catastrophic floods along the Odra, Elbe, Rhine and Danube Rivers in 2001 and 2002 in Poland, the Czech Republic, Germany and Austria.

Management plans are required for the sustainable use of floodplain resources. The FPC provides general outlines that can be used for the development of management strategies; however, considering regional differences in the status of floodplain integrity, watershed management and demographic and economic development, there is a need for specific strategies for each floodplain and even for different stretches of large river floodplains. For instance, the importance of floodplains for protein supply by fisheries is low in most Central European rivers; however, in most tropical countries, floodplain fishery provides accessible animal protein for millions of people and is one of the most important economic activities (Welcomme 1985).

Knowledge on wetland restoration has been increasing rapidly for several decades and ambitious restoration projects are being undertaken in North America and Europe (Mitsch and Jørgensen 2003). Some restoration projects have also been started in the tropics. These projects are excellent means of validating predictions of the FPC, as shown by Heiler *et al.* (1995) for the Danube River. Creating and maintaining natural variation of the pulsing hydrograph and the ability of the landscape to develop a dynamic floodplain appear to be the most important elements for conservation and restoration concepts (Sparks *et al.* 1990, 1998; Tockner *et al.* 1999).

CONCLUSIONS

Most freshwater systems are subjected to fluctuations in water levels. All systems that are not steeply bordered by mountains, dykes, or regulating channels are fringed with floodable areas. Flooding is controlled by climate type (catchment rainfall patterns and evapotranspiration), landscape morphology (declivity and connectivity) and local effects (log jams, tributary inflows, recent local precipitation). With the knowledge of these variables, inundation-duration curves can be plotted, as for instance, for a US coastal plain river (Benke *et al.* 2000), for a small alpine river (Arscott *et al.* 2000) and for the Pantanal wetland (Hamilton *et al.* 1996). This general pattern makes the central tenet of the FPC - that hydrological pulsing is the driving force for the performance of organisms and for patterns of ecological processes - a unifying theme in limnological conceptualization.

Today, 17 years after its first presentation, the FPC is widely accepted and applied by most river ecologists. It provides a conceptual framework for both research and management in river-floodplain systems. Several researchers have refined its tenets. Even in upstream areas, unpredictable flood pulses can be profitable for the stream community (Wantzen and Junk 2000), but this does not seem to be the case for regulated large rivers (Thorp *et al.* 1998). The characteristics of the pulse shape are crucial for the establishment and survival of many aquatic organisms (Welcomme and Halls 2001; Wagner and Schmidt, unpublished manuscript). Flood pulses homogenize water quality and habitat structure of formerly isolated water bodies (Marchese and Escurra de Drago 1992; Heckman 1994; Tockner *et al.* 2000). It has also become clear that there is no "either/or" distribution between productivity in the catchment, the river channel and the floodplain, but rather a variable combination of these three sources for the food webs of the river-floodplain continuum (Figure 3).

Recent studies have shown that predictions of the FPC on the development of adaptations and survival strategies of organisms have to be adjusted by additional information on paleoclimatological history (Adis and Junk 2002). The interaction of the flood pulse with other environmental variables, such as the light/temperature pulse, snow melting and prolonged ice cover in high-latitude floodplain systems and rainy and dry seasons in arid regions, is not sufficiently understood (Humphries *et al.* 1999). Also, the impacts of short- and long-term changes of the quality of the flood pulse on life history of organisms, communities and biogeochemical processes require additional studies. The FPC also makes predictions about organisms and processes during the terrestrial phase at low water periods (Adis and Junk 2002; Parolin *et al.* in prep) that require additional studies. New techniques, such as stable isotope determination, remote sensing, genetic tests and techniques for wetland restoration and management provide powerful tools to test and refine the FPC further.

ACKNOWLEDGEMENTS

We thank Rüdiger Wagner (MPIL-Schlitz) for discussions on the “phenological and physiological window of susceptibility”, Sabine Meier for editing the manuscript, Elke Bustorf for graphic design and Karen A. Brune for correction of the English. This paper is dedicated to the memory of Professor Jürgen Schwoerbel (1927-2002), one of the pioneers in modern running-water ecology.

REFERENCES

Ab’Saber A.N. 1988. O Pantanal Mato Grossense e a teoria dos refugios. *Revista Brasileira de Geographia,* 50: 9-57

Adis J. 1984. Seasonal Igapo-forests of Central Amazonian blackwater rivers and their terrestrial arthropod fauna. *In The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin*. pp. 245-268, Dordrecht, W. Junk Publishers.

Adis J. & Junk W.J. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: A review. *Freshwater Biology*, 47: 711-731.

Adis J., Marques M.I., Wantzen K.M. 2001. First observations on the survival strategies of terricolous arthropods in the northern Pantanal wetland of Brazil - scientific note. *Andrias*, 15: 127-128.

Agostinho A.A., Gomes, L.C. & Zalewski M. 2001. The importance of floodplains for the dynamics of fish communities of the upper river Paraná. *Ecohydrology & Hydrobiology*, 1: 209-217.

Agosthinho A.A., Thomaz S.M., Minte-Vera C.V. & Winemiller K.O. 2000. Biodiversity in the high Paraná River floodplain. *In* B. Gopal, W.J. Junk & J.A. Davis eds. *Wetlands Biodiversity*. pp. 89-118. Leiden, The Netherlands, Backhuys Publishers.

Amoros C. & Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47: 761-776.

Amoros C. & Roux A.L. 1988. Interaction between water bodies within the floodplains of large rivers: Function and development of connectivity. *Münstersche Geographische Arbeiten*, 29: 125-130.

Arscott D.B., Tockner K. & Ward J.V. 2000. Aquatic habitat diversity along the corridor of an Alpine floodplain river Fiume Tagliamento, Italy. *Archiv für Hydrobiologie*, 149: 679-704.

Bayley P.B. 1980. The limits of limnological theory and approaches as applied to river-floodplain systems and their fish production. *Tropical Ecology & Development*, 739-746.

Bayley P.B. 1991. The flood-pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers: Research & Management*, 6: 75-86.

Benke A.C., Chaubey I., Ward G.M. & Dunn, E.L. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern US coastal plain. *Ecology*, 81: 2730-2741.

Boulé M.E. 1994. An early history of wetland ecology. *In Global wetlands: Old world and new*. pp. 57-74.

Braum E. & Junk W.J. 1982. Morphological adaptation of two Amazonian characoids Pisces for surviving in oxygen deficient waters. *Int. Revue. Ges. Hydrobiol.*, 67: 869-886.

Bretschko G. & Leichtfried M. 1988. Distribution of organic matter and fauna in a second order, alpine gravel stream Ritrodat-Lunz study area, Austria. *Verh. Int. Verein. Limnol.*, 23: 1333-1339.

Clark J.R. & Benforado J. 1981. Wetland of bottomland hardwood forest. *Dev. Agric. Managed-Forest Ecol.* 11: Amsterdam, Oxford, New York, Elsevier Scientific Publishing Company.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302-1309.

Cummins K.W., Sedell J.R., Swanson F.J., Minshall S.G., Fisher S.G., Cushing C.E., Petersen R.C. & Vannote R.L. 1983. Organic matter budgets for stream ecosystems: Problems in their evaluation. *In* J.R. Barnes & G.W. Minshall eds. *Stream ecology: Application and testing of general ecological theory.* New York, Plenum Press. pp. 299-353.

Da Silva C.J., Wantzen K.M., Nunes da Cunha C. & Machado F.A. 2001. Biodiversity in the Pantanal Wetland, Brazil. *In Biodiversity in wetlands: Assessment, function and conservation, Volume 2*. pp. 187-215. Leiden, The Netherlands, Backhuys Publishers.

De Oliveira M.D. & Calheiros D.F. 2000. Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil. *Hydrobiologia*, 427: 101-112.

De Lamônica-Freire E. & Heckman C.W. 1996. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic Zone III: The algal communities in the Pantanal of Mato Grosso, Brazil, with a comprehensive list of the known species and revision of two desmid taxa. *Int. Rev. Ges. Hydrobiol.*, 81: 253-280.

Delong M.D., Thorp J.H., Greenwood K.S. & Miller M.C. 2001. Responses of consumers and food resources to a high magnitude, unpredicted flood in the upper Mississippi River Basin. *Regulated Rivers: Research & Management*, 17: 217-234.

Dettmers J.M., Wahl D.H., Soluk D.A. & Gutreuter S. 2001. Life in the fast lane: Fish and foodweb structure in the main channel of large rivers. *Journal of the North American Benthological Society*, 20: 255-265.

Dudgeon D. 2000. The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Review of Ecology and Systematics*, 31: 239-263.

Dynesius M. & Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern 3rd of the world. *Science*, 266: 753-762.

Elwood J.W., Newbold J.D., O'Neill R.V. & van Winkle W. 1983. Resource spiralling: An opearational paradigm for analyzing lotic systems. *In T.D.* Fontaine III & S.M. Bartell eds. *Dynamics of lotic ecosystems*. Ann Arbor, MI, USA, Ann Arbor Science Publishers. pp. 3-27.

Fisher T.R. & Parsley P.E. 1979. Amazon lakes: Water storage and nutrient stripping. *Limnol. Oceanogr*. L 24: 547-553.

Fredrickson L.H. & Reid F.A. 1988. *Waterfowl use of wetland complexes. U.S. Fish Wildlife Leaflet 13.2.1*. 6 pp.

Friedrich G. & Mueller D. 1984. Rhine West Germany. *In Ecology of European Rivers*. pp. 265-316. , Palo Alto, CA, USA, Blackwell Scientific Publications.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management*, 10: 199-214.

Furch K. 1984. Interannuelle variation hydrochemischer parameter auf der Ilha de Marchantaria. *Biogeographica*, 19: 85-100.

Galat D.L. & Zweimuller I. 2001. Conserving large-river fishes: Is the highway analogy an appropriate paradigm? *Journal of the North American Benthological Society*, 20: 266-279.

Gopal B. & Junk W.J. 2000. Biodiversity in wetlands: An introduction. *In Biodiversity in Wetlands: Assessment, function and conservation, Volume 1*. pp. 1-10. Leiden, The Netherlands, Backhuys Publishers.

Gopal B., Junk W.J. & Davies J.A. 2000. *Biodiversity in wetlands: Assessment, function and conservation, volume 1*. 353 pp. Leiden, The Netherlands, Backhuys Publishers.

Gopal B., Junk W.J. & Davies J.A. 2001. *Biodiversity in Wetlands: assessment, function and conservation, volume 2*. 311 pp. Leiden, The Netherlands, Backhuys Publishers.

Gutreuter S., Bartels A.D., Irons K. & Sandheinrich M.B. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2282-2291.

Haffer J. & Prance G.T. 2001. Climatic forcing of evolution in Amazonia during the Cenozoic: On the refuge theory of biotic differentiation. A*mazoniana*, XVI3/4: 579-607.

Hamilton S.K., Sippel S.J. & Melack J.M. 1996. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. *Arch. Hydrobiol*., 137: 1-23.

Hamilton S.K., Sippel S.J., Calheiros D.F. & Melack, J.M. 1997. An anoxic event and other biogeochemical effects of the Pantanal wetland on the Paraguay River. *Limnol. Oceanogr.*, 42: 257-272.

Heckman C.W. 1994. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone I: Physical and chemical causes and biological effects in the Pantanal of Mato Grosso, Brazil. *Int. Revue. Ges. Hydrobiol.*, 79: 397-421.

Heckman C.W. 1998. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: V aquatic invertebrate communities in the Pantanal of Mato Grosso, Brazil. *Int. Revue. Ges. Hydrobiol.*, 83: 31-63.

Heiler G., Hein T., Schiemer F. & Bornette G. 1995. Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. *Regulated Rivers: Research & Management*, 11: 351-361.

Hobbie J.E. & Likens G.E. 1973. The output of phosphorous, dissolved organic carbon, and fine particulate carbon from Hubbard Brook watersheds. *Limnol. Oceanogr.*, 18: 734-742.

Humphries P., King A.J. & Koehn J.D. 1999. Fish, flows and flood plains: Links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes*, 56: 129-151.

Illies J. 1961a. Versuch einer allgemeinen biozönotischen Gliederung der Fließgewässer. *Int. Revue Ges. Hydrobiol.*, 462: 205-213

Illies J. 1961b. Gebirgsbäche in Europa und in Südamerika - ein limnologischer Vergleich. *Verh. Internat. Verein. Limnol.*, 14: 517-523

Illies J. & Botosaneanu L. 1963. Problemes et methodes de la classification et de la zonation ecologiques des eaux courantes, consideres surtout du point de vue faunistique. *Mitt. Internat. Verein. Limnol.*, 12: 1-57.

IPCC 2001. *Technical summary, and summary for policy-makers. Third Assessment Report of Working Group I of the Intergovernmental Panel on Climatic Change.* (Available at http://www.ipcc.ch)

Irion G., Junk W.J. & de Mello J.A.S.N. 1997. The large central Amazonian river floodplains near Manaus: Geological, climatological, hydrological, and geomorphological aspects. pp. 23-46. *In* Junk W.J. ed. *The Central Amazon Floodplain - Ecology of a Pulsing System*. Springer Verlag, Berlin.

Irmler U. 1981. Überlebensstrategien von Tieren im saisonal überfluteten Amazonischen Überschwemmungswald. *Zool. Anz. Jena.*, 2061/2: 26.38.

Isaac V.J., Ruffino M.L. & McGrath D. 1998. In search of a new approach to fisheries management in the middle Amazon. *In* T.J. Quinn II, F. Funk, J. Heifetz, J. Ianelli, J. Power, J. Schweigert, P. Sullivan & C.I. Zhang eds. *Fishery stock assessment model*. pp. 889-902. AL, USA, Faibanks, Alaska Sea Grant College Program University of Alaska, As-SG-98-01.

Junk W.J. 1980. Áreas inundáveis - um desafio para limnologia. *Acta Amazonica*, 104: 775-795.

Junk W.J. 1985. The Amazon floodplain - a sink or source for organic carbon? *Mitt. Geol. Paläont. Inst. Univ. Hamburg*.

Junk W.J. 1989. Flood tolerance and tree distribution in central Amazonian floodplains. *In* L. B. Holm-Nielsen, I.C. Nielsen & H. Balslev eds. Tropical forests: Botanical dynamics, speciation and diversity. 47-64. London, Academic Press.

Junk W.J. 1999. The flood pulse concept of large rivers: Learning from the tropics. *Arch. Hydrobiol. Suppl.*, 1153: 261-280.

Junk W.J. 2000. The central Amazon River floodplain: Concepts for the sustainable use of its resources. *In* W.J. Junk, J.J. Ohly, M.T.F. Piedade & M.G.M. Soares eds. *The Central Amazon floodplain: Actual use and options for sustainable management*. pp. 75-94. Leiden, The Netherlands, Backhuys Publishers.

Junk W.J. 2002. Long-term environmental trends and the future of tropical wetlands. *Environmental Conservation*, 294. (forthcoming)

Junk W.J. & Piedade M.T.F. 1997. Plant life in the floodplain with special reference to herbaceous plants. *In* W.J. Junk ed. *The Central Amazon floodplain: Ecology of a pulsing system*. pp. 147-186. Berlin, Springer Verlag.

Junk W.J. & Weber G.E. 1996. Amazonian floodplains: A limnological perspective. *Verh. Internat. Verein. Limnol.*, 26: 149-157.

Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.*, 106: 110-127.

Junk W.J., Soares G.M., Carvalho F.M. 1983. Distribution of fish species in a lake of the Amazon River floodplain near Manaus Lago Camelao with special reference to extreme oxgen conditions. *Amazoniana*, 7: 397-431.

Junk W.J., Soares G.M. & Saint-Paul U. 1997. The Fish. *In* W.J. Junk ed. *The Central Amazon Floodplain - ecology of a pulsing system*. pp. 385-408. Berlin, Springer Verlag.

Junk W.J., Ohly J.J., Piedade M.T.F. & Soares M.G.M. 2000. *The Central Amazon floodplain: Actual use and options for sustainable management*. Leiden, The Netherlands, Backhuys Publishers. 584 pp.

Kern J. & Darwich A. 1997. Nitrogen turnover in the várzea. *In* Junk W.J. ed. *The Central Amazon floodplain - ecology of a pulsing system*, 119-136. , Berlin, Springer Varlag.

Kern J., Darwich A., Furch K. & Junk W.J. 1996. Seasonal denitrification in flooded and exposed sediments from the amazon floodplain at Lago Camalão. *Microbial Ecology*, 32: 47-57.

Knowlton M.F. & Jones J.R. 1997. Trophic status of Missouri River floodplain lakes in relation to basin type and connectivity. *Wetlands*, 17: 468-475.

Lae R. 1994. Effects of drought, dams, and fishing pressure on the fisheries of the central delta of the Niger River. *International Journal of Ecology and Environmental Sciences*, 20: 119-128.

Lewis W.M. Jr. 1988. Primary production in the Orinoco River Venezuela. *Ecology*, 69: 679-692.

Lewis W.M. Jr., Hamilton, S.K., Lasi, M.A., Rodríguez & Saunders M.A. III. 2000. Ecological determinism on the Orinoco floodplain. *BioScience*, 50: 681-692.

Lowe-McConnell R.H. 1975. *Fish communities in tropical freshwaters: Their distribution, ecology and evolution*. London, New York, Longman. 337 pp.

Lowe-McConnel R.H. 1987. *Ecological studies in tropical fish communities*. Cambridge, UK, Cambridge University Press.

Lytle D.A. 2001. Disturbance regimes and life-history evolution. *American Naturalist*, 157: 525-536.

Magrath, M.J.L. 1992. *Waterbird study of the lower Lachlan and Murrumbidgee Valley wetlands in 1990/1991. A report prepared for the NSW Department of Water Resources*.

Marchese M. & Ezcurra de Drago I.E. 1992. Benthos of the lotic environments in the middle Parana River system: Transverse zonation. *Hydrobiologia*, 237: 1-13.

Marchese M., Escurra de Drago I. & Drago E. 2002. Benthic macroinvertebrates and physical habitat relationships in the Paraná river-floodplain system. *In* M. McClain ed. *International Association of Hydrological Sciences. Special publication No.* 6. (forthcoming)

McGrath D., de Castro F., Câmara E. & Futema C. 1999. Community management of floodplain lakes and the sustainable development of Amazonian fisheries. *Advances in Economic Botany*, 13: 59-82.

Melack J.M. & Fisher T.R. 1983. Diel oxygen variations and their ecological implications in Amazon floodplain lakes. *Arch. Hydrobiol.*, 98: 422-442.

Minshall G.W. 1985. Developments in stream ecosystem theory. *Journal of Fisheries and Aquatic Science*, 42: 1045-1055.

Mitsch W.J. & Gosselink J.G. 2000. *Wetlands*. New York, USA, John Wiley & Sons.

Mitsch W.J. & Jørgensen S.E. 2003. *Ecological engineering and ecosystem restoration*. New York, John Wiley & Sons. (forthcoming)

Montgomery D.R. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association*, 35: 397-410.

Müller J., Irion G., Nunes de Mello J. & Junk W.J. 1995. Hydrological changes of the Amazon during the last glacial-interglacial cycle in Central Amazonia Brazil. *Naturwissenschaften*, 82: 232-235.

Naumann E. 1932. *Principles of regional limnology*. Stuttgart, Germany, Schweizerbart Publishers. 149 pp.

Neiff J.J. 1990. Ideas for an ecological interpretation of the Paraná. *Interciencia*, 156: 424-441

Nienhuis P.H., Leuven, R.S.E.W & Ragas, A.M.J. 1998. *New concepts for sustainable management of river basins*. Leiden, The Netherlands, Backhuys Publishers. 367 pp.

Nunes da Cunha C. & Junk W.J. 2001. Distribution of woody plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. *International Journal of Ecology and Environmental Sciences*, 27: 63-70.

Parolin P., de Simone O., Haase K., Waldhoff D., Rottenberger S., Kuhn V., Kesselmeier J., Schmidt W., Piedade M.T.F. & Junk W.J. Central Amazonian floodplain forests: Tree survival in a pulsing system. (In preparation)

Petermann P. 1999. Biogeographie einer Insel-Avifauna in der Várzea des mittleren Amazonas, am Beispiel der Ilha de Marchantaria. University of Saarland. (Doctoral dissertation)

Petr T. 2000. Interactions between fish and aquatic macrophytes in inland waters: A review. *FAO Fisheries Technical Paper*, 396: 1-185.

Petts G.E. & Amoros C. 1996. *Fluvial hydrosystems*. London, Chapman & Hall. 322 pp.

Pinay G., Decamps, H. & Naiman, R.J. 1999. The spiraling concept and nitrogen cycling in large river floodplain. *Archiv. Für Hydrobiologie*, 143: 281-291.

Poff N.L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Jr. N. Am. Benth. Soc.*, 16: 391-409.

Poff N.L. & Ward J.V. 1989. Implications of streamflow variability and predictability for lotic community structure - a regional-analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 1805-1818.

Poole G.C. 2002. Fluvial landscape ecology: Addressing uniqueness within the river discontinuum. *Freshwater Biology*, 47: 641-660.

Pringle C.M. 2001. River conservation in tropical versus temperate latitudes. *In Global Perspectives on River Conservation: Science, Policy and Practice*. pp. 373-383. New York, John Wiley & Sons Ltd.

Pringle C.M., Naiman R.J., Bretschko G., Karr J.R., Oswood M.W. Webster, J.R., Welcomme R.L. & Winterbourn M.J. 1988. Patch dynamics in lotic systems: The stream as a mosaic. *Jr. N. Am. Benth. Soc.*, 7: 503-524.

Puckridge J.T., Sheldon F., Walker K.F. & Boulton A.J. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, 49: 55-72.

Reid F.R., Kelley J.R. Jr., Taylor T.S. & Fredrickson L.H. 1989. Upper Mississippi Valley wetlands, refuges and moist-soil impoundments. *In* L. Smith, R. Pederson, R. Kaminski eds. *Habitat management for migrating and witering waterfowl in North America*. pp, 181-202. Lubbock TX, USA, Technical University Press.

Resh V.H., Hildrew A.G., Statzner B. & Townsend C.R. 1994. Theoretical habitat templets, species traits and species richness: A synthesis of long-term ecological research on the Upper Rhone River in the context of concurrently developed ecological theory. *Freshwater Biology*, 31: 539-554.

Resh V.H., Brown A.V., Covich A.P., Gurtz L.H.W., Minshall G.W., Reicem S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. 1988. The role of disturbance in stream ecology. *J. N. Am. Benth. Soc.*, 7: 443-455.

Richardson J.E., Pennington R.T., Pennington T.D. & Hollinsworth P.M. 2001. Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science*, 293: 2242-2245.

Richey J.E., Brock J.T., Naiman R.J., Wissmar R.C. & Stallard R.F. 1980. Organic carbon: Oxidation and transport in the Amazon River. *Science*, 207: 1348-1351.

Richter B.D., Baumgartner J.V., Powell J. & Braun D.P. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, 10: 1163-1174.

Robertson A.I, Bunn S.E., Boon P. & Walker K.F. 1999. Sources, sinks and transformations of organic carbon in Australian floodplain rivers. *Marine & Freshwater Research*, 50: 813-829.

Rood S.B. & Mahoney J.M. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environ. Manage.*, 14: 451-464.

Sabo M.J., Bryan C.F., Kelso W.E. & Rutherford A. 1999a. Hydrology and aquatic habitat characteristics of a riverine swamp: I. Influence of flow on water temperature and chemistry. *Regulated Rivers: Research & Management*, 15: 505-523.

Sabo M.J., Bryan C.F., Kelso W.E. & Rutherford A. 1999b. Hydrology and aquatic habitat characteristics of a riverine swamp: II. Hydrology and the occurrence of chronic hypoxia. *Regulated Rivers: Research & Management*, 15: 525-542.

Salo J., Kalliola R.J., Hakkinen I., Makinen Y., Niemala P., Puhaka M. & Coley P.D. 1986. River dynamics and the diversity of Amazon lowland forest. *Nature*, 322: 254-258.

Schwoerbel J. 1961. Über die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. *Arch. Hydrobiol. Suppl*, 25: 162-214.

Sedell J.R., Richey J.E., Swanson F.J. 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers? *Can. Spec. Publ. Fish. Aquat. Sci.*, 106: 49-55.

Southwood T.R.E. 1977. Habitat: The template for ecological strategies. *Journal of Animal Ecology*, 46: 337-365.

Sparks R.E., Nelson J.C. & Yin Y. 1998. Naturalization of the flood regime in regulated rivers. *BioScience*, 48: 706-720.

Sparks R.E., Bayley P.B., Kohlert S.L., Osborne L.L. 1990. Disturbance and recovery of large floodplain rivers. *Environmental Management*, 14: 699-709.

Stanford A. & Ward J.V. 1988. The hyporheic habitat of river ecosystems. *Nature*, 335: 64-66.

Statzner, B. & Higler B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology*, 16: 127-139.

Thienemann A. 1925. Die Binnengewässer Mitteleuropas. *Die Binnengewässer* 1. , Stuttgart, Germany, Schweizerbart Publishers.

Thorp J.H. & Delong M.D. 1994. The riverine productivity model: An heuristic view of carbon sources and organic-processing in large river ecosystems. *Oikos*, 70: 305-308.

Thorp J.H., Delong M.D., Greenwood K.S. & Casper A.F. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia*, 117: 551-563.

Tockner K. & Stanford J.A. 2002. Riverine flood plains: Present state and future trends. *Environmental Conservation*, 293: 308-330.

Tockner K., Malard F. & Ward J.V. 2000. An extension of the flood pulse concept. *Hydrological Processes*, 14: 2861-2883.

Tockner K., Schiemer F., Baumgartner C., Kum G., Weigand E., Zweimuller, I. & Ward, J.V. 1999. The Danube restoration project: Species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers: Research & Management*, 15: 245-258.

Townsend C.R. 1989. The patch dynamics concept of stream community ecology. *Jr. N. Am. Bentho. Soc.*, 8: 36-50.

Townsend C.R. 1996. Concepts in river ecology: Pattern and process in the catchment hierarchy. *Archiv für Hydrobiologie Supplementband*, 113 1-4: 3-21.

Townsend C.R. & Hildrew A.G. 1994. Species traits in relation to a habitat templet for river system. *Freshwater Biology*, 31: 265-275.

Triska F.J., Duff J.H. & Avanzino R. 1993. Patterns of hydrological exchange and nutrient transformation in the hyporheic zone of a gravel-bottom stream: Examining terrestrial-aquatic linkages. *Freshwater Biology*, 29: 259-274.

Van den Brink F.W.B., Beljaards M.J., Botts N.C.A. & van der Velde G. 1994. Macrozoobenthos abundance and community composition in 3 Lower Rhine floodplain lakes with varying inundation regimes. *Regulated Rivers: Research & Management*, 9: 279-293.

Van den Brink F.W.B., de Leeuw J.P.H.M., van der Velde G. & Verheggen G.M. 1993. Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the Lower Rhine and Meuse. *Biogeochemistry Dordrecht*, 19: 103-128.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell K.W., Cushing C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.*, 37: 130-137.

Vörösmarty C.J. 2002. Global water assessment and potential contributions from Earth Systems Science. *Aquatic Sciences*, 64: 328-351.

Wantzen K.M. & Junk W.J. 2000. The importance of stream-wetland-systems for biodiversity: A tropical perspective. *In* B. Gopal, W.J. Junk & J.A. Davies eds. *Biodiversity in Wetlands: Assessment, function and conservation*, 11-34, Leiden, The Netherlands, Backhuys Publishers.

Wantzen K.M., Machado F.A., Voss M., Boriss H. & Junk W.J. 2002. Seasonal isotopic changes in fish of the Pantanal wetland, Brazil. *Aquatic Sciences*, 64: 239-251.

Ward J.V. 1989. The four-dimensional nature of lotic ecosystems. *Jr. N. Am. Bentho. Soc.*, 8: 2-8.

Ward J.W. & Stanford J.A. 1983a. The serial discontinuity concept of lotic ecosystems. *In* T.D. Fontaine III & S.M. Bartell eds. *Dynamics of lotic ecosystems*, Ann Arbor, MI, USA, Ann Arbor Science Publishing. pp. 29-42.

Ward J.V. & Stanford J.V. 1983b.The intermediate-disturbance hypothesis: An explanation for biotic diversity patterns in lotic ecosystems. *In* T.D. Fontaine III & S.M. Bartell eds. *Dynamics of lotic ecosystems*, Ann Arbor, MI, USA, Ann Arbor Science Publishing. pp. 347-356.

Ward J.V. & Stanford J.A. 1995. The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research & Management*, 11: 105-119.

Ward J.V., Malard F. & Tockner K. 2001. Landscape ecology: A framework for integrating pattern and process in river corridors. *Landscape Ecology*, 17: 35-45.

Ward J.V., Tockner K. & Schiemer F. 1999. Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers: Research & Management*, 15: 125-139.

Wassmann R. & Martius C. 1997. Methane emissions from the Amazon floodplain. *In* W.J. Junk ed. *The Central Amazon Floodplain - Ecology of a Pulsing System*. pp. 137-143. Berlin, Springer-Verlag.

Weber G.E., Furch K. & Junk W.J. 1996. A simple modelling approach towards hydrochemical seasonality of major cations in a Central Amazonian floodplain lake. *Ecological Modelling*, 91: 29-56.

Welcomme R.L. 1979. *Fisheries ecology of floodplain rivers.* London, Longman. 317 pp.

Welcomme R.L. 1985. *River fisheries.*, FAO Fisheries Technical Paper 262. Rome, Food and Agricultural Organization of the United Nations. 330 pp.

Welcomme R.L. & Halls A. 2001. Some considerations of the effects of differences in flood patterns on fish populations. *Ecohydrology and Hydrobiology*, 13: 313-321

Williams D.D. 1989. Towards a biological and chemical definition of the hyporheic zone in two Canadian rivers. *Freshwat. Biol.*, 22: 189-208.

Winemiller K.O. 1989. Patterns of variation in life-history among South American fishes in seasonal environments. *Oecologia*, 81: 225-241.

Winterbourn M.J., Rounick, J.S. & Cowie, B. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research*, 15, 321-328.

Wittmann F. 2002. Species distribution, community structure, and adaptations of Amazonian várzea forests depending on the annual flood-stress, using remote sensing methods. University of Mannheim. (Doctoral dissertation)

A STRATEGY TO REHABILITATE NATIVE FISH IN THE MURRAY-DARLING BASIN, SOUTH-EASTERN AUSTRALIA

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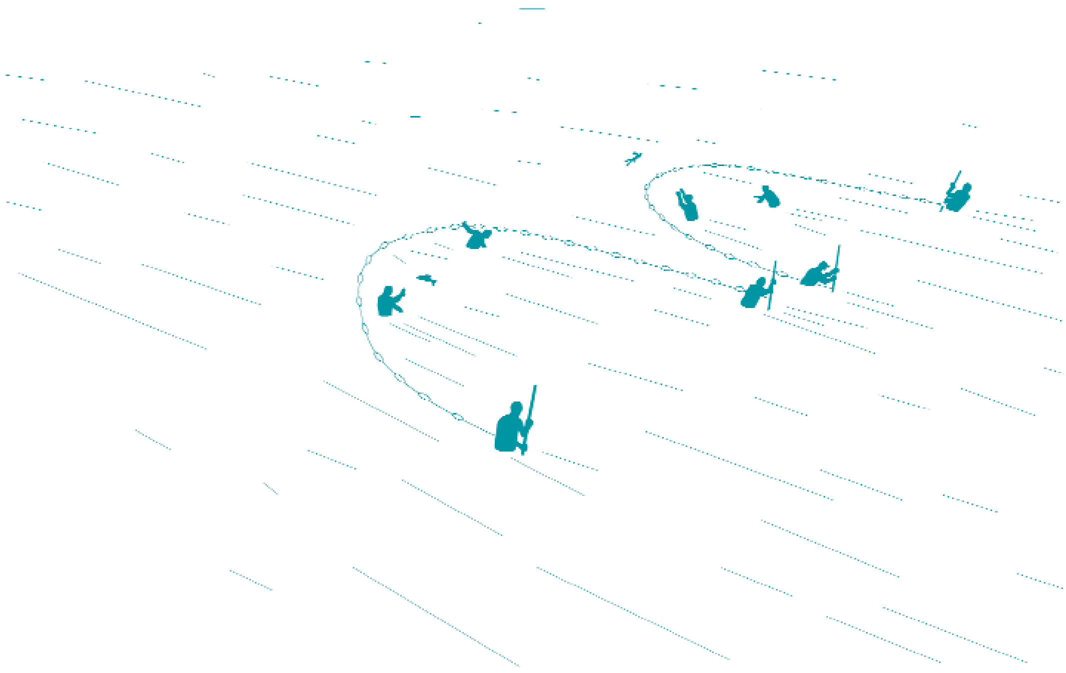


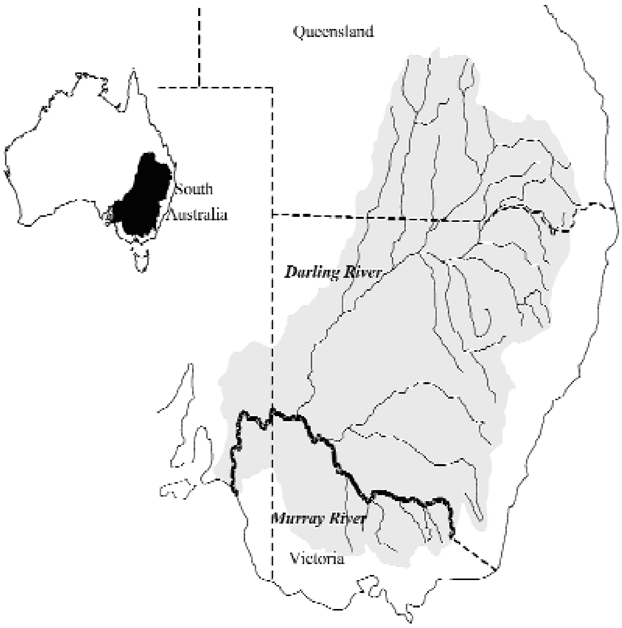
ABSTRACT

The Native Fish Strategy for the Murray-Darling Basin is a substantial shift in the restoration and conservation of native fish in Australia. It engages community ownership in the restoration of fish populations in large river systems that cross jurisdictional boundaries. The strategy is long-term (50 years) but operates as a series of 10-year 'working documents'. It introduces a management structure, which includes a scientific reference committee and a community advisory committee that includes representatives of many stakeholders groups, including indigenous peoples. The Murray-Darling is one of the world's largest catchments, covering more than 1 million km^2 and one seventh of the Australian landmass. This system flows over 2 500 km from source

to the sea and produces agricultural produce to the value of $Aus 1 billion each year. The basin crosses the boundaries of four states and together with the Commonwealth encompasses five legislative and many governmental jurisdictions. The natural ecological functioning of the Murray-Darling rivers is at risk. Native fish communities are only 10 percent of those prior to European settlement. Eight of the 35 native fish species are nationally threatened and 16 species are listed as threatened regionally. Eleven alien species of fish are now present and comprise 95.6 percent of the total catch in the Murray River region. Commercial fisheries are no longer viable and the recreational fishery has substantially declined. Without intervention the levels of native fish populations in the basin are expected to fall in the coming 40 to 50 years. The Native Fish Strategy seeks to rehabilitate fish populations to 60 percent of their estimated pre-European settlement levels after 50 years. Native fish management in the past has generally been single issue dominated and has been undertaken on an individual state-by-state basis. This new strategy is ecosystem based and uses on–ground management, not only to improve the status of native fish populations in the basin but also to increase understanding of the system. Factors contributiong to the deterioration of native fish populations and fish habitats include: flow regulation, habitat degradation, lowered water quality, man-made barriers to fish movement, the introduction of alien fish species, fisheries exploitation, the spread of diseases and translocation and stocking of fish. The Strategy delivers specific goals and targets through a series of strategic actions that involve government agencies, regional catchment organisations and a wide range of community groups.

INTRODUCTION

The Murray-Darling Basin is one of the world's largest catchments, covering more than 1 million km^2 and one seventh of the Australian landmass (Figure 1). This river system flows over 2 500 km from source to the sea and produces agricultural produce to the value of $Aus 1 billion each year. The basin crosses the boundaries of four states and a territory and together with the Commonwealth encompasses six legislative and many governmental departmental jurisdictions. Whilst water use has been coordinated across jurisdictions through the Murray-Darling Basin Commission (MDBC), native fish management has generally been single issue dominated and undertaken on an individual state-by-state basis. The draft *Native Fish Strategy* (Murray-Darling Basin Commission (MDBC) 2002) addresses this lack of coordination with its implementation facilitated by the MDBC. It is ecosystem based with a fundamental approach that uses on-ground management not only to improve the status of native fish in the Basin but also to increase our systems understanding. This Strategy has fish as its focus, rather than being an added component to other strategies (e.g. wetlands, salinity) and is a commitment between all jurisdictions to addressing their problems.



■ **Figure 1.** Map of the Murray-Darling Basin, southeastern Australia.

THE NEED FOR ACTION

The health of populations and communities of native fish species in the Murray-Darling Basin is an indicator of the overall health of the basin and its rivers (Harris 1995). If there is a decline in the native fish communities, this provides a warning that the natural ecological functioning of the rivers is at risk. The current poor status of native fish populations in the Murray-Darling Basin is alarming, with several indicators demonstrating the urgency of the current situation:

- Localised extinction of some native fish species (see Cadwallader and Gooley 1984);

- Threats to other species: eight of the 35 native fish species in the basin are nationally 'threatened' (Australian Society of Fish Biology 2001) and at least two are 'critically endangered'; 16 species are listed as threatened under state jurisdictions;

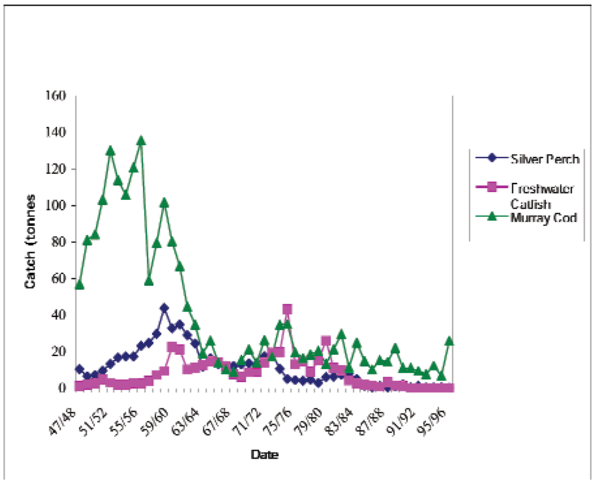
- Rapid decline in the conservation status of 'flagship' species such as silver perch *Bidyanus bidyanus* (Mitchell), freshwater catfish *Tandanus tandanus* (Mitchell) and Murray cod *Maccullochella peelii peelii* (Mitchell) across the basin (Cadwallader and Gooley 1984; Clunie and Koehn 2001a, 2001b);

- Presence of 11 alien species of fish that now make up a quarter of the basin's total fish species – carp *Cyprinus carpio* (L.) now make up an estimated 60 to 90 percent of the total fish biomass at many sites, with densities as high as one carp per square metre of river surface area (Harris and Gehrke 1997);

- Presence of two native fish species that are not native to the basin rivers (broad-finned galaxias *Galaxias brevipinnis* Gunther and spotted galaxias *Galaxias truttaceus* Valenciennes (Waters, Shirley and Closs 2002; P. Humphries, pers comm.);

- Loss of most commercial fisheries (Reid, Harris and Chapman 1997) (Figure 2); and

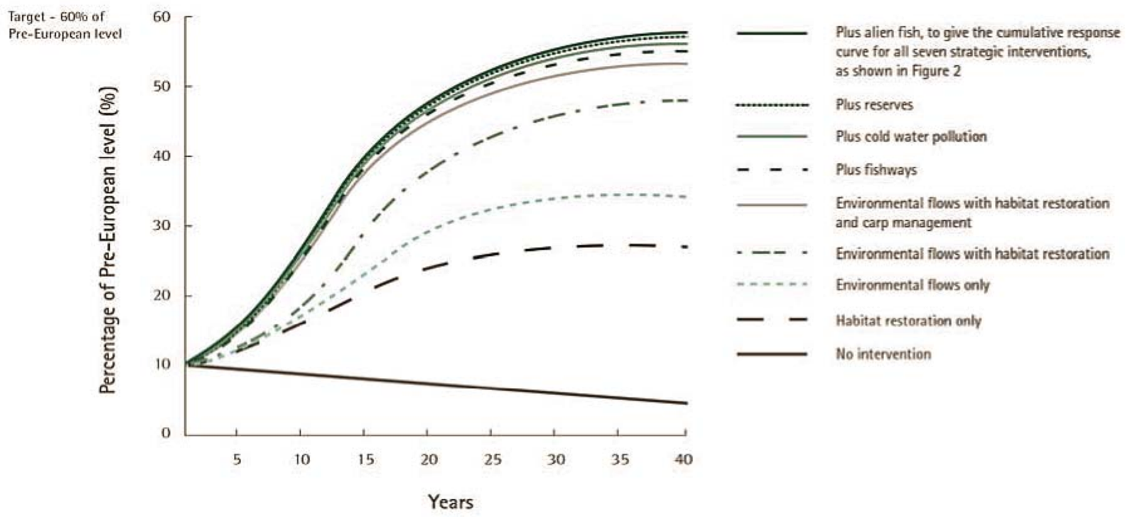
- Observed declines in recreational angling success – native fish species make up just 4.4 percent of the total catch in the Murray River region (Harris and Gehrke 1997).



■ Figure 2. Declines in catches per unit effort of the Murray cod, silver perch and freshwater catfish in New South Wales between 1947 and 1996 (data source: Reid *et al*. 1997).

If native fish in the Murray-Darling basin are to be rehabilitated to ensure viable populations, urgent action is needed to remediate existing threats. Actions must be coordinated and consistent across state boundaries. They need to build upon the knowledge gained through past research and management to rehabilitate fish habitats and to protect existing viable populations. Emphasis needs to be placed on rehabilitation rather than maintaining the status quo that would inevitably result in continuing declines and loss of species (Figure 3). As declines have taken place over many years, so must rehabilitation be undertaken over a similar timeframe – fifty or more years. The level of rehabilitation required to reverse declines will vary with species, communities and areas and should be assessed over the medium and longer terms.

A panel of fish experts has estimated that native fish populations within the Murray-Darling basin are currently at about 10 percent of their pre-European settlement levels (Figure 3). Without any intervention this is likely to fall to 5 percent over the next 40 to 50



■ **Figure 3.** Cumulative impact curves of actions to rehabilitate native fish communities in the Murray-Darling Basin as determined by an expert panel.

years. This panel believed that if only one strategic intervention were to occur, such as allocation of environmental flows, this may help to recover native fish populations to about 25 percent of their estimated pre-European settlement levels. They agreed that the actions detailed in the Strategy must be undertaken in an integrated way if they are to be effective. If undertaken singularly, the capacity of these interventions to recover the native fish populations of the basin beyond 25 percent of their pre-European level is questionable. The actions will also assist (at least in part) with the restoration of listed threatened fish and fish communities. Greater resourcing for developing a system of aquatic reserves and managing other alien fish species will also ensure a greater level of success with this approach.

A STRATEGIC APPROACH TO ACTION

The vision of this Native Fish Strategy is that the Murray-Darling basin sustains viable fish populations and communities throughout its rivers. The overall goal of this Strategy is to rehabilitate native fish communities in the Murray-Darling Basin back to 60 percent or better of their estimated pre-European settlement levels after 50 years of implementation. This means rehabilitating aquatic habitats and ecological processes in the Murray-Darling basin through management actions designed to restore healthy native fish communities. The improved status of native fish populations in the Murray-Darling basin will be the key criterion by which the public will judge the success of this Strategy.

This Strategy targets the causes as well as the symptoms of declining native fish species and focuses on long-term rehabilitation rather than restoration. As part of the *Integrated Catchment Management Policy Statement* for the basin (MDBC 2001), this Strategy provides a framework for improved management of native fish in the basin rather than prescribing specific management practices. The framework outlined in this Strategy will evolve with better knowledge and new research outcomes. Inter-state cooperation and coordination of actions and policies is an essential ingredient of the Strategy's framework. While the Strategy provides a 10-year framework, a sustained commitment needs to be maintained for the next 50 years. It provides direction of investment in on-ground fish management activities and associated research and investigations.

STRATEGY OBJECTIVES

The Strategy will address its goal and targets through strategic actions designed to achieve 13 objectives directed at improving the status of native fish populations in the basin. These objectives are to:

1 Repair and protect key components of aquatic and riparian habitats;
2 Rehabilitate the natural functioning of wetlands and floodplain habitats;
3 Improve key aspects of water quality that affect native fish;
4 Modify flow regulation practices;
5 Provide adequate passage for native fish;
6 Devise and implement recovery plans for threatened native fish species;
7 Create and implement management plans for other native fish species and communities;
8 Control and manage alien fish species;
9 Protect native fish from threats of disease and parasites;
10 Manage fisheries in a sustainable manner;
11 Protect native fish from the adverse effects of translocation and stocking;
12 Ensure native fish populations are not threatened from aquaculture; and
13 Ensure community and partner ownership and support for native fish management.

The MDBC has developed a standard for the development of all natural resource management strategies within the basin under its Integrated Catchment Management (ICM) Policy (MDBC 2001). The ICM policy is a commitment by governments and the community of the Murray-Darling basin to do all that needs to be done to manage and use the resources of the Basin in a way that is ecologically sustainable.

The ICM policy is based on setting targets for catchment health and building the capacities of governments and the basin community to achieve these targets (MDBC 2001). The approach will take another ten years to build. It will require substantial government, community and industry leadership and commitment and will significantly test the capacities of everyone to manage the natural resource base for the benefit of present and future generations.

The *Native Fish Strategy* is a work-in-progress and will address the following actions through a costed implementation plan. The implementation plan will be guided by the ICM policy principles related to investment (MDBC 2001):

- The economic, environmental and social benefits of the investment must be greater than the costs;
- Government investment will be used to stimulate private investment and to prevent unacceptable levels of resource degradation;
- Alternative investments will be considered and evaluated;
- Joint-venture partnerships with the community will be the preferred government investment approach; and
- Strong institutional arrangements, knowledge, sound planning and adequate monitoring, evaluation and reporting systems will support on-ground investment.

Implementing the driving actions of this Strategy will require a targeted and sustained effort across governments, catchment management organisations and communities. It is imperative to define the actions and associated responsibilities required within each catchment. This will need to be done in collaboration with government agencies and catchment groups in those catchments.

The prime responsibility for managing rivers falls to state governments. Many of the in-stream interventions needed to improve conditions for fish in rivers will require funding from the states. This will also be the case for any interventions on state-owned land. However, the Commonwealth through its funding programs may supplement state funds for these actions. Where interventions are required on private land, such as stream banks, states may use a number of mechanisms to encourage changes to the way land managers use and manage land and water resources. These mechanisms range from financial incentives through to regulation.

It is recommended that a new, inter-state management and science committee be established by the MDBC to draw all partners and managers together to achieve the Strategy's implementation plan. Implementation of the *Native Fish Strategy* requires a partnership between governments and the wider basin community. Important roles in the implementation of the Strategy will be held by individual landholders, indigenous communities, landcare groups, catchment management organisations, waterway managers, urban and rural community groups, local, State and Commonwealth Government agencies and the MDBC.

The use of targets is a way to measure progress towards achieving the Strategy outcomes. Partners to the Murray-Darling Basin *Initiative* use targets to ensure their own accountability for implementing the Strategy and to give the community confidence that the outcomes of the Strategy will be achieved. Targets will guarantee that all partners can agree on how healthy the native fish populations should be and how to measure trends in native population status, knowing the full costs associated with achieving this. Targets ensure the Strategy remains on track in reaching its long-term objectives for 50 years and beyond.

DRIVING ACTIONS

These 13 objectives identified will be achieved by implementing six key driving actions that include management, research and investigation and community engagement interventions:

- Rehabilitating fish habitat – helping to achieve objectives 1–8;
- Protecting fish habitat – helping to achieve objectives 1–8;
- Managing riverine structures (e.g. weirs and dams) – helping to achieve objectives 4–8;
- Controlling alien fish species – helping to achieve objectives 6–9;
- Protecting threatened native fish species – helping to achieve objectives 6 and 10; and
- Managing fish translocation and stocking – helping to achieve objectives 9–12.

All of the driving actions include a community engagement component designed to achieve objective 13.

MONITORING, EVALUATION AND REVIEW

The implementation of the driving actions will not see an immediate return on investment. While the rehabilitation of fish habitat and the management of riverine structures should result in changes within the next 10 to 15 years to native fish communities, the other driving actions are likely to take considerably longer before benefits become obvious. However, if this investment is delayed it will prove more costly to rehabilitate the basin's native fish communities. It is also important to provide additional knowledge to support the ongoing needs of the Strategy.

About 10 percent of the total budget allocated to implementing this Strategy will be used for monitoring, evaluation and review. This will seek to:

- Report annually against accountability indicators;
- Evaluate at any time the progress in achieving the Strategy's 13 objectives against process and implementation indicators;
- Audit cumulative actions every five years against the overall goals of rehabilitating the abundance and distribution of native fish populations to 60 percent of their estimated pre-European settlement levels; and
- Conduct an overall strategy review after five and ten years.

AUDITING CUMULATIVE ACTIONS AND THEIR IMPACTS ON FISH POPULATIONS

Assessment and monitoring are essential to determine the status of native fish populations and provide knowledge for the development and evaluation of indicators. There is a need to:

- Collate existing baseline data and new data for the establishment of long-term data sets;
- Develop a database/library that can catalogue data/results/outputs from projects;
- Develop a basin-wide fish distribution database;
- Undertake oral history projects, including collection of knowledge from indigenous communities, focusing on fish and fish habitats in an attempt to gain a historical perspective not available from other data sources;

- Assess ongoing condition of fish populations;
- Standardise the collection of data so that comparisons can be made both across the basin and over time;
- Collect scientifically valid data and provide scientific interpretation;
- Consider the timing and cost effectiveness of data collection (for example, it may be better to collect data only annually rather than seasonally, depending on the reason for collection);
- Use data collected by recreational and commercial fishers to assess and monitor fish populations; and
- Ensure data and information is shared with all stakeholders.

It is imperative that the key skills, resources and capacity to undertake monitoring and associated research are identified, developed and maintained across all partners, including the community. Review of the Strategy will involve using resource condition indicators that demonstrate improvement in the sustainability of native fish populations, including:

- major reviews of progress to be undertaken by external referees after five and ten years (specifically, the Strategy should be externally audited in 2007 and 2012); and
- evaluation of the science, objectives and milestones, to provide a better Strategy.

The central question is: Has the Strategy provided a strategic platform for the rehabilitation of native fish populations in the basin?

BEYOND THIS STRATEGY

The life of this Strategy extends to 2012. However, native fish management is a long-term challenge that will extend well beyond that date. As this Strategy is implemented, consideration will be given to the most appropriate framework for native fish management beyond 2012. In 2011, it will be important to finalise development of the 2012–22 Native Fish Strategy to ensure a Basin-wide approach to native fish management into the foreseeable future.

KNOWLEDGE GENERATION AND EXCHANGE

As fish are hidden under water, the general public awareness and understanding of issues relating to them is often less than for more visible and identifiable terrestrial animals. There is a clear need for the community to be educated about native fish, their status, importance and threats to them. A communication strategy will be developed and implemented, focusing on community awareness, consultation and engagement. The use of demonstration reaches where a series of restorative actions can be used to illustrate their value will be created. Prominent and substantial demonstration reaches are useful for integrating all relevant land and water programs into a comprehensive rehabilitation plan that uses the principles of adaptive management. They provide an excellent mechanism for improving public awareness, understanding and support for habitat rehabilitation and the protection of native fish species. In this context this Strategy seeks to:

- Engage the community and stakeholders through a comprehensive communication strategy;
- Initiate relevant scientific research that will provide new knowledge to support management actions in an adaptive context;
- Ensure that the Strategy's actions are monitored and evaluated to measure its success and provide a basis for adaptive management; and
- Demonstrate recovery of native fish through comprehensive rehabilitation of the key factors degrading demonstration river reaches.

Community involvement of this strategy is important. The use of a six-month public consultation period on the draft strategy, combined with a series of public forums in regional centres is evidence of the importance that has been placed on incorporation of the public perspective. The formation of a community advisory group provides an important new component to the management of fish in the Murray-Darling basin. It provides community ownership of actions and priorities and a link to the science underpinning the strategy. Implementation of the Strategy must be underpinned by science, within a framework of adaptive management, which must include the generation of new knowledge.

The *Native Fish Strategy* for the Murray-Darling Basin provides a substantial shift in the restoration and conservation of native fish in Australia. It is a model for engaging community ownership in the restoration of fish populations that could be used in other large river systems around the world with cross-jurisdictional boundaries. The strategy is long-term (50 years) but is structured as a series of 10-year 'working documents'. The Strategy introduces a management structure, which includes a scientific reference committee and a community advisory committee that includes representatives of many stakeholder groups, including indigenous peoples, which have always had strong spiritual and physical connections with the environment.

ACKNOWLEDGMENTS

The authors wish to thank Brian Lawrence and Jim Barrett from the Murray-Darling Basin Commission who funded and supported this document. Thanks to the expert panel of Mike Braysher, John Harris, Terry Hillman, Peter Jackson and Keith Walker and to Jenni Metcalf who edited the Draft Strategy and others who contributed to our writing of it. A full version of the *Draft Native Fish Strategy* is available at: www.mdbc.gov.au

REFERENCES

Australian Society for Fish Biology 2001. Conservation status of Australian fishes – 2001. *Australian Society for Fish Biology Newsletter,* 31(2): 37-41.

Cadwallader P.L. & Gooley G.J. 1984. Past and present distributions and translocations of Murray cod *Maccullochella peeli* and trout cod *M. macquariensis* Pisces: Percichthyidae in Victoria. *Proceedings of the Royal Society of Victoria,* 96: 33-43.

Clunie P. & Koehn J. 2001a. *Silver Perch: A Recovery Plan. Final report for project R8002 to Murray-Darling Basin Commission.* Canberra.

Clunie P. & Koehn J. 2001b. *Freshwater catfish: A recovery plan. Final report for project R8002 to Murray-Darling Basin Commission*. Canberra.

Harris J.H. 1995. The use of fish in biological assessments. *Australian Journal of Ecology,* 201: 65-80.

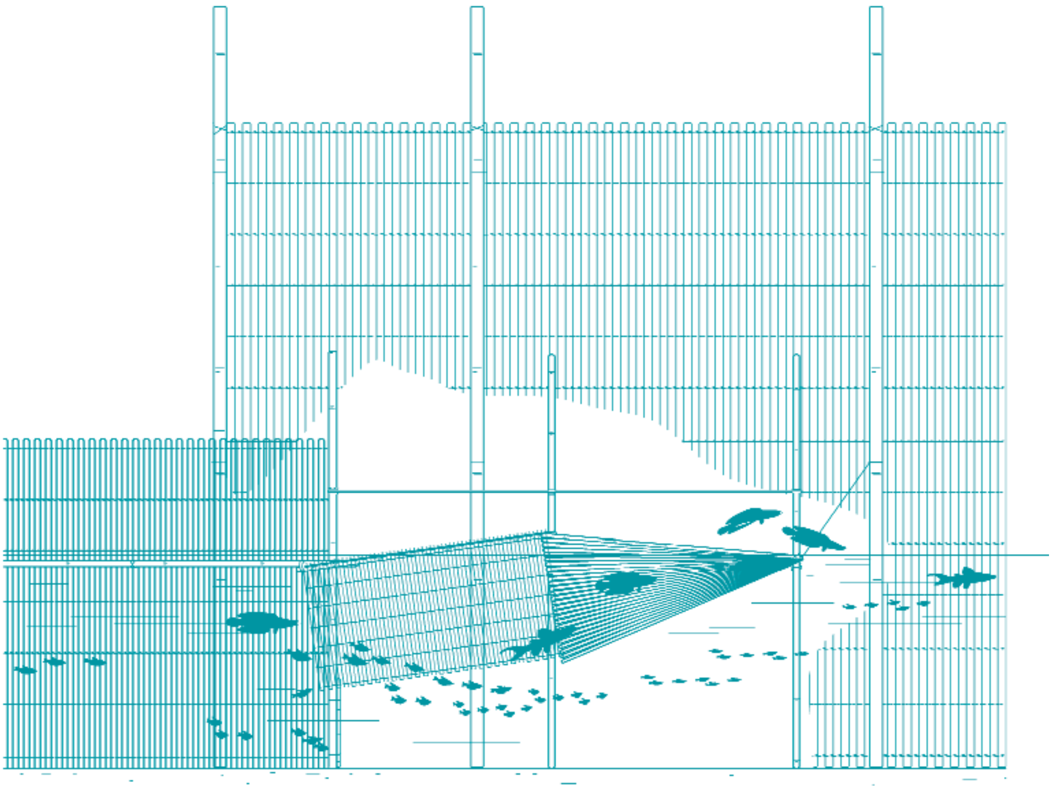
Harris J.H. & Gehrke P.C. 1997. *Fish and rivers in stress – the NSW rivers survey*. NSW Fisheries Office of Conservation & the Cooperative Research Centre for Freshwater Ecology. Cronulla & Canberra.

Murray-Darling Basin Commission 2001. *Integrated Catchment Management in the Murray-Darling Basin 2001-2010. Delivering a sustainable future*. Canberra, Murray-Darling Basin Commission. (Available at www.mdbc.gov.au)

Murray-Darling Basin Commission 2002. *Draft Native Fish Strategy for the Murray-Darling Basin.* Canberra, Murray-Darling Basin Commission. (Available at www.mdbc.gov.au)

Reid D.D., Harris J.H. & Chapman D.J. 1997. *NSW inland commercial fishery data analysis*. FRDC project No. 94/027 Report.

Waters J.M, Shirley M. & Closs G.P. 2002. Hydroelectric development and translocation of Galaxias brevipinnis: A cloud at the end of the tunnel? *Canadian Journal of Fisheries and Aquatic Sciences*, 591: 49-56.



AN OVERVIEW OF LEGAL ISSUES AND BROAD LEGISLATIVE CONSIDERATIONS FOR COMMUNITY-BASED FISHERIES MANAGEMENT

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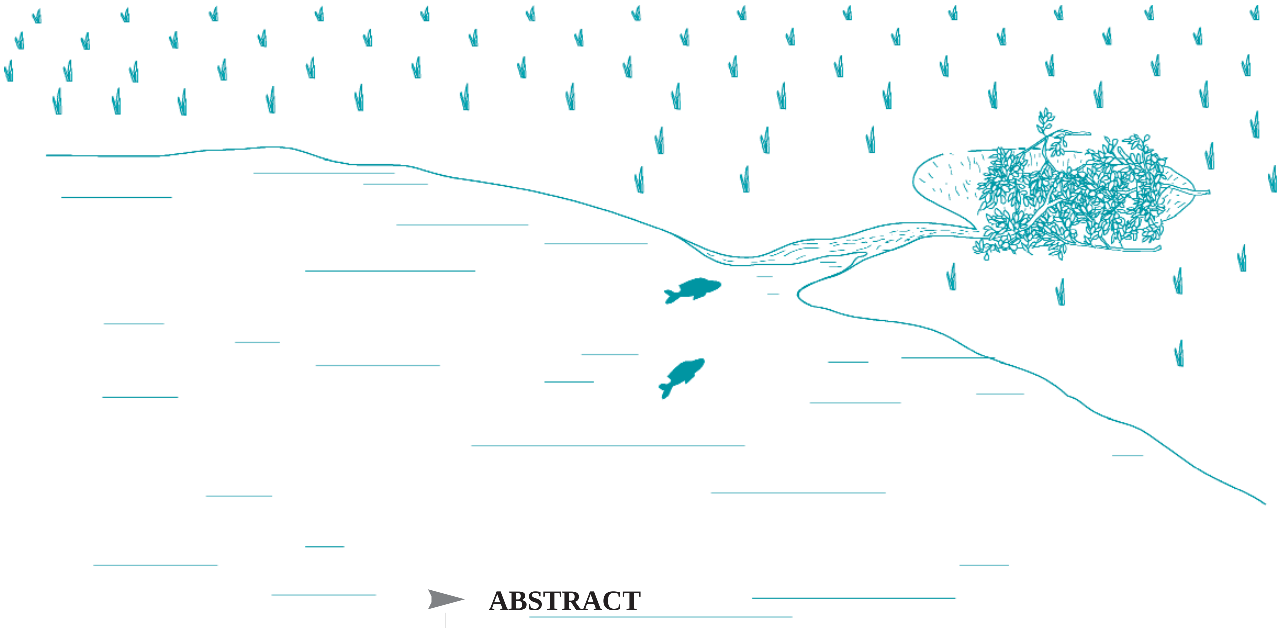


ABSTRACT

The fertile literature on community-based natural resource management (CBNRM) in general and in the fisheries sector in particular, shows that the implementation of such approaches to management will have a broad range of implications including policy, technical, institutional and legal implications. However, much discussion on utilising the community-based management approach in natural resource management to date has centred on its conceptual, economic and technical/management aspects. It is also important that the formal legal environment within which community-based management mechanisms be examined to determine whether it supports or will need necessary enhancement to support the implementation of CBNRM. It may even be necessary that such an examination takes place before or when CBNRM

is being considered for utiliszation or trial. The question as to whether community based fisheries management (CBFM) is legally sustainable must be asked of the whole legal framework of the state – from fundamental laws such as the constitution, to subsidiary legislation. Amendments to existing legislation or new legislation may be necessary to implement CBFM. There is no blueprint as to how a CBFM should be set up in a legal framework, what number of rights with respect to management of the fish resources should be accorded, what should be the level of participation by the local community and whether it be at the level of consultation during the management process or through formal representation in consultative, advisory or decision-making institutions within the fisheries management framework, or whether it should be a devolution of management authority or of implementation powers, or both. It is important, however, to ensure that the constitutionality of all these aspects of fisheries management should be ascertained and to ensure that enabling legislation for CBFM consider the following issues: security, exclusivity, permanence of rights vested, flexibility of its provisions so as to allow the states to exercise choice that reflects its unique needs, conditions and aspirations for CBFM, and to ensure that CBFM harmonizes with the overall fisheries management legal framework. Attaining the right balance in the CBFM legal framework however is difficult and depends largely on local circumstances.

INTRODUCTION

Global and local awareness of the fact that many of the world's fish stocks are over fished or depleted has seen moves to explore different approaches to fisheries management, including community based fisheries management (CBFM). The management of the fisheries resources of inland fisheries and large rivers systems resource management have obviously been part of this trend as evidenced by the amassing literature on the subject (e.g. Pomeroy 1994; Welcomme 2001). For the management of fisheries in Lake Kariba, FAO has assisted Zambia in a revision of its fisheries legislation to implement a community based management approach. This included the development of new fisheries legislation underpinning the creation of local and regional councils and committees having both management and enforcement functions and powers (Kuemlangan 1997).

When looking for reasons or causes for the failure to responsibly manage large parts of the world's fish resources, one finding commonly agreed upon is the failure of the open access regime to provide the framework for sustainable and responsible fisheries. Thus the last decades have witnessed an expanding interest in the different types of limited access regimes for governing utilisation of fish resources. Among the limited access regimes looked at is the property or rights based regimes (FAO 2002). In one form of property rights regime, referred to as the common property regime, the management of the resource is carried out by a community that collectively enjoys the rights to withdrawal and access. This means the community as a whole has a property right that can be more or less extensive. As is typical of property regimes, the creation of rights and their assignment to the community is recognised as an economic interest. This in turn stimulates an interest in the maintenance and protection of this bundle of rights and the resultant management goal of sustainable utilizsation of the resource.

One other recognisable trend in fisheries management approaches is the growing focus on increased stakeholder participation and devolution of management functions (FAO 2002). This in part is in recognition of the fact that the top-down management approach with management authority heavily concentrated in the central government administration and agencies has often been ineffective. Fisheries management and development functions in many jurisdictions has been the principal responsibility of government. This responsibility is often exercised through a central government authority which initiates government fisheries plans and policies, controls, monitors and undertakes surveillance of fishing and related activities, conducts research and enforces the laws and regulations concerning fisheries. In this command-and-control approach to management, the authority usually dictates the terms and conditions of involvement of principal actors in a given activity or group of activities. This approach to management of fisheries is effective only to the extent where the central authority has the full and required capacity to fulfil its mandate. However, a command-and-control approach to management gives little deference to the advice of stakeholders which often creates lack of understanding between the regulator and the regulated and often frustrates the effort of the central authority to achieve effective management. In the management of inland, near shore or coastal fisheries resources of many jurisdictions, there is a lot of interest in and broad consensus that the command and control approach to management should give way to wider participation by stakeholders in fisheries management through implementation of community-based fisheries management whereby stakeholders are involved directly or indirectly in the policy formulation and decision making processes or some technical aspects of the functions of the central authority. This approach provides for consultation of the stakeholders or for the stakeholders to have some form of representation in the decision making process. It promotes a more transparent and accountable management authority on the one hand and creates a more responsive stakeholder in terms of implementation of the management programmes and objectives and greater respect for and compliance with the directives of the relevant government authority on the other.

Regardless of the reason behind the pursuit of CBFM, there are socio-political dimensions that go beyond its mere introduction. There is a growing realiszation of the need for fostering sustainable development of the small-scale fishery. This fishery may form the backbone of the national economy, is important for the livelihood of the poor or provides inexpensive food for domestic consumers. The maintenance of a viable, decentralised settlement pattern to prevent large-scale migration of fishers to urban settlements is increasingly recognised as being of paramount importance to States. To this could be added the growing socio-political pressure for decentraliszation of governance (Kurien 1999). Indeed the introduction of and emphasis on community based management of fisheries resources has raised hopes that this approach to management will contribute to a more equitable distribution of any jurisdiction's fisheries resources, raised awareness about the fragility of the resource and the need to exercise caution in its exploitation and ultimately foster sustainable utilisation of the resources.

It is for the above socio-political dimensions and the other reasons given in the following sections of this paper that is important to examine legal issues and considerations for developing legal frameworks for CBFM. The substantive part of this paper provides an overview of broad legal issues relating to CBFM, which is preceded by a summary description of what CBFM is and the exposition of the current lack of consideration for legal issues relating to CBFM. The final part of the paper provides some basic considerations for legislating on CBFM.

WHAT IS COMMUNITY-BASED FISHERIES MANAGEMENT?

Community-based fisheries management, briefly put for the purposes of this discussion, is a form of participatory and common property rights based management which vests fishing rights in a group of individuals (communities) or involves the sharing of fisheries management and enforcement powers with local communities. It involves collective units (e.g. fishing communities) representing those who are directly involved in fisheries activities which may assume some or all control, monitoring and surveillance functions in relation to a fishery or are given differential rights to such fishery. In this arrangement, the central government authority performs the functions for which it is best suited (e.g. biological aspects of fisheries management, overall regulations) while the local communities are responsible for those tasks it can do best (e.g. gauging if there is excess fishing effort, local rules for fishing, monitoring, compliance).

WHY IS IT IMPORTANT TO CONSIDER THE LEGAL IMPLICATIONS OF CBFM?

The fertile documentation on the subject of community-based natural resource management (CBNRM) in general and in the fisheries sector in particular, shows that the implementation of such an approach to management by countries will have a broad range of implications including policy, technical, institutional and legal implications. However, much discussion on utilising the community-based management approach to natural resource management including in fisheries to date has centred on its conceptual, economic and technical/management aspects. Yet, once these technical aspects have been discussed, the the operational aspects, particularly, the formal legal environment within which community-based management will function, will also need examination to determine whether it supports or will need necessary enhancement to support the implementation of CBNRM. The World Bank Report (1999) from the International CBNRM Workshop discusses considerations for establishing community-based natural resource management (CBNRM). It underscores the legalising of institutions as a basic requirement for establishing CBNRM. Indeed, it may well be that such an examination takes place before or when CBNRM is being considered for utiliszation or trial. The failure to examine exhaustively the legal implications of CBFM as in CBNRM, may have been due to the wish to avoid legal complications when things appear to be going smoothly (Lindsay 1998). Plain oversight could be another reason for the lack of such examination in other instances.

In considering CBFM, particularly in the context of rights-based fisheries, examining legal issues is important for the following reasons: first, it is documented that effective implementation of CBFM systems depend on supporting legislative framework. (Berkes 1994; Ruddle 1994); second, there is some evidence is that CBFM systems have had a measure of success in jurisdictions like those in the Philippines and Japan where there exists a favourable legal environment exists (Alcala Vande Vusse 1994; Ruddle 1994). In addition, and with respect to traditional community-based marine resource management systems, the noted functional systems have been those that exist in jurisdictions that accord them legal recognition and are protected by government (Karlsen 2001; Pomeroy *et al*. 2001; Ruddle 1998). Third, discussing and dealing with the legal aspects of right-based management approaches in fisheries management could avoid the legal complications and adverse consequences of the kind such as that which arose in Iceland where the ITQ based fisheries management system introduced by the 1984 Fisheries Act was found to be unconstitutional. The latter may be an extreme example and one that relates more to the issue of individual transferable quotas. However, it has a valuable lesson for policy and decision makers that innovative approaches to management including rights-based management be reviewed from all perspectives and that they are found to be legally functional in the national context before they are comprehensively applied.

BROAD LEGAL ISSUES

The nature of the rights accorded to the local community, Property, and property rights and usufruct.

The discussion on community-based management often focuses on the rights of local communities at different levels. Some talk about the right to the resources themselves, some the right of the local community to manage the resources, some to the exclusive right to exploit the natural resources. What is touched upon here is fundamental economic rights including property, property rights and usufruct. In outline, the legal view of property can be summarised as follows. Property is not a thing, but a right established by socially constructed conventions. Property is a bundle of rights or interest in an asset that may be apportioned between different holders. Rights can be established and supported within a given community and are only declared as such when tested in courts. Rights can be established, qualified and extinguished by statute. (Leria & Vanvan Houtte 2000).

Quite clearly a community-based management regime can be classified as a common property right regime, given that the community is in possession of a sufficient number of rights or powers over the thing or resource they manage. However, each community-based management regime will prove to be unique both in terms of legal underpinnings and with regards to the institutional and management arrangements that support it. How it will be defined in the context of property regimes will depend on its characteristics and how many or few of the sticks in the bundle of rights are held by the community-based managers. The views here will probably vary, and and while some will claim that a common property regime exists, others will maintain that at the end of the day the state only accords the community usufruct rights, not property rights.

While it is useful to have a common theoretical foundation and understanding of the concepts when approaching this issue, it is in practical terms, difficult because the understanding of these concepts depends on the legal systems in which they exist. Given this background it is obvious that any discussion that tries, at the outset, to define whether a community-based management regime should or should not be regarded as a property rights regime will go down a long and hard road. Suffice it to say that a conscious consideration of what it is that one wishes to create and facilitate in advance is better than no consideration *ab ititio*. This must be done in close collaboration with the local communities, allowing the local community-based institutions to define, preside over and redefine the rules of resource use. Equally important is to recognise the place of the state legal framework and note that the establishment or perpetuation of a community-based natural resource management regime may require enhancing or establishing a legal framework to support it. In this broad context, the legal framework is viewed not only as an enabling factor for CBNRM, but also in terms of the constraints it imposes and therefore which should be removed.

The fundamental legal basis for CBFM

The question as to whether CBFM is legally sustainable must first be asked of the fundamental laws of a state. This is particularly important for those states that are established by constitution or whose legal systems recognize the constitution as the supreme law. If the fundamental law, whether it is the constitution, organic law or presidential or royal decrees, stipulates that certain prerequisites of CBFM are not possible, then this aspect of CBFM cannot be established legally. As touched upon above, there is no blueprint as to how a CBFM should be set up in a legal framework, what number of rights with respect to management of the fish resources should be accorded, what should be the level of participation by the local community and whether it be at the level of consultation during the management process or through formal representation in consultative, advisory or decision-making institutions within the fisheries management framework, or whether it should be a devolution of management authority or of implementation powers, or both. It is important however to ensure that constitutionality of all these aspects of fisheries management should be ascertained. In particular decentralization or delegation of resource management functions and appropriation of property or user rights could raise legal problems which are discussed as specific legal issues herein.

If it is the resolve of the government as reflected in national policies and directives to establish CBFM, then effort should be redirected at amending the fundamental laws of the land to enable this.

THE FUNDAMENTAL LEGAL BASIS AND DECENTRALIZATION

Decentralization does not necessarily mean people participation in governance of the full range of their own affairs and much less in the management of resources. Some may say that decentralization is really the effective establishment of central government at the local level. However, there are instances that decentralization may instil a culture of stakeholder participation in management of resources. In the latter context and as it relates to CBFM, the comprehension of the notion and ensuring its effective operation may come easier to communities where decentralization is a national policy supported by law. In this respect, decentralization or the delegation of mandate for the management of fisheries resources is essential for CBFM. Such mandates would come with formation of local governments and may vest in those governments the power to make subsidiary laws, and to administer and enforce laws. This feature is evidenced in the institutional framework of governance as reflected in fundamental laws such as the constitution, or if the constitution is silent on this issue, it may be an inherent culture in the system of governance.

The 1987 Constitution of the Philippines is an excellent example of a fundamental law that leaves no room for doubt by it clearly providing that CBFM shall be established through decentralization. Article X provides that there shall be a tier of local governments who shall be granted under a code for the local governments, powers, responsibilities and resources and all other matters relating to the organization and operation of local government units. In addition, it is an inherent policy that the State shall encourage non-governmental, community-based, or sector organizations that promote the welfare of the nation (Article II, Section 23). Further, Section 7 of the same Article states that the "Local Governments shall be entitled to an equitable share in the proceeds of the utilization and development of the national wealth within their respective areas, in the manner provided by law, including sharing the same with the inhabitants by way of direct benefits.

When considering the possibilities for decentralization of fisheries management functions, not only fundamental laws, but also subsidiary legislation that implement fundamental laws and enable decentralization must also be considered. Jurisdictions with a decentralized system of governance would most probably have in place a web of subsidiary legislation that confer resource management or enforcement powers to local government administration, local communities or stakeholders. These legislations may pertain to the establishment of local governments and their functions and administration (government and administrative laws), the management of other natural resources or the environment.Within the existing legal framework and pursuant to the constitution, other fundamental laws, main administrative laws, existing fisheries laws or other laws related to the management of coastal areas, e.g. environmental laws, a web of subsidiary legislation probably exists conferring management or enforcement powers to local government administration, local communities or stakeholders. When considering whether the existing legal framework allows for the introduction of CBFM this web of legislation is necessary to be assessed to clarify, sort out and resolve possible competing or overlapping authorities. The same holds true if the fundamental laws (e.g. the constitution) or framework laws (e.g. the main fisheries law) are revised with a view to introducing CBFM. Subsidiary legislation pursuant to these laws needs to be revisited to ensure compliance with the amended framework laws, and with other legislation as appropriate. While this is indeed a tedious and time consuming task, it is of crucial importance that the management powers and responsibilities of the community managers are clear and undisputed. For example, for the management of fisheries in the Lake Kariba, FAO assisted Zambia in a revision of its fisheries legislation to implement a community-based management approach. This included the development of a new fisheries legislation underpinning the creation of local and regional councils and committees having both management and enforcement functions and powers (Kuemlangan 1997).

THE FUNDAMENTAL LEGAL BASIS AND ALLOCATION OF OWNERSHIP OR OTHER SUBSTANTIAL RIGHTS

Like decentralization, the issue of the allocation of property and use rights should be asked also of fundamental laws as well as specific laws relating to natural resource development. This issue is often to be found in national constitutions, either addressed directly or indirectly if such appropriation is contrary to other constitutional principles or rights.

The Cambodian Constitution, for example, neither states explicitly the validity of allocating property or use rights nor prohibits such allocation. The Constitution as the supreme law of Cambodia states:

State property notably comprises land, mineral resources, mountains, sea, underwater, continental shelf, coastline, airspace, islands, rivers, canals, streams, lakes, forests, natural resources, economic and cultural centers, bases for national defence and other facilities determined as State property. The control, use and management of State properties shall be determined by law.

The State shall protect the environment and balance of abundant natural resources and establish a precise plan of management of land, water, air, wind, geology, ecologic system, mines, energy, petrol and gas, rocks and sand, gems, forests and forestry products, wildlife, fish and aquatic resources.

Given these provisions and reading them in the context of the whole Constitution, it can be safely deduced that property and use rights may be allocated under subsidiary legislation for as long as these legislation are gauged in terms that are not inconsistent with the Constitution.

The Icelandic example on the other hand shows us that it could be problematic to allocate property rights or other use rights because of constitutional constraints. The Supreme Court held in 1998 that in its current form then, the ITQ system breached constitutional rules on equal rights and rights to work on the one hand, and the constitutional rule against discrimination on the other. A legislative amendment to render them transferable satisfied the Court in 2000 that their transferability did not effect any discrimination.

There are examples of successful CBFM where local ownership (or other substantial property rights) over fish resources is recognized by law. This is the case in Samoa where local council by-laws entrench traditional management and conservation practises (Taua 1999).

The establishment of CBFM in the context of the creation of property rights systems, with all their implications of the inclusion of some and exclusion of others, to a greater or lesser degree of permanence, conflicts directly with the hallowed right of the public to take fish from public waters. This has been expressed differently in various jurisdictions - in Iceland, for example, it was couched in terms of violating the constitutional principles of economic freedom and equality before the law.

For this reason, the introduction of property rights in fishing has encountered considerable difficulty, and sometimes, downright opposition. Even though a serious barrier, this need not be the end of initiatives towards CBFM.

Where the constitution or other fundamental law stands in the way of the allocation of such rights the political will to amend these laws must be mustered in order to implement CBFM. Otherwise such practises will continue to suffer from the effects of a weak legal basis.

THE NEED FOR NATIONAL LEGISLATION AND SOME PRINCIPAL LEGISLATIVE CONSIDERATIONS

In addition to the need for enabling legislation that is consistent with fundamental laws and which elaborate basic constitutional principles relating to CBFM, there is also the basic need for security and enforceability of a right. Legal insecurity and uncertainty is likely to originate from legal regimes which do not allow for local people to establish enforceable legal rights to the resources on which they depend, or to play a meaningful role in the planning and managing of such resources.

Legislation provides mechanisms for site-specific delegation to local people of some measures of management responsibility over state land and fisheries resources, either on an indefinite basis or for a definite period. A balance is normally sought through this mechanism for ensuring that the state level concerns for efficiency in fisheries management and the local-level concerns for self-governance, self-regulation and active participation are realised while defining the extent of their mandates.

Local institutions cannot define the rules by which they interact with an outsider. CBFM must naturally exist inside its larger legal environment and linked with sovereign authority, which is the state, and thus needs a legal status that outsiders can recognize and interact with. They need legal protection from trespass and the criminal behaviour of outsiders. They need state law to give legal recognition to community-based rules and to tell outsiders that they have to abide by those rules. This is elaborated hereunder in the discussion on security as a principal legislative issue.

Community rules cannot define the limits of state power. Thus it is crucial that national legislation address to what extent the state will respect local autonomy and where and under what conditions it will retain the power to intervene. From a property rights regime perspective, this touches upon the fundamental question of who owns the natural resources. Iceland, which has one of the worlds most advanced ITQ systems, has chosen to include as Article 1 of their 1990 Act Relating to the Management of Fisheries the following text: "Marine resources that are found in Icelandic waters and are utilized are the common property of the Icelandic nation. (…) The issuing of fishing permits, in accordance to this legislation, does not constitute any claim to ownership or irrevocable claims by individual parties over fishing rights."

Most fishing nations that implement a rights-based fisheries regime have retained the power to allocate and withdraw rights and change the regulations governing their administration. If the rules governing a rights-based regime are explicit in the form of legislation, it is less problematic in administering them and deflecting legal challenges.

State law has also an important role to play in providing protection for individuals against the abuse of local power.

Importantly, state law is needed to provide basic guidelines for protection of important wider social interests, such as environmental protection. In particular where wide rights have been allocated to the local community, this question surfaces strongly. Where the local community is given ownership (and other property rights) of natural resources, where does the State stand with respect to protection of wider interests? On the one hand the answer is simple, as the government always retains a regulatory function by which it can act to protect legitimate interests of outsiders, including future generations. On the other hand there is a problem of defining those interests. A wide definition and continued intervention by the state on this ground would clearly diminish the local authority.

SECURITY

When considering a legal framework for CBNRM, security of the rights allocated to the community are fundamental. Security can be described as the ability of the community to withstand challenges of others to the right. In particular when these rights take the form of property or use rights this aspect gains in importance. Such rights can be challenged by other individuals by displacement or court verdict. They may be challenged by the state, which can withdraw or terminate the right in accordance with law. Security requires, among other things, that there be clarity as to what the rights are, that the rights cannot be taken away or changed unilaterally and unfairly, and that rights are enforceable against the state (including local government institutions). An aspect of security is certainty both about the boundaries of the resources to which the rights apply and about who is entitled to claim membership in the group. Another important aspect which has been touched upon but not stated outright is the need for the to law to recognise the holder of the rights.

EXCLUSIVITY

This is the ability to hold and manage the right without outside interference. The right must be exclusive. This requires accessible, affordable and fair avenues for seeking protection of the rights, of solving disputes and for appealing decisions of government officials. The ability to enforce the right is an important aspect of exclusivity. Other fishers may interfere with a local community's ability to harvest the fish in the manner they want. More significantly, the state by regulations, license conditions, gear, area and time restrictions etc. usually interferes to a considerable extent. The lines of authority need to be drawn clearly in order to provide for the exclusive exercise of the rights and powers allocated a local community.

PERMANENCE

This is the time span of the rights allocated a local community. In particular when the local community takes on wide management responsibilities and rights the security of permanence and duration is crucial. The duration of rights should be either in perpetuity or for a period that is clearly spelled out and is long enough for the benefits of participation to be fully realized.

FLEXIBILITY

- Flexibility is the community-based managers need for flexibility or legal space to exercise choice that reflects their unique needs, conditions and aspirations.
- Legal regimes should allow flexibility in deciding what the objectives of management should be and the rules that will be used to achieve those objectives.
- Flexibility is required in regard to how state law handles the recognition of local groups.
- Flexibility is needed on the definition of management groups and areas of jurisdiction.

INTEGRATING CBFM INTO THE BROADER FISHERIES MANAGEMENT LEGAL FRAMEWORK

CBFM will obviously have to exist within the wider legal and fisheries management framework given that the CBFM mechanism is usually introduced to achieve fisheries management goals. This must be properly reflected in legislation and in the policy making process by securing a role for the community managers in the overall picture of state fisheries management. To address this concern a number of matters may be considered for inclusion in legislation, or where they already exist, appropriate linkages will need to be made: (i) the policy-making framework and process must consider the place of the community managers in relation to overarching policy makers. Where the process of making and notifying a management plan is spelt out in legislation, securing the community managers a place in the planning process is paramount. Management planning should not be limited, but should enable any appropriate management unit divisions (Stewart 2002), (ii) the decision rules required for determining total fishing effort, e.g. total national quotas, need to address the role of the community managers in taking such decisions. In the same context, the relationship between the overall fishing effort and fishing effort within the community management area should be tackled, (iii) the delegation of responsibility, including regulatory powers to community managers and the structure of the management authority, (iv) enforcement powers of the community managers and its place in overall fisheries surveillance and enforcement, (v) if community managers will exercise judicial powers, this should be explicitly stated. For trans-boundary waterways including large river systems where international obligations relating to the use of the shared waterways features strongly, it is paramount to ensure that CBFM legal framework is compatible with the relevant international legal framework.

CONCLUSIONS

The fundamental question that needs to be asked in this respect and one which, unfortunately, has been raised rarely, "Is CBNRM legally sustainable?" (Lindsay 1998). A related question would be, "Do the circumstances require that a legal framework be established to support CBFM?"

Community-based management or other forms of rights-based management of natural resources as well as other approaches to management attempt to address fisheries problems in fisheries management including the fisheries of large river systems. It has been put that institutional and legal issues are the cause of most fisheries management problems (Garcia and Grainger 1997 *et al.*). This should be caution enough to suggest that the legal aspects of fisheries management approaches be thoroughly thrashed out. This requires a multidisciplinary approach. This requires, among others, as Fisher (1996) puts it in a discussion on legal regimes for fishery resource management, "It behoves scientists and lawyers to collaborate by providing their input and expertise not only when problems arise, but in anticipation of problems. In practice, this means that a multidisciplinary approach should be adopted for fisheries resource management from initial investigation through assessment and evaluation to policy formulation and implementation leading to operational involvement until termination of the project. The same is true for the adoption of community-based resource management in fisheries in large river systems which invariably support the livelihood of many riparian communities."

Ultimately, it would have to be asked what the necessary elements for an appropriate legal framework that supports the effective implementation of CRBM would be. In addition, any law established for utilization of rights-based fisheries must be practical and flexible in effect to respond to the needs for effective implementation of such a management approach. In the final analysis and as Lindsay aptly puts it, it is a question of balance in establishing the legal framework for community-based management (Lindsay 1998). Attaining that required balance however is not easy and depends largely on local circumstances.

REFERENCES

Alkala A.C. and Vande Vusse F.J. 1994. *In* R.S. Pomeroy ed. *Proceedings of the workshop on community management and common property of coastal fisheries and upland resources in Asia and the Pacific: Concepts, methods and experiencss.* Manila, ICLARM. pp. 12-19.

Berkes F. 1994. Property rights and coastal fisheries. *In* R.S. Pomeroy ed. *Proceedings of the workshop on community management and common property of coastal fisheries and upland resources in Asia and the Pacific: Concepts, methods and experiences.* Manila, ICLARM. pp. 51-62.

FAO 2002. Law and sustainable development since Rio-legal issues and trends in agriculture and natural resources management. *FAO Legislative Study* 73, Rome.

Garcia S. & Grainger R. 1997. Fisheries management and sustainability: A new perspective of an old problem? In D.A. Hancock, D.C. Smith, A. Grant & J.P. Beumer eds. *Developing and sustaining world fisheries resources. The State of science and management. 2nd World Fisheries Congress,* pp. 631-654.

Karlsen G.R. 2001. Can formalisation help? The introduction of fisheries co-management in the inshore fisheries of Dingle, Co. Kerry, Ireland. *Marine Policy,* 25: 83-89.

Kuemlangan B. 1997. Zambia draft fisheries legislation - preliminary report, August 1997. FAO Technical Cooperation Programme Project TCP/ZAM/6613. (Unpublished)

Kurien J. 1999. Community property Rights: Re-establishing them or a secure future for small-scale fisheries. *FAO Fisheries Technical* Paper No. 404/1 - Use of Property Rights in Fisheries Management.

Leria C. & Van Houtte A. 2000. Rights-based fisheries: A legal overview. *In Current fisheries issues and the Food and Agriculture Organization of the Unites Nations.* Publication in association with the Center for Oceans Law and Policy, University of Virginia School of Law. pp. 263-300.

Lindsay J. 1998. *Designing Legal Space: Law as an enabling tool in community-based management.* International Workshop on Community-Based Nautral Resource Management, Washington, DC, May 10-14, 1998.

Pomeroy R.S. ed. 1994. *Proceedings of the workshop on community management and common property of coastal fisheries and upland resources in Asia and the Pacific: Concepts, methods and experiences.* Manila, ICLARM.

Pomeroy R.S., Katon B.M. & Harkes I. 2001. Conditions affecting the success of fisheries co-management: Lessons from Asia. *Marine Policy,* 25: 197-208.

Ruddle K. 1994. Changing the focus of coastal fisheries management in R.S. Pomeroy ed. *Proceedings of the workshop on community management and common property of coastal fisheries and upland resources in Asia and the Pacific: Concepts, methods.* Manila, ICLARM. pp. 63-86.

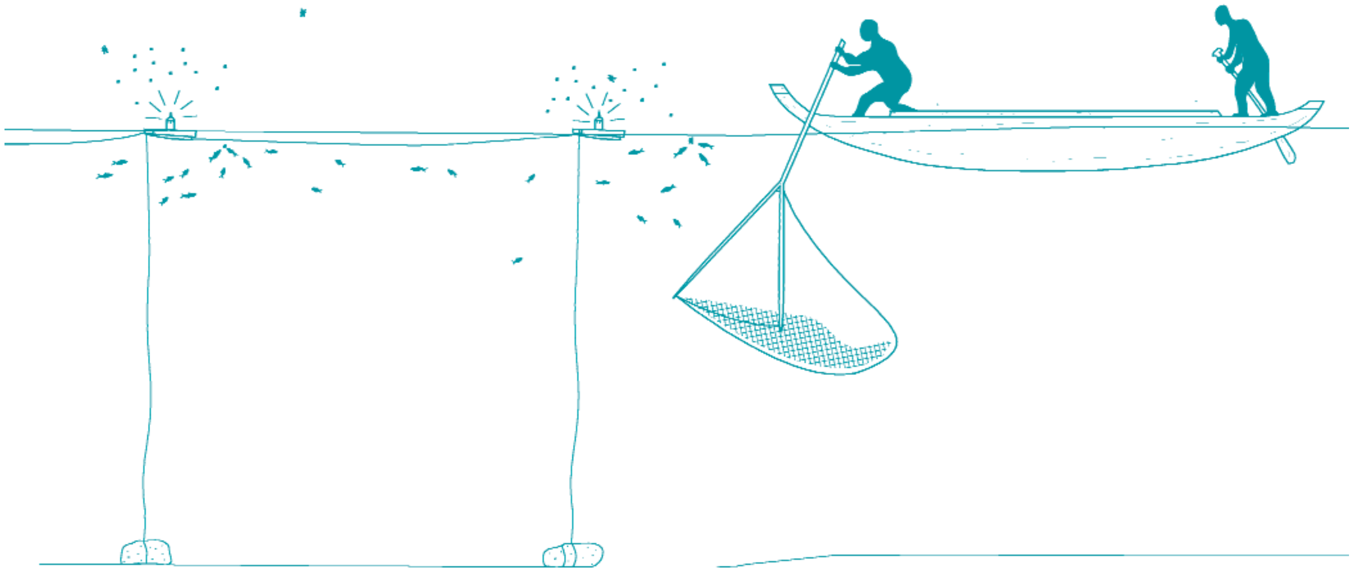
Ruddle K. 1998. The context of policy design for existing community-based fisheries management systems in the Pacific Islands. *Special Ocean & Coastal Management Issues,* 40(2-3), 105-126.

Stewart C. 2002. Legislating for property rights in fisheries. Rome, FAO Legislative Study. (forthcoming)

Taua A. 1999. *Community-based fisheries management in Samoa.* FishRights99 Conference. Fremantle, Austratia.

Welcomme R.L. 2001. *Indland Fisheries-Ecology and Management.* London, FAO. 358 pp.

The World Bank 1999. Report from the International CBNRM Workshop, Washington, DC, 10-14 May 1998. (Available at http://www.world-bank.org/wbi/conatrem/)



BIODIVERSITY STATUS OF FISHES INHABITING RIVERS OF KERALA (S. INDIA) WITH SPECIAL REFERENCE TO ENDEMISM, THREATS AND CONSERVATION MEASURES

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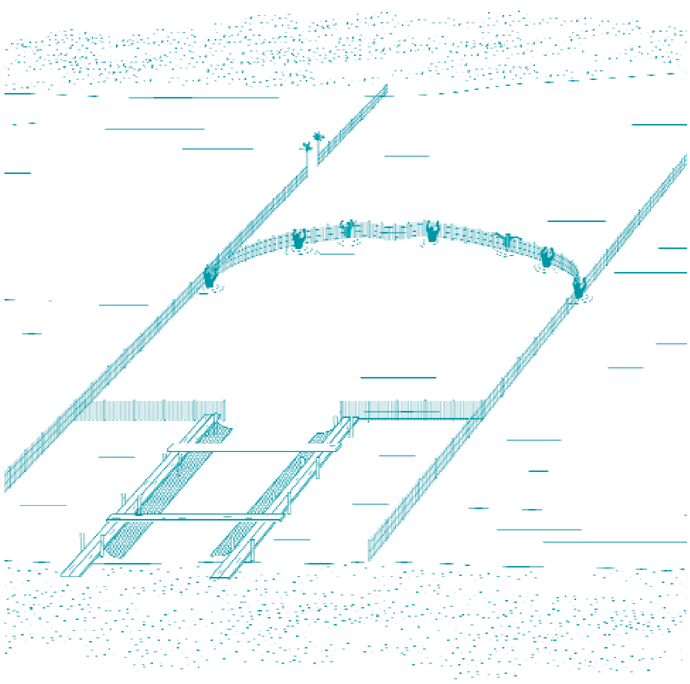


ABSTRACT

The identification of 175 freshwater fishes from 41 west flowing and 3 east flowing river systems of Kerala were confirmed. These can be grouped under 106 ornamental and 67 food fishes. The biodiversity status of these fishes was assessed according to IUCN criteria. The results showed that populations of the majority of fish species showed drastic reduction over the past five decades. Thirty-three fish species were found to be endemic to the rivers of Kerala. The distributions of the species were found to vary within and between the river systems and some of the species exhibited a high degree of habitat specificity. The diversity and abundance of the species generally showed an inverse relationship with altitude. The serious threats faced by the freshwater fishes of Kerala are mostly in the form of human interventions and habitat alterations and conservation plans for the protection and preservation of the unique and rare fish biodiversity of Kerala are also highlighted.

INTRODUCTION

Kerala is a land of rivers which harbour a rich and diversified fish fauna characterized by many rare and endemic fish species. The Western ghats are recognised as one of the 21 biodiversity hotspots of the world. A data base on fish biodiversity is essential as a decision making tool for conservation and management of fish germplasm, declaration of part of the rivers as aquatic sanctuaries, protection and preservation of endangered species and mitigation of anthropogenic activities so as to fulfil India's obligations under conventions on biological diversity with special reference to Articles 6 and 8 of UNEP (1992). Notable studies on the freshwater fish fauna of Kerala are those of Day (1865, 1878, 1889); Pillai (1929); John (1936); Hora and Law (1941); Silas (1951a, 1951b); Remadevi and Indra (1986); Pethiyagoda and Kottelat (1994); Kurup (1994); Kurup and Ranjeet (2002); Easa and Shaji (1995); Menon and Jacob (1996); Manimekalan and Das (1998); Ajithkumar *et al* (1999); Raju *et al.* (1999a and b) and Biju, Thomas and Ajithkumar (1999). In the present paper an attempt is made to prepare a consolidated list of freshwater fishes of Kerala and to assess their biodiversity status as per IUCN criteria. Their patterns of distribution have been delineated giving special emphasis to endemism and various anthropogenic threats which aggravate the degree of their endangerment. This communication also deals with various management plans relevant to the conservation of freshwater fish biodiversity of Kerala.

MATERIALS AND METHODS

Data on qualitative and quantitative abundance of fish species inhabiting various rivers were gathered during extensive surveys and sampling carried out as part of various externally aided research projects such as the ongoing NAT-ICAR project on Fish germplasm inventory evaluation and genebanking of freshwater fishes of Kerala, the ICAR sponsored population characteristics, bionomics and culture of *Labeo dussumieri* (1987-1990), the Kingdom of Netherlands financed project entitled exploited fishery resources of Vembanad lake (1988-1990). Experimen-tal fishing was conducted from not less than 10 sites on each river. Habitat diversity was given foremost importance during selection of locations within the river system. The sites for habitat inventory were selected based on channel pattern, channel confinement, gradient and streambed and bank materials. All the physical habitat variables in the selected reaches were studied (Anon. 2000). The position of the selected zones was determined using hand held GPS, altitude was estimated using electronic altimeter, conductivity and TDS using Lynx microprocessor based conductivity meter. Dissolved oxygen levels at each survey location were measured using Eutech cyberscan DO100 dissolved oxygen meter. Light intensity on the surface water and flow velocity was measured using Lux meter and water current meter, respectively. Total alkalinity and hardness were estimated based on Clesceri, Greenberg and Trussell (1989). The specimens were collected using various types of fishing methods such as cast nets (16 mm, 18 mm, 22 mm), gill nets (32 mm, 38 mm, 64 mm, 78 mm, 110 mm), drag nets (4 mm, 15 x 3 mtrs), scoop nets and other local contrivances. Collections were made from all selected locations during 8:00-18:00 h and 20:00-06:00 h. Visual observations were also carried out if the water was clear with a view to assess the distribution of the fish and abundance. Special care was taken to maintain uniformity in fish catch per unit effort (CPUE) (effort in hours) so as to compare the populations at selected locations of a river system. Density of fish populations at each location was estimated as abundance index

$$AI = \frac{(n(k))}{NxTotal*FU}*100$$

where *AI* = Abundance index, *n(k)* = number of individuals of the species k caught at the study site and *N* = Number of individuals of all fish species caught at that site, *FU* = Fishing unit as described by Arun (1997). The Shannon-Weaver diversity index

$(H=\Re\ n_1/n\ Ln\ n/n$

Where H = Diversity index, n_1 = number of individuals in species of a population or community, n = number of individuals in sample from a population for each river systems were calculated using the software Primer 5. Apart from this, the catches of the freshwater fishes from the landing centres and markets adjacent to the respective rivers were also inspected and specimens were collected for detailed examination. Samples were preserved in 8 percent formalin and kept for identification. Fishes were identified following Day (1878); Talwar and Jhingran (1991); Jayaram (1981, 1999); Kishori Lal Tekrival and Arunava Rao (1999). About 125 research papers on the freshwater fish fauna of Kerala available during the period 1965-2000 were also consulted towards compiling the past data of abundance and availability for assessing biodiversity status. The status of each species, whether threatened or endemic, was assigned based on IUCN categorization (NBFGR 1998).

RESULTS

Biodiversity status of the freshwater fishes delineated

One hundred and seventy five fish species under 13 orders, 29 families and 65 genera were collected and identified from the rivers and streams of Kerala. The name of the species, together with their commercial importance, status as per IUCN criteria and the river sources from where their occurrence has been recorded are shown in Table 1. This includes 25 new species recorded and described in the recent past. Of the 175 species, 4 species are exotic and alien. Among the species listed under threatened category, 18 were critically endangered while 38 species are endangered, whereas 28 species are vulnerable. There are 48 species under the non-threatened category, among which 21 are nearly threatened with low risk whereas 34 species belonged to low risk of least concern. (Figure 1). Among the 18 critically endangered species, 7 are confined to only a single locality while 5 species are found in 2 locations in the same river (Table 2). Among the endangered species, 5 are confined to a single location while 6 are from 2 locations of the same river system. The distributions of 15 species are found to be restricted to 2 rivers, while 12 species are recorded from 3 rivers (Table 3). Species such as *Lepidopygopsis typys*, *Silurus wynaadensis*, *Gonoproktopterus micropogon periyarensis*, *Osteochilichthys longidorsalis*, *Horaglanis krishnai and Labeo potail* are critically endangered and among them, *Silurus wynaadensis, Osteochilichthys longidorsalis, Horaglanis krishnai and Labeo potail* have shown a population reduction of 99 percent over the past two decades. The distributions of these fishes are restricted to one or two locations. *Silurus wynaadensis*, *Labeo potail* and *Osteochilichthys longidorsalis* are reported from the upstream locations of Kabbini and Chalakkudy rivers respectively where as *Horaglanis krishnai* is known to be only recorded from the subterranean wells of Kottayam district. While delineating the distribution pattern of freshwater fishes, it could be seen that more than 90 percent of the fishes so far reported from Kerala were encountered from the 5 major rivers. (Kabbini, Kallada, Bharathapuzha, Periyar and Chalakkudy).

Table 1: List of freshwater fish species reported from the Kerala part of Western Ghats

No	Name of Species	Ornamental/Food fish	IUCN Status	River Source
1	*Ambassis gymnocephalus*	Ornamental	LRlc	Chalakkudy
2	*Ambassis nalua*	Food fish*	DD	Travancore
3	*Amblypharyngodon chakaensis*	Ornamental*	CR	Veli Lake, Trivandrum
4	*Amblypharyngodon melettinus*	Ornamental**	DD	Achenkoil
5	*Amblypharyngodon microlepis*	Ornamental**	LRnt	Chalakkudy, Bharathapuzha
6	*Amblypharyngodon mola*	Ornamental*	LRlc	Kabbini River
7	*Anabas testudineus*	Ornamental*	VU	Achenkoil, Chalakkudy
8	*Anguilla bengalensis*	Food fish**	EN	Periyar
9	*Anguilla bicolor*	Food fish**	DD	Chalakkudy

No	Name of Species	Ornamental/Food fish	IUCN Status	River Source
10	*Aorichthys aor*	Food fish*	DD	Chaliyar River
11	*Aplocheilus blocki*	Ornamental*	DD	Valapatnam
12	*Aplocheilus lineatus*	Ornamental*	LRlc	Chalakkudy
13	*Awavous gutum*	Ornamental*	LRlc	Achenkoil, chalakkudy
14	*Balitora brucei*	Ornamental*	DD	Achenkoil
15	*Balitora mysorensis*	Ornamental*	DD	Bhavani, Bharathapuzha
16	*Barilius bakeri*	Ornamental**	LRnt	Periyar, Kabbini
17	*Barilius barna*	Ornamental*	LRnt	Bharathapuzha
18	*Barilius bendelesis*	Ornamental**	LRnt	Bharathapuzha
19	*Barilius canarensis*	Ornamental**	DD	Periyar
20	*Barilius gatensis*	Ornamental**	LRlc	Chalakkudy, Achenkil,Periyar, Manimala, Bharathapuzha, Kabbini, Meenachil
21	*Batasio travancoria*	Ornamental*	EN	Chalakkudy
22	*Bhavania australis*	Ornamental**	LRnt	Kabbini
23	*Catla catla*	Food fish***	VU	Achenkoil
24	*Chanda nama*	Ornamental*	LRlc	Achenkoil,Kabbini,Pamba
25	*Channa gachua*	Food fish**	VU	Travancore
26	*Channa leucopunctatus*	Food fish**	DD	Travancore
27	*Channa marulius*	Food fish***	LRnt	Pamba, Achenkoil
28	*Channa micropeltes*	Food fish**	CR	Pamba, Kallada
29	*Channa panctatus*	Food fish*	LRnt	Chalakkudy
30	*Channa striatus*	Food fish**	LRlc	Chalakkudy, Achenkoil, Kabbini, Kallada, Bharathapuzha
31	*Chela dadiburjori*	Ornamental**	DD	Bharathapuzha
32	*Chela fasciata*	Ornamental**	EN	Bharathapuzha
33	*Chela laubuca*	Ornamental**	LRlc	Kabbini
34	*Cirrhinus mrigala*	Food fish**	LRlc	Reaservoirs of Kerala
35	*Cirrhinus reba*	Food fish	VU	Kabbini
36	*Clarias dayi*	Food fish**	DD	Wynaad
37	*Clarias dussumieri*	Food fish**	VU	Chalakkudy
38	*Clarias gariepinus*	Food fish***	Intr.	Farms of kuttanad
39	*Crossocheilus latius latius*	Ornamental*	DD	Kabbini
40	*Crossocheilus periyarensis*	Food fish*	VU	Periyar
41	*Ctenopharyngodon idellus*	Food fish***	Intr.	Resrvoirs of Chalakkudy and Periyar
42	*Cyprinus carpio*	Food fish***	LRlc	Achenkoil
43	*Danio aequipinnatus*	Ornamental**	LRlc	Valapatnam,Chaliyar
44	*Danio malabaricus*	Ornamental**	LRlc	Achenkoil, Kabbini, Kallada, Meenachil
45	*Dayella malabarica*	Ornamental*	CR	Chalakkudy
46	*Eleotris fusca*	Ornamental*	LRlc	Chalakkudy
47	*Esomus danricus*	Ornamental**	LRlc	Chalakkudy, Moovattupuzha
48	*Esomus thermoicos*	Ornamental**	LRlc	Bharathapuzha,Pambar
49	*Etroplus maculatus*	Ornamental*	LRIc	Bharathapuzha, Kabbini, Achenkoil, Pamba, Meenachil, Kallada
50	*Etroplus suratensis*	Food fish*	LRlc	Chalakkudy, Bharathapuzha
51	*Garra gotyla*	Ornamental*	VU	Kabbini

No	Name of Species	Ornamental/Food fish	IUCN Status	River Source
52	*Garra hughi*	Ornamental*	EN	Pambar
53	*Garra mcClellandi*	Ornamental*	EN	Chaliyar,Periyar tiger reserve
54	*Garra menoni*	Ornamental*	VU	Bharathapuzha,Pambar
55	*Garra mullya*	Ornamental*	LRlc	Pamba, Kallada, Meenachil, Bharathapuzha
56	*Garra periyarensis*	Food fish*	EN	Periyar
57	*Garra surendranathinii*	Ornamental***	EN	Periyar
58	*Glossogobius giuris*	Food fish*	LRlc	Chalakkudy, Bharathapuzha
59	*Glyptothorax anamalaiensis*	Ornamental***	CR	Anamalai hills
60	*Glyptothorax annandalei*	Ornamental*	EN	Kabbini
61	*Glyptothorax davissinghi*	Ornamental*	DD	Nilambur, Chaliyar
62	*Glyptothorax housei*	Ornamental**	DD	Kallada
63	*Glyptothorax lonah*	Ornamental**	LRnt	Kabbini
64	*Gonoproktopterus curmuca*	Food fish**	EN	Chalakkudy, Kallada, Bharathapuzha
65	*Gonoproktopterus dubius*	Food fish**	EN	Kabbini
66	*Gonoproktopterus kolus*	Food fish**	EN	Chalakkudy
67	*Gonoproktopterus micropogon periyarensis*	Food fish**	EN	Periyar
68	*Gonoproktopterus thomassi*	Food fish**	EN	Kallada
69	*Heteropneustes fossilis*	Food fish**	VU	Chalakkudy, Bharathapuzha, Kabbini
70	*Homalaptera menoni*	Ornamental**	EN	Bharathapuzha
71	*Homalaptera montana*	Ornamental**	CR	Anamalai hills
72	*Homaloptera pillai*	Ornamental**	VU	Bharathapuzha
73	*Horabagrus brachysoma*	Food fish**	EN	Chalakkudy, Kallada, Achenkoil
74	*Horabagrus nigricollaris*	Food fish**	CR	Chalakkudy River
75	*Horadandia atukorali*	Ornamental*	EN	Cherthala
76	*Horaglanis krishnai*	Ornamental*	CR	Kottayam
77	*Horalabiosa joshuai*	Ornamental*	CR	Silentvalley-Bharathapuzha
78	*Gonoproktopterus kurali*	Food fish**	EN	Periyar River
79	*Labeo ariza*	Food fish*	CR	Periyar
80	*Labeo calbasu*	Food fish**	LRnt	Chalakkudy
81	*Labeo dussumieri*	Food fish**	EN	Pamba, Achenkoil
82	*Labeo rohita*	Food fish**	LRlc	Achenkoil
83	*Lepidocephalus thermalis*	Ornamental*	LRlc	Periyar
84	*Lepidopygopsis typus*	Ornamental**	CR	Periyar
85	*Macrognathus aral*	Food fish*	LRnt	Periyar
86	*Macrognathus guentheri*	Food fish*	VU	Chalakkudy, Pamba,Periyar
87	*Macropodus cupanus*	Ornamental*	LRlc	Valapatnam
88	*Mastacembelus armatus*	Food fish*	LRlc	Pamba, Bharathapuzha, Kabbini, Kallada, Meenachil, Achenkoil
89	*Mastacembelus oatesi*	Food fish*	LRnt	Chalakkudy
90	*Megalops cyprinoides*	Food fish*	LRlc	Periyar
91	*Microphis concalus*	Ornamental*	VU	Uppala, Periyar, Moovattupuzha
92	*Mystus armatus*	Food fish*	LRlc	Bharathapuzha, Kabbini, Chalakkudy
93	*Mystus cavasius*	Food fish*	LRnt	Periyar, Bharathapuzha, Kabbini, Chalakkudy
94	*Mystus gulio*	Food fish*	LRlc	Periyar, Bharathapuzha, Kabbini, Kallada
95	*Mystus keletius*	Food fish*	DD	Periyar
96	*Mystus menoda*	Food fish*	DD	Achenkoil

No	Name of Species	Ornamental/Food fish	IUCN Status	River Source
97	*Mystus oculatus*	Ornamental**	LRlc	Kabbini
98	*Nandus nandus*	Ornamental**	LRnt	Pamba, Achenkoil, Chalakkudy
99	*Nemacheilus botia*	Ornamental***	LRnt	Travancore
100	*Nemacheilus denisoni denisonii*	Ornamental***	VU	Bharathapuzha, Pambar, Manimala
101	*Nemacheilus evezardii*	Ornamental*	EN	Kabbini
102	*Nemacheilus guentheri*	Ornamental*	LRlc	Bharathapuzha, Achenkoil,Pambar, Kabbini
103	*Nemacheilus keralensis*	Ornamental***	EN	Meenachil
104	*Nemacheilus menoni*	Ornamental**	EN	Periyar
105	*Nemacheilus monilis*	Ornamental***	EN	Kabbini
106	*Nemacheilus nilgiriensis*	Ornamental*	DD	Kabbini
107	*Nemacheilus pambarensis*	Ornamental***	DD	Chinnar
108	*Nemacheilus periyarensis*	Ornamental***	DD	Periyar
109	*Nemacheilus pulchellus*	Ornamental**	DD	Periyar
110	*Nemacheilus semiarmatus*	Ornamental***	VU	Pamba, Kallada
111	*Nemacheilus striatus*	Ornamental**	DD	Wynaad
112	*Nemacheilus triangularis*	Ornamental***	LRnt	Chalakkudy, Kallada, Meenachil
113	*Nemachielus petrubenarescui*	Ornamental**	DD	Kabbini River
114	*Neolissochilus wynaadensis*	Food fish*	CR	Kabbini
115	*Notopterus notopterus*	Food fish**	LRnt	Kabbini
116	*Ompok bimaculatus*	Food fish**	VU	Periyar, Bharathapuzha, kabbini, Kallada
117	*Ompok malabaricus*	Food fish**	CR	Bharathapuzha
118	*Oreochromis mossambicus*	Food fish**	Intr	Pamba, Achenkoil, Bharathapuzha, Kabbini, Kallada, Meenachil
119	*Osteochilus thomassi*	Food fish**	EN	Periyar
120	*Osteobrama bakeri*	Ornamental***	EN	Kallada, Achenkoil
121	*Osteobrama cotio peninsularis*	Ornamental*	VU	Periyar
122	*Osteochilichthys nashii*	Food fish**	VU	Kabbini
123	*Osteochilichthys longidorsalis*	Ornamental*	CR	Chalakkudy
124	*Osteochius brevidorsalis*	Ornamental*	EN	Kabbini
125	*Pangasius pangasius*	Ornamental*	CR	Kuttanad
126	*Pangio baashai*	Ornamental*	DD	Chaliyar
127	*Pangio goensis*	Ornamental*	EN	Manimala
128	*Parambassis dayi*	Ornamental*	VU	Chalakkudy, Chaliyar , Pamba , Bharathapuzha
129	*Parambassis thomassi*	Ornamental**	LRnt	Bharathapuzha, Kabbini, Kallada, Meenachil, Pamba
130	*Pisodonophis boro*	Not categorised	EN	Periyar
131	*Pristolepis fasciata*	Ornamental**	DD	Travancore
132	*Pristolepis marginata*	Ornamental**	VU	Achenkoil
133	*Pseudambassis ranga*	Ornamental*	LRlc	Chalakkudy
134	*Pseudeutropius mitchelli*	Food fish*	DD	Bharathapuzha
135	*Puntius amphibius*	Ornamental*	LRlc	Chalakkudy, Bharathapuzha, Kabbini, Meenachil, Kallada
136	*Puntius barmanicus*	Ornamental*	DD	Pamba
137	*Puntius carnaticus*	Food fish***	LRnt	Kabbini
138	*Puntius chalakkudiensis*	Ornamental***	EN	Chalakkudy
139	*Puntius chola*	Ornamental**	VU	Kabbini
140	*Puntius conchonius*	Ornamental***	VU	Kabbini
141	*Puntius denisonii*	Ornamental***	EN	Achenkoil

No	Name of Species	Ornamental/Food fish	IUCN Status	River Source
142	*Puntius dorsalis*	Ornamental*	VU	Chalakkudy, Periyar, Moovattupuzha
143	*Puntius fasciatus*	Ornamental**	LRnt	Chalakkudy, Kabbini, Kallada, Meenchil,
144	*Puntius filamentosus*	Ornamental**	LRlc	Achenkoil, Pamba, Bharathapuzha, Kabbini, Meenchil, Kallada
145	*Puntius jerdoni*	Ornamental***	VU	Achenkoil
146	*Puntius lithopidos*	Ornamental**	EN	Periyar
147	*Puntius melanostigma*	Ornamental*	EN	Travancore, Kerala part of Nilgiri biosphere
148	*Puntius micropogan micropogan*	Food fish**	DD	Chalakkudy
149	*Puntius ophicephalus*	Food fish*	CR	Periyar River
150	*Puntius pinnuratus*	Ornamental*	DD	Kallada, Central Kerala
151	*Puntius sarana sarana*	Food fish**	VU	Bharathapuzha
152	*Puntius sarana subnasutus*	Food fish**	VU	Chalakkudy, Bharathapuzha, Kallada
153	*Puntius singhala*	Ornamental**	DD	Bharathapuzha
154	*Puntius sophore*	Ornamental**	LRnt	Periyar,Keecheri, Bharathapuzha
155	*Puntius thomassi*	Food fish**	EN	Kallada
156	*Puntius ticto*	Ornamental**	LRlc	Chalakkudy, Manimala, Bharathapuzha, Meenachil
157	*Puntius vittatus*	Ornamental**	VU	Kabbini, Chalakkudy
158	*Rasbora daniconius*	Ornamental**	LRnt	Most of all Rivers
159	*Salarias reticulates*	Ornamental**	DD	Chalakkudy
160	*Oncorhychus mykiss*	Food fish***	Intr	Pambar, Periyar, Bharathapuzha
161	*Salmostoma acinaces*	Ornamental**	VU	Chaliyar,Kabbini
162	*Salmostoma boopis*	Ornamental*	LRlc	Achenkoil, Bharathapuzha, Kabbini
163	*Salmostoma clupeoides*	Ornamental*	LRlc	Periyar, Kabbini
164	*Salmostoma Sardinella*	Food fish*	LRnt	Chalakkudy
165	*Schismatogobius deraniyagali*	Food fish*	DD	Chaliyar
166	*Sicyopterus griseus*	Ornamental**	EN	Chalakkudy
167	*Silonia childreni*	Not categorised	EN	Periyar River
168	*Silurus wynaadensis*	Food fish*	CR	Kabbini
169	*Tetradon travancoricus*	Ornamental**	VU	Chalakkudy
170	*Tor Khudree*	Food fish**	VU	Periyar, Kallada
171	*Tor mussullah*	Food fish**	CR	Chalakkudy
172	*Tor putitora*	Food fish**	EN	Kabbini
173	*Tor tor*	Food fish**	EN	Chandragiri
174	*Travancoria jonesi*	Ornamental**	EN	Chalakkudy
175	*Travancoria elongata*	Ornamental**	DD	Chalakkudy

*Important CR-Critically endangered
**Highly important EN-Endangered
***Very highly important VU-Vulnerable
LRnt-Low risk nearly threatened
LRlc-Low risk least concern
DD-Data deficient
Intr - Introduced

Table 2: Critically endangered fresh water fishes of Kerala and the regions where they are found

Sl No	Name of the Species	River source	Location	Habitat	Endemism
		Species restricted to a single location			
1	*Amblypharyngodon chakaensis*	Travancore	Veli lake	Lake	ENK
2	*Horabagrus nigricollaris*	Chalakkudy	Chalakkudy upper reaches	Pool-riffle	EWG
3	*Horaglanis krishnaii*	Subterranean wells	Kottayam	Subterranean channels	ENK
4	*Horalabiosa joshuai*	Pambar	Chinnar wild life sanctuary	Riffle	EWG
5	*Lepidopygopsis typus*	Periyar	Thannikkudy	Riffle	ENK
6	*Silurus wynaadensis*	Kabbini	Vythiri	Pool-riffle	ENK
		Species restricted to a single river			
1	*Labeo ariza*	Periyar	———		EWG
2	*Neolissochilus wynaadensis*	Kabbini	Vythiri, Aranagiri	Pool-Riffle	ENK
3	*Ompok malabaricus*	Bharathapuzha	Kannadipuzha	Deep Pools	EWG
4	*Osteochilichthys longidorsalis*	Chalakkudy	Parambikulam, Vazhachal	Riffle	ENK
5	*Pangasius pangasius*	Pamba	Kuttanad	Pools	——-
6	*Tor mussullah*	Chalakkudy	Vazhachal	Rapids	EWG
		Species restricted to one or more rivers			
1	*Balitora mysorensis*	Bhavani	Bharathapuzha Mukkali Mannarkkad	Rapids	EWG
2	*Channa micropeltes*	Pamba, Kallada	Thenmala dam, Rose mala	Pool	ENK
3	*Dayella malabarica*	Chalakkudy,Achenkoil	Pulikkakkadavu, Mannar	Lacustrine	EWG
4	*Glyptothorax anamalaiensis*	Anamalai hillstrams	Noolpuzha	Pool riffle	EWG
5	*Homalaptera Montana*	Anamalai hills	Puthuthottam estate	Cascade	EWG
6	*Puntius ophicephalus*	Periyar, Pamba	Ummikuppanthodu	Rocky Pools	EWG

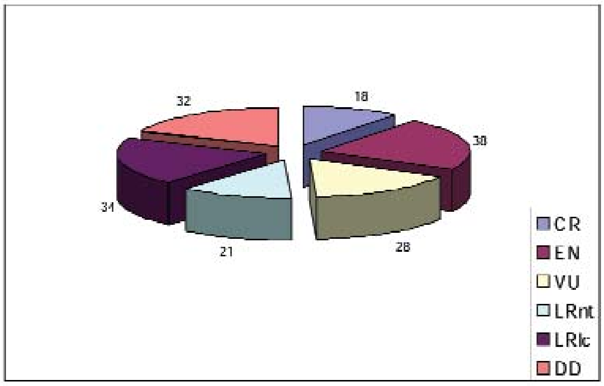
Table 3: Endangered fresh water fishes of Kerala and the regions where they are found

Sl No	Name of the Species	River source	Location	Habitat	Endemism
		Species restricted to a single river system			
1	*Chela fasciata*	Bharathapuzha	Thootha	Riffle	ENK
2	*Garra hughi*	Pambar	Chinnar wild life sanctury	Riffle	EWG
3	*Glyptothorax davissinghi*	Chaliyar	Nilambur	————	EWG
4	*Gonoproktopterus micropogon periyarensis*	Periyar	Thannikkudy	Run	ENK
5	*Homalaptera menoni*	Bharathapuzha	Silent Valley	Riffle	EWG
6	*Horadandia attukorali*	Cherthala	Kollam, Cherthala	Pools at low lands	EWG
7	*Osteo chilus thomassi*	Periyar	————	——————	EWG
8	*Osteochius brevidorsalis*	Kabbini	Noolpuzha	Riffle-pool	EWG
9	*Puntius thomassi*	Kallada	Kulathupuzha	Rapid	EWG
10	*Silonia childreni*	Periyar	Periyar lake	Pool	EWG
11	*Travancoria elongata*	Chalakkudy	Vazhachal	Rapid	EWG
12	*Travancoria jonesi*	Chalakkudy	Parambiculam	———	EWG
13	*Tor putitora*	Kabbini	Kalindi	Riffle	……
		Species restricted to two river systems			
1	*Anguilla bengalensis*	Periyar,Kabbini	Neryamangalam Panamaram	Pools	EWG
2	*Esomus thermoicos*	Bharathapuzha, Pambar	————-	Pools and Ponds	EWG
3	*Garra mcClellandi*	Chaliyar,Periyar, Bharathapuzha	Thekkadi Mannarkkad	Riffles and Runs	EWG
4	*Garra surendranathinii*	Periyar,Chalakkudy	Thannikkudy, Parambikulam	Riffles and runs	ENK
5	*Gonoproktopterus kolus*	Chalakkudy, Periyar	Parambikulam, Palakkayam	Runs and Pools	EWG
6	*Gonoproktopterus thomassi*	Kallada,Chalakkudy	Kulathupuzha	Run	EWG
7	*Gonoproktopterus kurali*	Periyar ,Kallada	Periyar lake, Thenmala	Runs, Pools	EWG
8	*Labeo dussumieri*	Pamba, Achenkoil	Pavukkara, Prayikkara	Pools at low lands	ENK
9	*Nemacheilus evezardii*	Kabbini,Pambar	Begur, Chinnar wid life sanctury	Rapids	EWG
10	*Nemacheilus monilis*	Kabbini, Pambar	Begur	Rapid	EWG
11	*Osteobrama bakeri*	Kallada, Achenkoil	Ottakkal, Prayikkara	Runs, Pools	ENK
12	*Pangio goensis*	Manimala,Chaliyar	————	————	EWG
13	*Puntius lithopidos*	Travancore, Periyar	————-		EWG

Sl No	Name of the Species	River source	Location	Habitat	Endemism
14	*Puntius melanostigma*	Travancore,Kerala part of Nilgiri biosphere	————-	Run	EWG
15	*Sicyopterus griseus*	Chalakkudy, Bharathapuzha	Vanchikkadav Mannarkkadu	Riffle, pools	EWG
	Species found in more than two river systems				
1	*Batasio travancoria*	Chalakkudy, Pamba, Kallada,Manimala	———	———-	ENK
2	*Glyptothorax annamalaensis*	Anamalai hills	————	———-	EWG
3	*Glyptothorax annandali*	Kabbini, Bharathapuzha and Moovattupuzha Rivers	————-	————	EWG
4	*Gonoproktopterus curmuca*	Chalakkudy, Kallada, Bharathapuzha	Malakkappara, Thenmala, Mannarkkasdu	Runs and Pools	EWG
5	*Horabagrus brachysoma*	Chalakkudy, Kallada, Achenkoil,Periyar	Punalur,Prayikkara, Parumala	Runs and Pools	ENK
6	*Puntius denisonii*	Achenkoil, Bharathapuzha, Chandragiri	Chuttippara, Mannarkkad Kasargod	Rocky Pools	ENK

Endemic freshwater fish diversity of Kerala

Of the 175 fish species reported, 33 species were found to be confined to the water bodies of Kerala (Table 4, Figure 1). This group includes species such as *Puntius denisonii, Nemacheilus keralensis, Oseobrama bakeri, Chela laubuca, Gonoproktopterus micropogon periyarensis, Silurus wynaadensis Neolissochilus wynaadensis, Puntius ophicephalus, Garra surendranathinii, Garra menoni*. The distribution of these species varies both within a river system and also between river systems and many of these fishes have a highly restricted distribution. While assessing the biodiversity status of these fishes, it appeared that 9 species are critically endangered while 10 are endangered. *Lepidopygopsis typus, Labeo potail* and *Gonoproktopterus micropogon periyaresis* are critically endangered and species such as *Puntius denisonii, Osteobrama bakeri, Chela fasciata,* are endangered according to the IUCN crieria. Currently many of the endemic, high value ornamental fishes are exploited for commercial purposes from the wild, thus aggravating their degree of endangerment. However, the quantities of these fishes exploited for trade purposes are not available. The rehabilitation of populations of endemic fishes through standardisation of captive breeding techniques and massive seed ranching are necessary for restoration and replenishment of their stock.



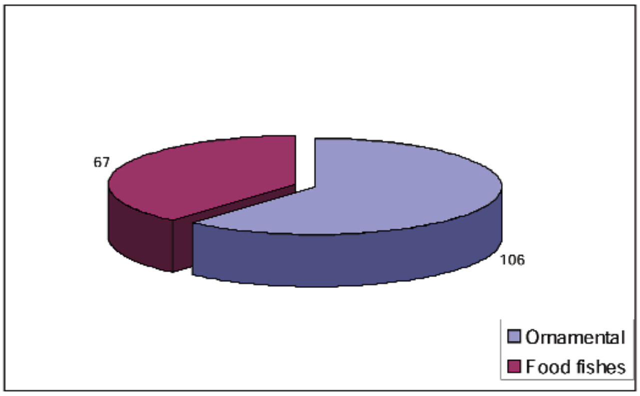
■ **Figure 1.** Biodiversity status of the freshwater fishes of Kerala based on IUCN

Table 4: List of Endemic freshwater ornamental fishes of Kerala and their biodiversity status and regional distribution

Sl. No.	Scientific name of the species	Status as per IUCN	Regional distribution
1	*Horadandia attukorali*	EN	Pathiramanal islands
2.	*Amblypharyngodon chakaensis*	CR	Veli lake, Trivandrun
3.	*Barilius bakeri*	LRnt	Western ghats of Kerala
4.	*Gonoproktopterus micropogon periyarensis*	EN	Periyar lake
5.	*Puntius chalakudiensis*	EN	Chalakkudy River
6.	*Puntius ophicephalus*	CR	Head waters of Periyar
7.	*Osteobrama bakeri*	EN	Kottayam ,Nilambur
8	*Neolissochilus wynadensis*	CR	Head waters of Cauveri River
9.	*Crossocheilus periyarensis*	CR	Western Ghats of Kerala
10.	*Garra hughi*	EN	Cardamom and Palani hills, Western ghats)
11.	*Garra menoni*	VU	Kunthi River, Silent valley
12	*Garrra periyarensis*	EN	Periyar Tiger Reserve, Periyar
13	*Garra surrendranathinii*	EN	Upstreams of Chalakkudy, Pamba and Periyar
14	*Lepidopygopsis typus*	CR	Periyar River
15	*Homaloptera menoni*	VU	Bhavani River
16	*Homaloptera pillai*	VU	Kunthi River, Silent Valley
17	*Travancoria elongata*	DD	Chalakkudy River
18	*Travancoria jonei*	EN	Upstreams of Periyar, Chalakkudy Rivers
19	*Nemacheilus keralensis*	EN	Western ghats of Kerala
20	*Pangio bashaii*	DD	Chalikkal River, A tributary of River Chaliyar
21	*Batasio travancoria*	EN	Western ghats of Kerala
22	*Horabagrus brachysoma*	EN	Rivers and backwaters of Kerala
23	*Horabagrus nigricollaris*	CR	Chalakkudy River, Kerala
24	*Chela laubuca*	DD	Kabbini
25	*flyptothorax anamalaiensis*	CR	Base of Anamalai hills of Kerala part of Western Ghats
26	*Glyptothorax housei*	DD	Anamalai hills
27	*Horaglanis krishnii*	CR	Kottayam district
28	*Pristolepis marginata*	VU	Mnanthavadi River, Kerala
29	*Channa micropeltes*	CR	Kallada River and Thenmala dam
30	*Silurus wynaadensis*	CR	Kabbini River, Wynaad
31	*Dayella malabarica*	EN	Parambiculam, Chalakkudy River
32	*Nemacheilus periyarensis*	DD	Mlappara,Periyar
33	*Salarias reticulates*	DD	Thumburmuzhi,Chalakkudy

Ornamental, Cultivable and Food fishes of Kerala

Of 175 species identified from the diverse river systems of Kerala, 106 are ornamental while 67 species are food fishes (Figure 2). Among the 106 ornamental species, 10 species including *Puntius denisonii* (Red line torpedo fish), *Puntius arulius* (Arulibarb), *Puntius conchonius* (Rosy barb), *Puntius filamentosus* (Tiger barb), *Puntius ticto ticto* (Ticto barb), *Puntius vittatus* (Koolie barb), *Puntius fascialtus* (Melon barb), *Parambassis thomassi* (Glass fish), *Hrabagrus brachysoma* and *Horabagrus nigricollaris* (Yellow cat fishes) have already secured positions in the national and international markets as ornamental fishes. The rest of the species have tremendous potential for development as candidates for the international ornamental fish market. Captive breeding and seed production technology of most of these fishes are not yet standardised and this forms the major bottleneck for their introduction in domestic and international trade. *Puntius carnaticus* and *Gonoproktopterus thomassi* have already been identified as potential candidate species suitable for aquaculture and can be developed as substitutes for Grass and Chinese carps in composite farming. 67 species of potential food fishes were recorded from the Kerala part of the Western Ghats, including species like *Mastacembeles armatus*, *Gonoproktopterus curmuca*, *Gonoproktepterus micropogon periyarensis*, *Channa marulius*, *Channa striatus*, *Mystus guliio*, *Mystus cavasius*, *Anguilla bengalensis* and *Puntius sarana subnasutus*.



■ **Figure 2.** Percentage of ornamental relative to food fish species reported from Kerala

Fish diversity and altitude

Examination of fish biodiversity at various altitudes from 6 rivers of Kerala showed that species diversity was inversely related to altitude (Table 5). In the Bharathapuzha river system between altitudes of 0-774 m the Shannon-Weaver diversity index varied from 0-2.9 and the diversity indices showed maximum value between altitudes of 0-65 m while it was lowest at altitudes ranging from 580-645 m. The presence of quite large numbers of waterfalls in this region might have contributed to the biodiversity decline of this reach. In the Chalakudy River system the diversity index ranged between 1.76- 3.8 between altitudes of 0-1032 m. The highest diversity was found between 0-65 m while it was lowest at reaches between 516-580 m. In the Pamba River system the Shannon Weaver diversity index ranged between 0.67-2.64 between altitudes of 0-161 m. The diversity was highest at altitudes between 0-65 m while it was lowest from 903-968 m. In the Periyar River system between altitudes of 0-839 m the diversity ranged between 1.55-3.056. Highest fish diversity was observed in the lower stretch (0-65 m), while the diversity was poor at 194-452 m due to the commissioning of some mega hydroelectric projects. In the Kallada River system the diversity was highest in the stretch between 258-323 m altitude. Interestingly, in lower stretches with an altitude of 0-65 m the diversity was poor due to habitat alteration on account of various human interventions. The fish diversity in the entire river system was in the range between 0.99-2.25. In the Kabbini river system the study was confined only in the upstream habitats having an altitude of 710-968 m and the diversity index in this stretch ranged between 1.24-3.57. The remaining parts of the river system pass through Karnataka state. At Kabbini the highest fish diversity was observed at an altitude ranging between 710-774 m, while it was lowest at altitudes ranging from 903-968 m. The results of this study revealed that fish diversity was highest in the lower stretches of the Chalakudy River system (0-65 m) while it was lowest in the upstream reaches of the Bharathapuzha River system at an altitude between 581-600 m (Table 5). Among the six river systems studied, the Chalakudy and Kabbini River systems showed the highest diversity index ranging between 1.76-3.8 and 1.24-3.37 respectively. In contrast, in the upstream reaches of the Periyar River system, between 774-968 m biodiversity showed an unusually increasing trend. This is due to the dominance of some critically endangered endemic species such as *Lepidopygopsis typus*, *Gonoproktopterus micropogon periyarensis* and *Crossocheilus periyarensis* which show high degrees of habitat selectivity and can sustain themselves only in the microhabitats prevailing in these areas. Abundance of *L. typus* showed a positive correlation with amount of bedrock substrate, chute type microhabitat, overhanging boulders, overhanging vegetation, total shade and stream cover. Optimum habitat of *G. micropogon periyarensis* was found as midchannel pools with comparatively good depth, overhanging vegetation, slope and excellent shade while that of *C. periyarensis* is lateral pools and scour-out pools with enough woody debris, overhanging vegetation and tree cover. According to Freeman, Bowen and Crance (1997), animals preferably occupy areas that best support survival, growth or reproduction. It may, therefore, be inferred that altitude has a clear-cut influence on the type of habitat prevailing in different reaches of the river systems. Survey and sampling conducted at six major river systems of Kerala also discloses that out of the 7 types of channel reaches, regime reaches showed the highest species diversity followed by pool-riffle and cascade. The contribution of regime reaches decreases with increasing altitude; meanwhile cascade and pool-riffle reaches are invariably high in the upstream habitats. Though beyond an altitude of 645 m, the contribution of these habitats shows a decrease and the river reaches are mostly represented by bedrock and step-pool type of habitats, the species diversity in these habitats are relatively minimal, with the presence of a few species characterised by very peculiar morphological adaptations which can only survive in these regions.

Table 5: Shannon-Weaver diversity index at different altitudes in six major river systems of Kerala

Altitude Range (m)	Name of the river system					
	Bharathapuzha	Chalakkudy	Pamba	Periyar	Kallada	Kabbini
0-65	2.9	3.8	2.64	3.056	0.99	-
65-129	1.76	2.73	2.33	-	-	-
129-194	1.86	-	-	2.68	2.13	-
194 -258	-	3.28	2.2	1.55	1.8	-
258-323	1.9	2.21	2.4	1.69	2.25	-
323-387	1.76	-	-	-	1.5	-
387-452	-	2.58	1.44	1.88	-	-
452-516	1.9	2.97	-	-	-	-
516-581		1.76	-	2.05	1.44	-
581-645	0	-	1.62	1.88	-	-
645-710	-	-	-	2.27	1.37	-
710-774	1.2	2.24	-	1.81	1.45	3.37
774 -839	-	2.74	1.72	2.76	-	3.25
839-903	-	2		2.66	-	1.24
903-968	-	-	0.67	2.79		2.84
968-1032	-	2.75	-	-	-	-
1032-1097	-	-		-	-	-
1097-1161	-	-	2.44	-	-	-

Habitats of critically endangered species

Microhabitat details of 7 critically endangered and endemic species are shown in Table 6. In the Kabbini River system the habitat of *Silurus wynaadensis* species is characterized by an average sinuosity of 1.21 while the entrenchment ratio, w/d ratio and the slope are 0.09, 5.3 and 0.09 respectively. The dominant substrate is sand and the stream comes under the A1 type in Rosgen's classification (Anon. 2000). The microhabitat of *Neolissochilus wynaadensis* is also located in the same river, where the average sinuosity, entrenchment ratio, w/d ratio and slope range between 1.2-1.6, 0.09-1.2, 3.2-5.3 and 0.06-0.09 respectively. Substrate is dominated by sand and the stream comes under the A5 type in Rosgen's classification. The Periyar River system requires special conservation measures due to the presence of five endemic and critically endangered species in its upstream region. *Lepidopygopsis typus, Nemacheilus menoni, Garra periyarensis* and *Gonoproktopterus micropogon periyarensis* were found in microhabitats characterised by a sinuosity ranging between 1-1.4 while the entrenchment ratio, w/d ratio and slope are in the range of 1-1.1, 0.87-28 and 0.1-0.15 respectively. The substratum is dominated by bedrock. The streams fall into both A1a+ and F1b classes. The sinuosity, entrenchment ratio, w/d ratio and slope are in the range of 1-1.3, 1-1.09, 1.14-28 and 0.1-0.15 respectively in the microhabitat of *Crossocheilus periyarensis*. The substrate is dominated by bedrock and the species found only in A1a+ type streams.

Biodiversity threats to the freshwater fishes of Kerala

The available information on the freshwater fishes of Kerala is mostly on systematics, distribution and abundance (Pillai, 1929; John 1936; Chacko 1948; Menon 1951, 1993; Kurup 1994; Easa and Shaji 1995; Zacharias, Bharadwaj and Jacob 1996; Ajith Kumar *et al* 1999; Raju Thomas *et al* 1999; Biju *et al* 2000; Kurup 2001; Kurup and Ranjeet 2002). The present database is compared against past data to determine the degree to which the fishes have become depleted over the last 50 years. Anthropogenic activities are the main cause for the alarming decline of fish populations in most of the rivers of Kerala. Unsustainable and unethical fishing by using fish poisons, dynamiting and a wide array of prohibited fishing methods are rampant in the uplands and lowlands of most rivers. Habitat destruction of natural spawning and breeding grounds of the fishes through sand extraction and construction of physical obstructions across rivers has contributed to the population decline and the endangerment of the freshwater fishes. Many of the species reported as endangered are now found only in areas protected under Forest and Wildlife jurisdiction, which clearly indicates the reasons for their endangerment.

Table 6: Major physical habitat variables at the area of occurrence of some critically endangered species

Name of the species	Habitat variables					
	Entrenchment ratio	W/D ratio	Slope	Sinuosity	Dominant substrate	Stream type (Rosgen's II level)
Silurus wynadensis	0.09	5.3	0.09	1.21	Sand	A1
Neolissochilus wynadensis	0.09-1.2	3.2-5.3	0.06-0.09	1.2-1.6	Sand	A1
Lepidopygopsis typus	1-1.1	0.87-28	0.1-0.15	1-1.4	Bed rock	A1a+ and F1b
Nemacheilus menoni	1-1.1	0.87-28	0.1-0.15	1-1.4	Bed rock	A1a+ and F1b
Garra periyarensis	1-1.1	0.87-28	0.1-0.15	1-1.4	Bed rock	A1a+ and F1b
Gonoproktopterus micropogon periyarensis	1-1.07	0.87-28	0.1-0.15	1-1.4	Bed rock	A1a+and F1b
Crossocheilus periyarensis	1-1.09	1.14-28	0.1-0.15	1-1.3	Bed rock	A1a+F 1b

The various types of destructive fishing activities practiced along the river systems of Kerala are summarized below.

Use of small meshed fishing gears

The use of small meshed fishing gears is prevalent in downstream sections of most of the rivers including the Achenkoil, Kallada and Pamba. Such practices, which are adopted for short-term profit, kill the fry and fingerlings of the fishes thus ultimately leading to regular growth over fishing and consequent reductions in populations.

Fishing using chemical and herbal poisons

Diverse types of fish poisons both of plant chemical origin are widely used in upstream, middle and downstream parts of most rivers.

Use of chemicals as poisons

Copper sulphate and bleaching powder are widely used in areas of rivers where water velocity is low. Fishes become inactivated or intoxicated and fishes including fingerlings are easily caught.

Use of insecticides as poisons

Insecticides and pesticides are used as a fish catching method, specifically for fishes that are either nocturnal or dwelling in small caves or crevices.

Seeds, bark and leaves of plants as poisons

Leaves, stems and seeds of different types of plants are used as poisons in shallow or low velocity waters. The seeds of palm, Othalathumkaya, Vakkanakkaya are regularly used for fishing.

Dynamiting

Dynamiting is a major method for catching food fishes but is less commonly used to catch ornamental varieties since it kills fishes instantaneously.

Electro-fishing

Electro-fishing is increasing in popularity in the down streams of the rivers like the Achenkoil and Pamba. It is mainly targeted at larger fishes; however, smaller, ornamental fishes are also killed by this method.

Destruction and modification of habitats

Destruction of fish habitat is another major cause of the decline in the ornamental fish population. Dams, bunds and levees act as barriers for free migrations of fish in the rivers. Deforestation accelerated the decline of fish populations due to excessive siltation and soil erosion.

Introduction of exotic species

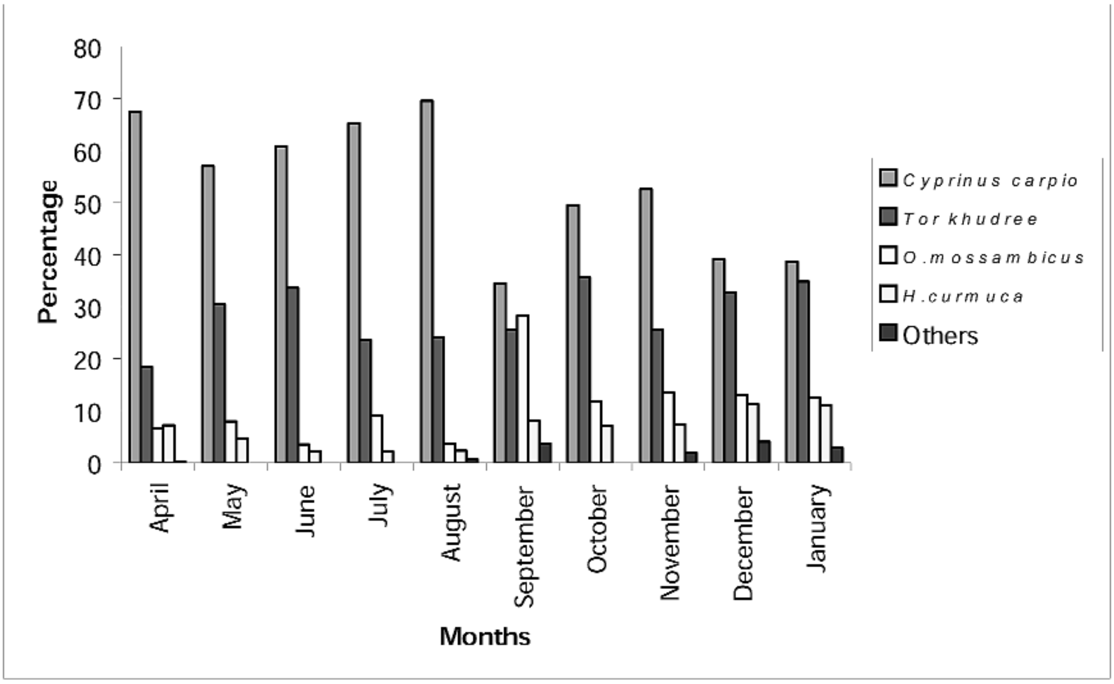
The introduction of exotic and alien species to the natural waters of Kerala has resulted in competition for food and space and ultimately in the decline of indigenous species. In Periyar Lake, which is well known as one of the biodiversity hotspots of Kerala, exotic species such as *Cyprinus carpio* have already established breeding populations and contribute more than 70 percent of the exploited stock. A high percentage of diet overlap exists between native fish species like *Tor khudree*, *Gonoproktopterus curmuca*, *Lepidopygopsis typus* and exotic species like Tilapia *(Oreochromis mossambicus)* and Common carp *(Cyprinus carpio)* (Table 7). Percentage contribution of exotics in the landing showed clear cut preponderance over indigenous fish species by weight (Figure 3). Tilapia has established its populations in almost all rivers of Kerala. The exotic high yielding African catfish (*Clarias gariepinus)* is another potential danger to the indigenous species. Alien species such as Catla (*Catla catla*), Rohu *(Laboe rohita)* and Mrigal *(Cyrrhinus mrigala)* have been cultured in most of the reservoirs and ponds of Kerala and consequently a gradual reduction of the endemic populations in these water bodies.

Water quality

Agriculture in the catchment area has aggravated water pollution by the application of pesticides and insecticides as well as having brought about a reduction in the available space for the free movement of the fishes. Over 200 medium and large-scale industries and 2 000 small-scale industries discharge effluents containing heavy metals such as mercury, zink and cadmium above the permitted level. There are regular mass mortalities of fish in the major rivers. The ammonia content of effluents discharged into these rivers was reported to be 432-560 ppm. Pollutants such as acids, alkalis, fluorides and radioactive materials were detected in the effluent waters of the industries at the Cochin area as a result of which the Eloor-Varappuzh areas of the Cochin backwaters are being transformed into a barren contaminated zone. According to the data compiled by the KWBSP, 10 types of pesticides with a

Table 7: Diet overlap of fish species in Periyar Lake, (Underlined figures indicates high overlap)

Fish species	O.mossambicus	Tor khudree	G.curmuca	C.carpio	G.micropogan periyarensis
O.mossambicus	-	0.78	0.48	0.33	0.21
Tor khudree	-	-	0.39	0.57	0.27
G.curmuca				0.42	0.35
C.carpio					0.32
G.micropogan periyarensis					



■ **Figure 3.** Percentage catch composition by weight of fish species from April 2002 to January 2003 total quantity of 490 tons are used in Kuttanad, the rice bowl of Kerala and samples of sediments and clams collected from the lower Kuttanad region had high concentrations of organic pesticides (Nair 200).

Over fishing

Over fishing of potential ornamental species without assessing their population size could lead to their extinction in the near future. Unfortunately, with the targeting of half a dozen fishes for the domestic and international trade, the stock size of these fishes has declined drastically and, as a result, most of them are now endangered. In addition, the spreading of fish diseases, especially in the downstream reaches of the rivers has resulted in mass mortalities of fishes such as barbs. Ever since from the outbreak of EUS in 1991, its recurrence had been invariably reported during the past 12 years from different water bodies of Kerala, thus acting as another major biodiversity threat to the inland fishes of Kerala.

MANAGEMENT MEASURES RELEVANT FOR CONSERVATION OF THE FRESHWATER FISHES OF KERALA

Management measures aimed at conserving freshwater fish biodiversity should be inserted into the fishery policies of the Govt. of Kerala. In addition the information given can be utilized by central and state government agencies, such as the Western Ghat Development Authority, Kerala Fisheries Management Society, local NGOs etc. who are deeply involved in implementing various measures for the protection of the fish biodiversity of the state.

Further measures should include:

The data base on population size and geographical distribution of endangered and endemic species should be strengthened by undertaking extensive micro geographical surveys. The knowledge of area of distribution and information on the micro geographical characteristics of the habitats of these ecologically sensitive fishes will be inputs for establishment of aquatic reserves for the conservation of the species.

Information regarding migration, breeding behaviour and spawning grounds of threatened fishes should be generated through extensive surveys and analysis. Such a database is essential for both *ex situ* and *in situ* conservation of the species.

Techniques should be developed for the captive breeding and broodstock development of fishes of potential economic importance. These should be standardised and the commercial scale exploitation of the species only be encouraged after standardising these techniques. Such information should be extended to the small and large-scale aquarists for the enhancement of ornamental fish exports.

Broodstock maintenance centres and hatcheries should be established exclusively for indigenous endangered and critically endangered fishes for their *in situ* conservation and aqua ranching as a substitute for their natural recruitment.

Investigation on the invasive nature of exotic species in the natural habitats should be carried out with a view to establish how many of them could achieve natural breeding populations and also to what extent their feeding spectrum habits overlap with that of the indigenous fishes. The functioning of the committee constituted under Govt. of India to quarantine and control the exotic species introduction to the country should be made more effective. The introduction of exotic and alien species of fishes in open waters for the purpose of resource augmentation, as is currently practiced in many of the freshwater dams of Kerala, should be discouraged and before any exotic species are introduction, its potential threat to local species should be studied and the introduction shall be subjected to the establishment of non threatening nature of the species.

CONCLUSION

The present study shows that the rivers and streams of Kerala have exceptional fish biodiversity with a high degree of endemism due to the presence of many rare and localised forms. These areas are conspicuous among the biodiversity hot spots of the world and therefore call for protection and preservation as bio reserves. Long-term management plans are needed to conserve and preserve this treasury of fish germplasm. Measures should include standardisation of captive breeding and seed production technology of endangered and critically endangered fishes and their massive ranching in the rivers. Efforts should be made to regulate various human interventions that are being imposed in the freshwater habitats of the fishes and strict regulations should be imposed on the introduction of exotic and alien fish species in the natural waters. The present study also revealed that the physical habitat variables play a leading role in the distribution of fishes in streams and the habitat alteration brought about in various rivers contribute significantly to the endangerment of freshwaters in the rivers of Kerala.

ACKNOWLEDGEMENTS

The authors thank the Director, School of Industrial Fisheries, Cochin University of Science & Technology for providing the necessary facilities. The financial assistance from ICAR-NAT project on Germplasm inventory, evaluation and gene banking of freshwater fishes is gratefully acknowledged.

REFERENCES

Ajithkumar C.R., Remadevi K., Raju Thomas K. & C.R. Biju. 1999. Fish fauna, abundance and distribution in Chalakudy river system, *Kerala. J. Bombay Nat. Hist. Soc*. 96(2): 244-254.

Anon, 2000. Part of manual on habitat and biological inventory under NATP Germplasm inventory and genebanking of freshwater fishes. Lucknow, India, National Bureau of Fish Genetic Resources.

Arun L.K. 1997. *Patterns and processes of fish assemblage in Periyar Lake-valley system of Southern Western Ghats, KFRI Research Report*. Peechi, Kerala, Kerala Forest Research Institute.

Biju C.R., Thomas R. & Ajithkumar C.R., 1999. Fishes of Parambikulam Wildlife Sanctuary, Palakkad District, Kerala. *J. Bombay. Nat. Hist. Soc*. 96(1): 82-87.

Chacko P.I. 1948. Development of fisheries of Periyar lake. *J. Bombay Nat. Hist. Soc.* 48(1): 191-192.

Clesceri L.S., Greenberg,A.E. & Trussell, R.R. 1989. *Standard methods for the examination of water and waste water, 17th edition*. APHA-AWWA-WPCF, USA.

Day 1865. *The fishes of Malabar*. London, Bernard Quaritch.

Day. 1878. *The fishes of India, being a natural history of the fishes known to inhabit the seas and freshwaters of India, Burma and Ceylon.* Dawson, London 1: 778; 2:195 plates reprint 1958.

Day F.1889. *Fauna of British India, Including Ceylon and Burma. Fishes 1*. 548 pp. 2: 509. London, Taylor and Francis.

Easa P.S. & Shaji C.P., 1995. *Freshwater fish diversity in Kerala part of the Nilgiri Biosphere Reserve. Research Report*. Peechi, Kerala Forest Research Institute.

Freeman M.C., Bowen Z.H. & Crance J.H. 1997. Transferability of habitat suitability criteria for fishes in warm water streams. *North American Journal of Fisheries Management*, 17:20-31

Hora S.L. & Law N.C. 1941. The freshwater fishes of Travancore. *Rec. Ind. Mus*. 43: 233-256.

Jayaram K.C. 1981. *Fresh water fishes of India handbook. Zoological survey of India*. Culcutta.

Jayaram K.C. 1999. *The freshwater fishes of the Indian region. Narendra Publishing House*. New Delhi. 509pp

John C.C. 1936. Freshwater fish and fisheries of Travancore. *J. Bombay Nat. Hist. Soc*. XXXV: 132-157

Kishori Lal Tekriwal & Arunava Rao A. 1999. *Ornamental and aquarium fish of India*. Waterlooville, UK, Kingdom Books. 144 pp.

Kurup B.M. 1994. An account on threatened fishes of river systems flowing through Kerala. *In Proc. Nat. Sem. Endangered Fish India*. pp. 129-140

Kurup B.M. 2001. River and Streams of Kerala part of Western Ghats as hotspot of exceptional biodiversity with great degree of endemism. *In* M.R. Meenakumari, B. Joseph, J. Sankar, T.V. Pravin P. & L. Edwin eds. *Proc. Riverine and Reservoir Fisheries of India Boopendranath*. p 204-217. Society of Fisheries Technologists India, Cochin.

Kurup B.M. & Ranjeet. K. 2002. Invasion of exotic fish population in Periyar lake, Kerala: A hotspot of fish biodiversity. *In* Proc. Life History Traits of Freshwater Fish Population for its Utilization in Conservation. Lucknow, India, NBFGR-NATP, AC-15. pp.1–4.

Manimekalan A. & Das H.S. 1998. *Glyptothorax davissinghi* Pisces: Sisoridae, a new catfish from Nilambur in the Nilgiri Biosphere Reserve, South India. *J. Bombay Nat. Hist. Soc.* 95: 87-91.

Menon A.G.K. 1951. Notes on fishes in the Indian Museum XLVI. On a new fish of the genus *Labuca* from Cochin. *Rec. Indian Mus*. 49: 1-4.

Menon A.G.K. 1993. Rare and endangered fishes of Malabar, Seminar on the conservation of endangered fauna of Malabar paper 1, Abstracts, p. 1.

Menon A.G.K. & P.C. Jacob. 1996. *Crossocheilus periyarensis*, a new cyprinid fish from Thannikkudy Thekkadi, Kerala, S. India. *J. Bombay Nat. Hist. Soc*. 95: 87-91.

Nair B.N. 2000. *Report of the expert committee for fisheries management studies, Kerala*. Directorate of Fisheries,Vikas Bhavan, Thiruvananthapuram. pp.1-213.

NBFGR 1998. *Conservation assessment and management plan C.A.M.P Workshop Report*. India, Zoo Outreach Organisation/CBSG. pp. 1-156.

Pethiyagoda R. & Kottelat M. 1994. Three new species of fishes of the genera *Osteochilichthys* Cyprinidae, *Travancoria* Balitoridae and *Horabagrus* Bagridae from the Chalakkudy river, Kerala, India. *J. South Asian Nat. Hist*., 11: 97-116.

Pillai R.S.N. 1929. A list of fishes taken in Travancore from 1901-1915. *J. Bombay Nat. Hist. Soc.* XXX: 111-126.

Raju Thomas K., Biju C.R. & Ajithkumar C.R. 1999. Extension of range of *Esomus thermoicos* Pisces: Cyprinidae: Rasborinaeto Kerala. *J. Bombay Nat. Hist. Soc*., 96(1): p. 163.

Raju Thomas K., Biju C.R. & Ajithkumar C.R. 1999. Distribution of Pangio goaensis TilakCyprini-Formes: Cobitidae in Manimala River, Southern Kerala. *J. Bombay Nat. Hist. Soc* 96(3): 479.

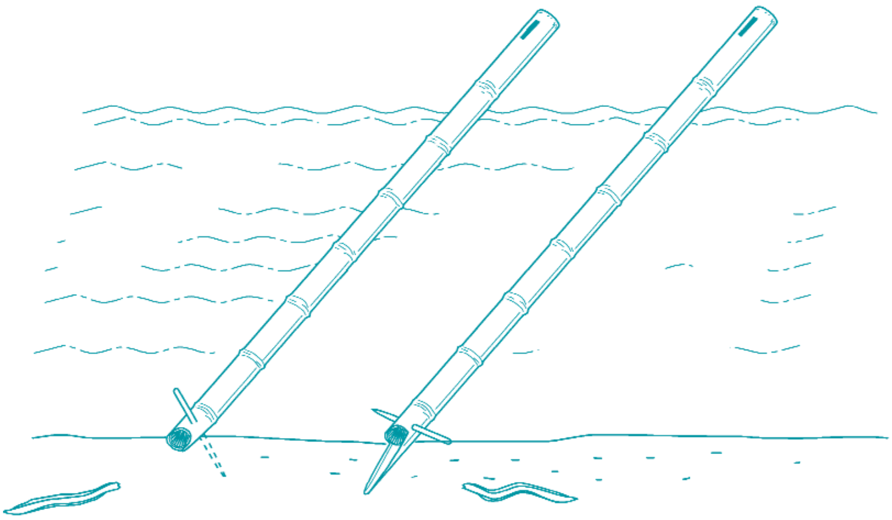
Remadevi K. & Indra T.J. 1986. Fishes of Silent Valley. *Rec. Zool. Surv. India*. 841(4): 243-257.

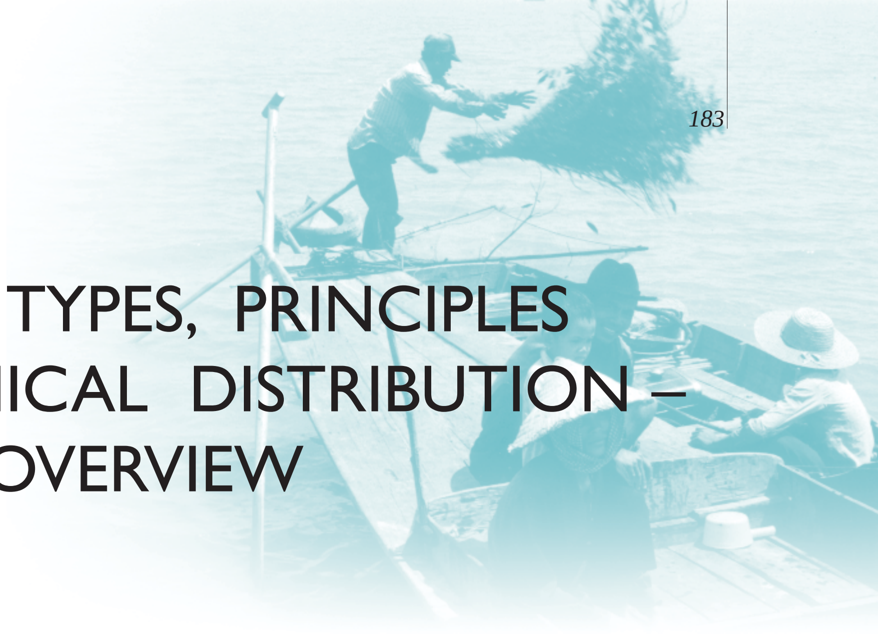
Silas E.G. 1951a. On a collection of fishes from the Anamalai and Nelliampathy hill ranges Western Ghatswith: Notes on its zoogeographical significance. *J. Bombay Nat. Hist. Soc.* 49: 670-681.

Silas E.G. 1951b. Fishes from the high ranges of Travancore. *J. Bombay Nat. Hist. Soc.* 502: 323-330.

Talwar P.K. & Jhingran A.G. 1991. *Inland fishes of India and adjacent countries*. New Delhi, Oxford & IBH Publishing Co.

Zacharias V.J., Bharadwaj A.K. & Jacob P.C. 1996. Fish fauna of Periyar Tiger Reserve. *J. Bombay Nat. Hist. Soc*. 93(1): 39-43.





FISH PASSES: TYPES, PRINCIPLES AND GEOGRAPHICAL DISTRIBUTION – AN OVERVIEW

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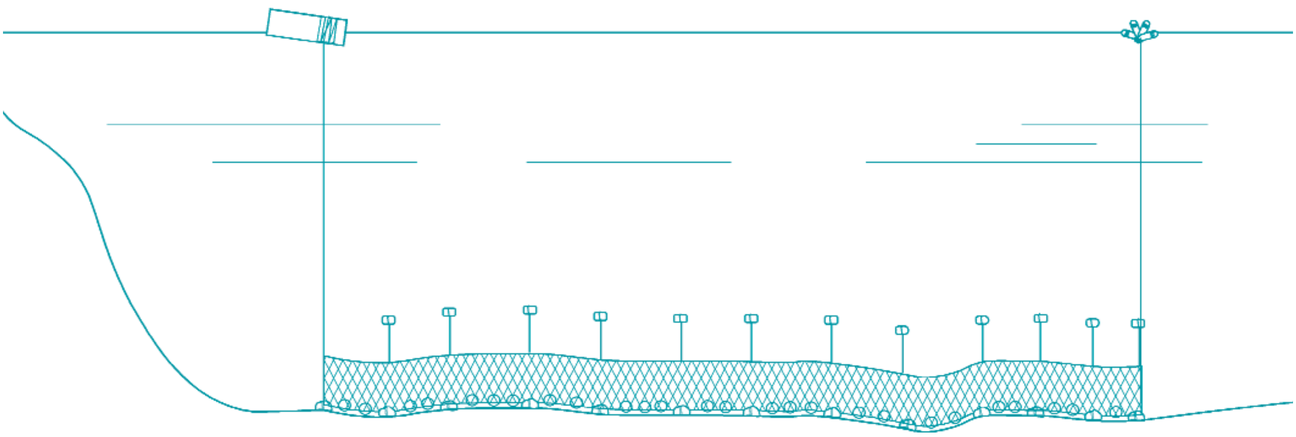


INTRODUCTION

Barriers across rivers often have negative impacts on natural fish populations and, along with other factors, may contribute to the diminished abundance, disappearance or even extinction of species. An example of this is the extinction of the salmon (*Salmo salar*) in the River Rhine, a stock that supported a thriving fishery in the first half of the twentieth century. Dams are threatening many aquatic species in Europe and North America, as well as in other continents where even far less is known about the biology, behaviour, fishery and population dynamics of the fish species concerned. There is increasing concern today that fisheries and the associated livelihoods are being threatened as a consequence of dam construction.

Fish migrations take place in all three directions, upstream, downstream and laterally but only the first two are dealt with in this paper. The general principle of upstream fish passage facilities (called fish passes, fishways or sometimes even “fish ladders”) is to attract fish that move up the river to a specific location in the river downstream of the obstruction so as to induce them (actively), or even make them (passively), pass upstream by opening a waterway (fish pass in the strict sense) or by trapping them in a tank and transferring them upstream (fish lift or transport systems such as trucking).

Upstream passage technologies are well developed for certain anadromous species, mainly salmonids (e.g. salmon, trout) and clupeids (e.g. shad, alewives, blueback herring) in North America and Europe. Upstream passage can be provided through several types of fish pass, including pool-type fish passes, Denil type (or baffle-type) fish pass, nature-like bypass channels, fish lifts and fish locks or collection and transportation facilities. Special designs for catadromous species (mainly eel) have been developed in Europe, Japan, New Zealand and Australia.

The design of a fish pass, the effectiveness of which is closely linked to the water velocities and flow patterns, should take into account the behaviour of the target species. Thus the water velocities in the pass must be compatible with their swimming capacity and behaviour. A large water level difference between pools, excessive aeration or turbulence, large eddies or low flow velocities can act as a barrier for fish. In addition to hydraulic factors, fish are sensitive to other environmental parameters (level of dissolved oxygen, temperature, noise, light, odour, etc.), which can have a deterrent effect.

Downstream fish passage technologies are much less advanced than those for upstream passage and are the areas most in need of research. Obviously, this is partly due to the fact that efforts towards re-establishing free movement for migrating fish began with the construction of upstream fish passage facilities and that downstream migration problems have only more recently been taken into consideration. Second, the development of effective facilities for downstream migration is much more difficult and complex. Research continues to improve downstream passage, especially at large obstacles where satisfactory solutions were scarce (EPRI 1994). As a general rule, problems concerning downstream migration have been thoroughly examined in Europe and North America with regard to anadromous species and more particularly to salmonids. Comparatively little information is available for other species.

A large number of systems exist to prevent fish from being entrained into water intakes but they are by no means as effective as bypasses. They may take the form of physical barriers, which physically exclude fish from turbine intakes, or behavioural barriers that attract or repel fish by means of applying stimuli to elicit behavioural responses. Bypasses for downstream passage can be complemented with such systems. The design of effective facilities for assisting the downstream passage of fish must, of course, take into account the swimming ability and behaviour of the target species and the physical and hydraulic conditions at the water intake.

UPSTREAM FISH PASSAGE FACILITIES

Pool-type fish passes

The concept of pool-type fish passes, which are widely used, is very old. An official survey carried out in France in the nineteenth century by Philippe (1897) revealed that there were more than one hundred. The principle behind pool passes is the division of the height to be passed into several small drops by forming a series of pools. The passage of water from one pool to another is either by surface overflow, through one or more submerged orifices situated in the dividing wall separating two pools, or through one or more notches or slots. Often, hybrid pool passes exist, for example with part of the flow through a notch, slot or over the dividing wall in combination with submerged flow through an orifice.

The main parameters of a pool pass are the dimensions of the pools and the geometric characteristics of the cross-walls separating the pools (dimensions and heights of the weirs, notches, slots and orifices). The upstream and downstream water levels also influence the functioning of the pass.

The pools have a twofold objective, i.e. to ensure adequate dissipation of the energy of water, with no carryover of energy from one pool to another and to offer resting areas for fish. There is a large diversity of pool-type fish passes throughout the world, which differ in the dimensions of the pools, the type of interconnection between pools, the differential heads between pools, the flow discharge and the slope. The discharge can vary from a few dozen litres to several cubic metres per second (Larinier 1992a, 1998; Bates 1992; Clay 1995). Design criteria are based on the swimming capacities and behaviour of the species involved as well as hydraulic models and field experience. Ideally, the drop between pools should not be more than 0.30 m. The pool volume is determined by a maximum energy dissipation in the pools that limits turbulence and aeration. This criterion seems to be commonly accepted nowadays but must be adapted for different species, i.e. between 200 watts m^{-3} for salmonids and less than 100 watts m^{-3} for small species and juveniles (Larinier 1990; 1992a; Bates 1992; DVWK 1996; Beitz pers. comm. 1999; FAO/DVWK 2002).

Pool passes with deep and narrow interconnections, like vertical slot type fish passes, can accommodate significant variations in upstream and downstream water levels without the need for regulatory devices.

Experience shows that when pool-type fish passes are well designed with respect to the different hydraulic criteria they can allow passage of most species (Travade *et al.* 1998).

Denil fish passes

Mr. Denil, a civil engineer, developed the first baffle fish passes in Belgium in the 1910s, mainly for Atlantic salmon. The principle is to place baffles on the floor and/or the walls of a rectangular flume with a relatively steep slope (10 to 25 percent) to reduce the mean velocities of the flow. These baffles, in shapes of varying complexity, cause secondary helical currents that ensure an extremely efficient dissipation of energy of the flow. The shape of the original baffles was later simplified with good results (Larinier 1983, 1992b; Lonnebjerg 1980; Rajaratnam and Katopodis 1984).

A disadvantage is that no resting zones for fish exist in a Denil pass and fish must swim through without stopping. If the total drop is very high and the pass, consequently, becomes very long, the fish must make an excessive effort for a period which may exceed the limits of its endurance and thus result in failure. Therefore, one or several resting pools should be provided at intervals that depend on the swimming performance of the target species (Larinier 1992b).

This type of pass is relatively selective and is really only suitable for individuals > 30 cm of salmon, sea-run trout, marine lamprey and large rheophilic potamodromous species such as barbel. Significant adaptations are needed if smaller fish are to pass.

Three designs of Denil fish passes are now in common use which are mainly distinguished by the shape and the material of the baffles, the slope and the width of the pass (OTA 1985; Larinier 1990; Amstrong 1996; Nakamura pers. comm.1999). The herringbone patterned baffles (super active-type baffles) are placed only on the bottom, while the two sides of the channel are kept smooth. The width of such a design is not limited, i.e. several unit-patterns can be juxtaposed according to the size of the river and the discharge required.

Nature-like bypass channels and fish ramps

The nature-like bypass channel, being very similar to a natural stream, is a waterway designed for fish passage around a particular obstruction. As noted by Parasiewitz *et al*. (1998), the function of a nature-like bypass channel is, to some degree, restorative in that it replaces a portion of the flowing water habitat which has been lost due to impoundment. These channels are characterised by a very low gradient. The energy is dissipated through a series of riffles or cascades positioned more or less regularly, similar to those in natural water courses, rather than the distinct and systematically distributed drops of pool type passes (Gebler 1998). The main disadvantage of this solution is that it needs considerable space in the vicinity of the obstacle and cannot be adapted to significant variation in upstream level without special devices (gates, sluices). These control devices may cause hydraulic conditions that make fish passage difficult.

As with any other fish pass, it is recommended that the fish entrance to the artificial river be located as close to the obstruction as possible. Given the very low gradient, for reasons of limited space it is sometimes difficult to position the entrance immediately below the obstruction, which means it must be placed further downstream. This may restrict the efficiency of these passes and, consequently, make them less useful for large rivers.

Fish ramps are constructions that are integrated into the weir but cover only a part of the river width; with as gentle a slope as possible to ensure that fish can ascend. Independently of their slope, all these structures are called ramps; in general the incorporation of perturbation boulders or boulder sills is required to reduce flow velocity (DVWK 1996; FAO/DVWK, 2002).

Fish locks

A fish lock consists of a large holding chamber located at downstream level of the dam linked to an upstream chamber at the forebay level by a sloping or vertical shaft. Automated control gates are fitted at the extremities of the upstream and downstream chambers (Travade and Larinier 1992; Clay 1995). The operating principle of a fish lock is very similar to a navigation lock. Fish are attracted into the downstream holding pool, which is closed and filled along with the sloping shaft. Fish exit the upstream chamber through the opened gate. A downstream flow is established within the shaft through a bypass located in the downstream chamber to encourage the fish to leave the lock.

The efficiency of such a fish facility depends mainly on the behaviour of the fish which must remain in the downstream pool during the whole of the attraction phase, follow the rising water level during the filling stage and leave the lock before it empties. The velocity and turbulence in the downstream holding pool must, of course, be acceptable for the fish. On the other hand, the lock chamber should not be filled too quickly during the lifting phase, since thus would cause excess turbulence and aeration, which might encourage the fish to remain in the lower chamber. The fish should have sufficient time to leave the lock in order to prevent any chance of being swept back downstream when the lock empties.

Numerous locks have proved to be either not very efficient, or else totally inefficient. The main drawback of the lock is that it has a limited capacity (in terms of the number of fish that it can handle) compared to that of a traditional fish pass; this is due to the discontinuous nature of its operation and the restricted volume of the lower chamber. The fish attracted into the lock may also leave the downstream chamber before the end of the trapping stage.

The fish locks constructed at the first dams on the Columbia River (Bonneville, The Dalles, McNary) and elsewhere in the United States were abandoned in favour of pool-type fish passes. Similarly, most locks in France are considered to be ineffective (some of them for obvious design reasons) and pool fish passes have replaced some. Difficulties due to fish behaviour have been solved in the United States (Rizzo 1969), and in Russia (Pavlov 1989). More recently Beitz (1997) forced fish to pass upstream in Australia by installing a crowder in the holding pool and a follower to coax fish towards the surface of the lock during the filling phase.

Fish lifts

In fish lifts, fish are directly trapped and lifted up in a trap or a trough together with water. At the top of the dam, the trap or trough empties its contents into the forebay. In order to limit the height of the trap in the case of significant downstream water level variation and to ensure easier maintenance, the fish lift can be installed upstream of a short section of conventional fish passes.

Where the number of fish to be passed is very large and can reach hundreds of thousands of individuals, it is no longer possible to hold the fish in the confined volume of the trap. High mortality may occur for some species. Therefore, the design is improved by incorporating a large holding pool into which migratory fish are attracted. A mechanical crowder is used to force fish to enter the area above the tank. The attraction water for the fish lift enters partly at the upstream end of the tank, partly through side or floor diffusers and gratings. Crowder gates at the entrance remain in a V-trap position to prevent fish moving back out through the entrance. Fish collected in the tank are released into an exit channel with low downstream velocities to swim up into the forebay (Travade and Larinier 1992).

The main advantages of fish lifts compared to other types of fish passage facilities lie in their cost, which is practically independent of the height of the dam, in the little space needed and in their low sensitivity to variations in the upstream water level. They are also considered to be more efficient for some species, such as shad, which have difficulties in using more traditional fish passes. The main disadvantages lie in the higher cost of operation and maintenance. Furthermore, the efficiency of lifts for small individuals (e.g. young eel) is generally low because sufficiently fine screens cannot be used for operational reasons.

Navigation locks

The passage of migratory fish through navigation locks is generally fortuitous, given the low attraction of these facilities, which are located in relatively calm zones to enable boats to manoeuvre. Tests carried out in the United States have shown that less than 1.5 percent of migrating fish use the lock at the Bonneville dam on the Columbia River (Monan *et al.* 1970).

However experiments have shown that navigation locks may constitute a significant back-up facility, or even a useful alternative to the construction of a fish pass at existing sites, providing that their operation is adapted to fish passage. The first condition that must be fulfilled is that sufficient attraction flow is created in the downstream approach channel to the lock. Opening the filling sluice of the lock with the downstream gates open can do this. Once the lock is full, it seems that it is necessary to maintain sufficient surface velocity to encourage fish to proceed upstream. As an example, more than 10 000 shad passed through the Beaucaire navigation lock on the Rhône River in 1992 in 49 lock operation cycles (Travade and Larinier 1992). However, the use of navigation locks as fish passage facilities is limited because the required mode of lock operation is often incompatible with navigation requirements.

Collection and transportation facilities

The technique of trapping and transporting migrants is often used as a transitory measure before upstream fish facilities are constructed. For example in the case of a series of dams when the building of fish passes occurs in stages, trapping and transportation can be an interim measure. Fish can be released further upstream in the river near the spawning areas or transported to a hatchery, which is often the case for salmonids during the first stage of restoration programmes. Trapping and transportation can be a more long-term measure in the case of dams where the construction of a pass would be difficult, or in the case of a series of dams where one dam is close to the next, thus creating a reach without valuable habitat for breeding.

Pavlov (1989) describes a floating fish trap used in Russia as part of a system of trapping and transporting fish over dams. It consists of a floating barge, anchored in place and equipped with pumps to provide attraction flow. After a period of attraction, a crowder concentrates fish over a lifting device, which then lifts them to the transportation chute of a container vessel. The container vessel is self-propelled and transports fish upstream. This system has the advantage of being able to be placed anywhere in the tailrace and in the path of migrating fish.

Fish passes for catadromous species

Research efforts to adapt fish passes to the needs of catadromous species, which enter fresh water and migrate upstream as juveniles, have been much less intense and are only relatively recent. Specially designed fish passes for young eels are being developed in Europe, Canada and New Zealand (Porcher 1992; Clay 1995; Mitchell 1995). Research programmes have been more recently launched in Australia, Japan and France to design and test fish passes suitable for very small fish.

Location of fish passes

For a fish pass to be considered efficient, the entrance must be designed in such a way that fish find it with a minimum of delay (Bates 1992). The width of the entrance is usually small in proportion to the overall width of the obstacle and its flow represents only a limited fraction of the total river flow. The only active stimulus used to guide the fish towards the entrance is the flow pattern at the obstruction. The attraction of a fish pass, i.e. the fact that fish find the entrance more or less rapidly, depends in particular on the location of its entrance and the hydraulic conditions (flow discharges, velocities and flow patterns) in the vicinity of the entrance. The flow that comes out of the entrance must neither be masked by the turbulence of discharge to the turbines or the spillway, nor by re-circulating zones or static water.

In the case of a wide river, fish may reach the obstacle on either side and therefore it may be necessary to provide not only several entrances to one fish pass but even more than one fish pass because a single pass cannot be expected to attract certain species that migrate along the opposite bank.

The siting of the pass entrance at an obstruction is not the only factor to be taken into account when choosing the location for fish pass. The exit of the fish pass should neither be situated in a fast flowing zone near a spillway, weir or sluice, where there is a risk of the fish being swept back downstream, nor in a static area, or re-circulating zone in which the fish could become trapped.

Finding the best position for entrances to the fish pass is not easy and rarely obvious, especially at hydroelectric dams. The hydraulic barrier to the fish may be right at the exit of the draft tubes, upstream of a zone of large turbulent eddies resulting from turbine discharges. On the other hand when the residual energy from the turbine water is significantly high, the hydraulic barrier may occur further downstream. Finally the location of the hydraulic barrier can vary at the same site, depending upon which turbines are in use at any one time.

When the barrier zones cannot be clearly identified at a particular site and are likely to vary depending on dam operating conditions, meaning that the correct fish pass entrance locations are not obvious, the effectiveness will be considerably improved by installing several entrances at points which appear, *a priori* to be the most favourable. The problem is extremely complicated and difficult to solve in the case where the fish passage facility is intended to suit several species whose swimming abilities and migratory behaviour are very different, or sometimes even unknown. This gives rise to the necessity to define the target species clearly at the outset of the project.

The discharge through the fish passage facility must be sufficient to compete with the flow in the river during the migration period. It is difficult to give precise criteria, but generally the flow passing through the fish pass must be of the order of 1-5 percent of the competing flow. It is clear that the higher the percentage flow of the watercourse passing through the fish pass, the greater the attraction of the pass will be. Although it is quite possible to direct a large fraction of the flow of the river through the fish pass in the case of small rivers, this is not the case in large rivers where the mean flow can exceed several hundred cubic metres per second. It then becomes difficult, in terms of cost, to maintain a sufficient flow through the facility, particularly during high water periods. On major rivers an attraction flow of around 10 percent of the minimum flow of the river (for the lower design flow) and between 1 and 1.5 percent of the higher design flow seem to be satisfactory for a well located fish pass to work.

When a large quantity of water is needed to attract fish into a fish pass (several cubic metres per second) only a fraction should be allowed through the fish pass itself in order to limit the size and the cost of the facilities. The auxiliary flow needed to boost up the attraction is then injected at low pressure and velocity through screens in the downstream section of the pass, or at the entrance itself. The simplest option is to add the auxiliary flow (or supplementary attraction flow) by gravity, after dissipation of the energy in a pool. At large dams, the auxiliary flow can also be created either by pumping water from the downstream pool or by sending water from upstream through one or several small special turbines that reduce, to a certain extent, the electric energy production losses and thus, in general, please the energy companies (Bates 1992; Larinier 1992a).

EFFECTIVENESS AND EFFICIENCY OF UPSTREAM FISH FACILITIES

The answer to the question "are fish passes effective mitigation means" is not obvious. The biological objectives of building a fish pass vary according to site and even on the same site depending on the species considered. The concept of effectiveness is therefore very variable and can only be defined with respect to an objective.

The concepts of effectiveness and efficiency may be used to clarify the degree of mitigation provided by a fish pass. Effectiveness is a qualitative concept, which consists in checking that the pass is capable of letting all target species through, within the range of environmental conditions observed during the migration period. Effectiveness may be measured through inspections and checks, i.e. visual inspection, trapping, video checks (Travade *et al.* 1998).

The efficiency of a fish pass is a more quantitative description of its performance. It may be defined as the proportion of stock present at the dam which then enters and successfully moves through the fish pass in what is considered an acceptable period of time. The methods giving an insight into the efficiency of a pass are more complicated than those for effectiveness. Marking and telemetry are valuable techniques to assess the overall efficiency of fish passes and the cumulative effect of various dams along a migration path.

The targeted effectiveness for a given site must be defined with respect to the biological objectives sought. It is therefore related to the species considered, the number of obstacles on the river and the position of the obstacle on the migration route.

The objective of a pass designed for diadromous species, such as salmon and located downstream of all the spawning grounds, is that the whole migrating population passes through. If numerous obstacles characterize this river, the aim is to minimize the time needed by the fish to enter the pass, so that the migrating fish reach the reproduction areas "on time". The efficiency of a fish pass is expressed both in terms of the percentage of the population which negotiate the obstacle and the migration delay, i.e. how long the population, or part of the population, takes to pass the obstacle. On the other hand, if the fish pass is located upstream of some spawning grounds, the requirements on percentage and time taken may be less stringent because fish may reproduce downstream. Whatever the case, the fish pass must be sufficiently efficient so as not to constitute a limiting factor in the long-term maintenance of migrating stock.

When dealing with a fish pass for potamodromous species whose biological objective is, above all, to avoid the sectorisation of populations in the various reaches, it is not necessary that all individuals of a population move upstream. The pass will be effective if a "certain number" of individuals, i.e. a significant proportion with respect to the population downstream of the obstacle, gets through the pass.

When the causes of poor performance (in terms of effectiveness and/or efficiency) of fish facilities are analysed, certain factors are frequently revealed (Larinier 1992; Nakamura 1993; OTA 1995):

Lack of attraction of the facility, resulting from a poor position of the fish pass or insufficient flow at the entrance of the facility in relation to the flow discharge into the river.

Poor design of the facility with regard to the variations in water levels upstream and downstream during the migration period, resulting in undersupply or oversupply of flow to the fish pass, or excessive drop at the entrance. This may be due to poor appreciation of the range of the upstream and/or downstream water levels during the project planning phase, or a subsequent change in these levels.

Poor dimensions, i.e. pools with insufficient volume causing excessive turbulence and aeration, excessive drop between pools, insufficient depth for the fish, or the flow pattern in the pools not suitable for the target species.

Frequent clogging up or obstruction of the fish passage facility, resulting from inadequate protection against debris, or too exposed a position, or quite simply inadequate maintenance on the part of the operator.

Malfunctioning of parts which regulate the flow discharge and the drops between pools (automatic sluice gates, etc.), or which ensure the functioning of the facility in the case of fish lifts and fish locks (automatic sluice gates, hoist for the tank, moving screens, etc.).

However, there are limits to the effectiveness of a fish pass. Even if 100 percent effective, a pass may prove insufficient to maintain the balance of a migratory population in the long term. In addition to problems arising from obstructed fish passage there are indirect effects such as a change in hydrological regime, water quality, an increase in predation and the loss or deterioration of the habitat upstream or downstream, which may also be limiting factors. These aspects are however species-specific and/or site-specific. Other mitigation measures, for example specific water flow management for fish at certain times of the year, may prove indispensable.

BARRIERS AND DOWNSTREAM FISH PASSAGE FACILITIES

Physical barriers

Fish are often entrained and pass through the turbines at generating facilities. One solution to prevent this involves stopping them physically at water intakes using screens that must have a sufficiently small grid size to physically prevent fish from passing through. These screens have to guide fish towards a bypass, which is done most effectively by placing them diagonally to the flow, with the bypass in the downstream part of the screen.

Sufficient screen area must be provided to create low flow velocities to avoid fish impingement. The velocity of the flow towards the screen should be adapted to suit the swimming capacities of the species and stages concerned. Physical screens can be made of various materials: perforated plates, metal bars, wedgewire, plastic or metal mesh. Uniform velocities and eddy-free currents upstream of screens must be created to effectively guide fish towards the bypass (ASCE 1995; Larinier and Travade 1999).

Behavioural barriers

Knowledge about visual, auditory, electrical and hydrodynamic stimuli has led to the development of a large number of experimental barriers, i.e. bubble screens, sound screens, fixed and movable chain screens, attractive or repellent light screens, electrical screens and hydrodynamic (‘louver’) screens.

Results obtained in particular cases with various screens (visible chain, light and sound screens) have not been of any great use because of their specificity (efficiency as a function of species and size), low reliability and their susceptibility to local conditions (water turbidity, hydraulic conditions). The use of behavioural barriers, which are still experimental, must be considered with caution (OTA 1995).

Surface bypasses in connection with surface bar racks or deep intakes

Surface bypasses associated with existing conventional trash racks or angled bar racks with relatively narrow spacing have become one of the most frequently prescribed fish protection systems for small hydroelectric power projects, particularly in the Northeast of the United States and in France. These structural guidance devices act as physical barriers for larger fish (downstream migrating adults) and behavioural barriers for juveniles. The efficiency is closely related to the ratio of fish length versus spacing and to response of fish to hydraulic conditions at the front of the structure and at the bypass entrance. Tests showed that under optimal conditions, efficiency can reach 60-85 percent (Larinier and Travade 1999). Flow discharge in the bypass has also been proven to be critical. The design criteria currently applied in the United States and France call for a minimum discharge of 2 percent to more than 5 percent of the turbine discharge (Odeh and Orvis 1998; Larinier and Travade 1998).

In the Columbia River Basin, there is a major effort under way to develop surface bypasses associated with relatively deep-water intakes. Various design configurations are being evaluated. The volume of bypass flow required to be sufficiently attractive is thought to lie in the 5 percent to 10 percent range. The design goal of theses bypasses is to guide at least 80 percent of the juvenile fish (Ferguson, Poe and Carlson 1998).

Downstream migration of eels

The problem of the downstream migration of eels (*Anguilla* spp.) at hydroelectric power stations is critical in the light of their size and the numerous fatalities that result. No specific solution has been implemented in North America or Europe due to the relatively recent awareness of eel migration. Only physical barriers are likely to work, but their installation would mean redesigning most water intakes (increase in the surface area of the filter due to smaller grid spacing). Due to the demersal behaviour of the species, there is no certainty that the approach used for juvenile salmonids with surface bypasses combined with existing trash racks would be efficient. Experiments on bottom bypasses need to be carried out, although it must be recognised that even if this technique were to prove efficient, there would be a considerable challenge to design facilities that did not create significant maintenance problems. The principle of behavioural light screens appears promising, taking into account the species repulsion to light (Hadderingh, van Der Stoep and Hagraken 1992). Stopping turbines during downstream migration is a solution already envisaged, as is the capture of individuals upstream of the obstacles for *Anguilla rostrata* in the United States (Euston, Royer and Simons 1998) and *Anguilla dieffenbachii* in New Zealand (Mitchell 1995). However, these solutions assume that the downstream migration period is both predictable and sufficiently short, which does not appear to be the case for the European eel (*Anguilla anguilla*) if we consider downstream migration monitoring (Larinier and Travade 1999).

FISH PASSES AROUND THE WORLD

The following review is not exhaustive. It aims to explore the current use of fish passes throughout the world, the target species, the state of technology and the current philosophy. Some countries are not mentioned because the state-of-the-art is poorly documented or of doubtful scientific bases.

North America

There are about 76 000 dams in the United States, including around 2 350 operating hydroelectric projects. Among these hydroelectric generating facilities, only 1 825 are non-federal projects licensed by the FERC (Federal Energy Regulatory Commission) (Cada 1998). Upstream facilities and downstream passage technologies are respectively in use at 9.5 and 13 percent of the FERC-licensed hydropower plants (OTA 1995). Fish passage requirements are most common along the Pacific and Atlantic coast, which supports the most important anadromous fisheries and in the Rocky Mountains, which have valuable recreational fisheries.

The main advances in upstream passage technology came from the west coast of United States and Canada where fish passage facilities have gradually become more sophisticated over the years since the building of Bonneville Dam, the first dam with large fish pass on the Columbia River about 60 years ago (OTA 1995). Currently, about 40 large-scale hydropower stations are in place on the Columbia River. Upstream passage technologies are considered to be well developed and well understood for the main anadromous species including salmonids (Pacific salmon and steelhead trout) and clupeids (American shad, alewife and blueback herring, Alosa spp.), as well as striped bass (*Morone saxitilis*). Upstream passage fish facilities have not been specifically designed for potamodromous species, although some of these fish will use them (carp, northern squawfish, suckers, shiner, whitefish, chub, dace, crappie, catfish, trout etc.). Most of these fish passes are pool-type fish passes with lateral notches and orifices (Ice-Harbor-type pool fish pass), or vertical slot pool fish passes where it is necessary to accommodate higher upstream and downstream variations in water levels (Clay 1995).

For smaller facilities, vertical slot fish passes are the most frequent type of design in British Columbia and pool-and-weir fish passes in Washington and Oregon (Washburn and Gillis 1985). The Denil fish pass is not widely used in the West coast, except in Alaska for salmon (*Oncorhynchus* spp.) where its light weight and mobility when constructed of aluminium, have proven useful for installations at natural obstructions that are inaccessible except by helicopter (Ziemer 1962; Clay 1995).

On the East coast of the United States and Canada, advances in fish pass design are more recent since anadromous species restoration programs on the main rivers of New England (Connecticut, Merrimack, Penobscot, St Croix River) were launched in the sixties of the last century. Fish passes of all types have been used to pass the following target species: Atlantic salmon (*Salmo salar*), shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*), striped bass (*Morone saxatilis*), smelt (*Osmerus mordax*) and sea-run brook trout (*Salvelinus fontinalis*). Fish lifts have been successfully used to pass large populations of shad on the Connecticut, Merrimack and Susquehanna rivers. Denil fish passes have been used in Maine, namely for salmon and alewife. Fish pass development in the Maritimes appears to have followed the Maine experience closely with the exception that Denil fish passes were not widely constructed (Washburn and Gillis 1985). For the same species, pool-and-weir fish passes are preferred, with drops varying from 0.15 m for smelt and up to 0.60 m drop for salmon (Conrad and Jansen 1983). In the East coast of Canada, Clay (1995) reported there are 240 fish passes.

For central Canada and the United States, Clay (1995) lists 40 fish passes used by potamodromous species such as catostomids, cyprinids, ictalurids, esocids, gadids and percids, as well as salmonids such as Salvelinus, Coregonus, Thymallus.

Francfort *et al*. (1994) completed a detailed study of the costs and benefits of measures used to enhance upstream and downstream fish passage at dams, using data of operational monitoring studies from 16 key projects across the United States which represent the measures most commonly used in the United States. At least six of the case study projects have successfully increased the upstream passage rates or downstream passage survivals of anadromous species. The most significant success are the two fish lifts at the Conowingo Dam which are an essential part of the Susquehanna River shad restoration programme and which have to cope with an increasing number of adult shad, i.e. from 4 000 to over 80 000 between 1984 and 1992 (Cada 1998). Although all projects had conducted some degree of performance monitoring of their fish passage mitigation measures, there were substantial differences in the extent and rigour of the studies: for some projects monitoring was limited to studies during a single season or based only on visual observations. For most case study projects benefits could be expressed only in terms of the increased numbers of fish transported around the dam. The influence of these increased numbers on the subsequent size of the fish populations was rarely known (Cada 1998).

EUROPE

A recent inventory suggests that there are approximately 380 fish passes in England and Wales. More than 100 have been built since 1989 (Cowx 1998). For many years fish passes have been built almost exclusively for Atlantic salmon and sea-run brown trout. The awareness of the need for the passage of potamodromous species ('coarse' fish) and other non-salmonid diadromous species such as shad (allis and twaite) or eel is more recent. The most commonly used fish pass is the pool-type fish pass (Beach 1984) in England and Wales and more recently floor baffle Denil fish passes (Amstrong 1996). In Scotland, submerged orifice fish passes, pool and weir passes and fish locks were used in the fifties of the last century.

In France, recent legislation, adopted in 1984, requires that free passage must be assured through all obstructions situated on designated 'migratory fish' rivers. The diadromous species considered are Atlantic salmon, sea-run brown trout, sea lamprey, Allis shad and eel. The only potamodromous species taken into account by the law are brown trout, northern pike and European grayling. Consequently, more than 500 fish passes have been built or retrofitted over the last 17 years. As a result of experience gained, in particular from experiments with hydraulic models and on-site monitoring, certain advances have been made in the choice and design criteria for upstream fish facilities. Denil fish passes are only used for Atlantic salmon, sea-run brown trout and sea lamprey on small rivers. Fish lifts or large pool-type passes with large and deep passages (vertical slot or deep notches) are used for shad. When several species must be taken into account, the recommended fish pass is the pool type (Larinier 1998).

In Germany and Austria, design and construction of fish passes has also been actively pesued over the last 15 years. Fish pass design tends to take into consideration many of the potamodromous species (brown trout, cyprinids, percids, etc.). The most common fish pass used is the natural-like bypass channel (Parasiewicz *et al.* 1998). However, where land is limited, more conventional pool and weir fish passes are used (DVWK 1996; FAO/DVWK 2002).

Pavlov (1989) reviewed fish passes in the former USSR. Conventional pool and weir fish passes are used for salmonids. He describes fish facilities built in the Caspian basin, Azov and Black seas and in particular on the Volga, Don and Kuban rivers where target species were Acipenseridae, Clupeidae, Cyprinidae, namely *Vimba vimba*, Percidae and Siluridae. Very large fish locks, fish sluice, fish lifts and mobile devices for fish collection and transport have been designed for these species.

Although a law was passed in Portugal in 1962 that required the installation of fish passes to maintain fish migrations, this was hardly enforced until 1990. After 1991, all projects of new weirs and dams were analysed and if migratory fish populations were concerned a fish pass has to be installed. About 50 new fish passes were built. The problem of the old dams without a fish pass, or with an inefficient pass, remains but the philosophy is changing and the question of maintaining fish migration corridors for diadromous or potadromous is now on the agenda. The first inefficient fish pass will be removed and a new one will be installed in Coimbra Dam on river Mondego for shad (J. Bochechas pers. comm.).

A total of 115 fishpasses were catalogued in Spain (Elvira, Nicola and Almodovar 1998), with about one third constructed after 1990. These fish passes are mainly located at weirs and dams of moderate height. The commonest fish pass found is the pool and weir fish pass, including vertical fish slot. In addition, Denil type and other non-standard designs have been used. Distribution is not uniform, since 87 percent of them are located within the two northernmost basins, North and Ebro. Many of the fish pass facilities were built in rivers where Atlantic salmon and brown trout (both resident and sea trout) are present. The effectiveness was estimated with 58 percent being highly suitable, 15 percent adequate, 19 percent low and 8 percent totally ineffective.

In Northern Europe, the main migratory fish species considered are Atlantic salmon and brown trout, which always had a special value for the inhabitants. Several whitefish species (coregonus sp.), grayling (*Thymallus thymallus*), northern pike (*Esox lucius*) and some cyprinids make shorter migrations both in freshwater and between the brackish water of the gulf of Bothnia and rivers running into it. In the coastal areas lamprey (*Lampetra fluviatilis*) is of great commercial value (Laine, Kamula and Hooli 1993). Norway has a very long tradition for building fishways and has been the predecessor in fishway construction in Scandinavian countries. There are now about 420 fishways. Most of these facilities are of the pool and weir type, but some are Denil fishways. The first fishways were excavated in rock and were usually large pools separated by narrow passes. About 25 percent of the fishways are on regulated rivers and 75 percent on rivers with natural obstructions (Grande 1990). Most of the Norwegian fishways are for salmon. There are just a few for brown trout, grayling and coregonids. Most Swedish fishways are pool and weir type fishways. Combinations of pool and Denil fishways have been built for inland fish, the first of them in the 1950s.

ASIA

There are probably about 10 000 fish passes installed on Japanese rivers (Nakamura and Yotsukura 1987). They are mainly designed for anadromous salmonids (*Oncorhynchus* spp.), Japanese eel, gobies (*Rhinogobius* spp.) and the ayu (*Plecoglossus altivelis*), which is a very valuable amphidromous species whose juveniles (50-60 mm long) migrate upstream. Recently, riverine species have also been selected as target species (Nakamura 1993). Over 95 percent of fish passes are conventional pool and weir fish passes, the others are vertical slot and Denil type. Most of the first fish passes designed for ayu were not efficient because they were imitations of European designs that were only suitable for larger fish (Nakamura *et al.* 1991). Following the two Symposia on fish passes held in Gifu in 1990 and 1995, a large effort is being made to improve and adapt fish pass design to Japanese species: ‘the improvement of fish passes is progressing so rapidly that it is known as a fishway revolution‘ (Nakamura 1993).

As noted by Wang (1990) and Clay (1995), China has a vast system of reservoirs (about 86 000) and the fisheries of these reservoirs are intensively exploited and maintained by stocking from hatcheries, so that little need has been felt to construct fish passes. The first fish passes are only 40 years old (Wang 1990) and around 60 to 80 fish passes have been built (Nakamura 1993). The main target species are potamodromous species, mainly four species of carp and catadromous species, mainly Japanese eel. Most fish passes are pool-type.

Zhili, Qinhao and Keming (1990) describe the Yangtang fishway on the Mishui River, which passes 45 species and more than 580 000 fish per year. The fish pass effectiveness was fairly well monitored (5 000 hours of observation annually). The effect of the fish pass seems to be significant, statistics of fish harvest showed that the annual fish output in the upstream part of the Mishui River increased to 3.5 times compared with that in the years before the fishway building. This fish pass has been specifically designed to pass very small fish, with very low turbulence in pools and low drops (about 0.05 m) between pools. The attraction flow (16 $m^3 s^{-1}$) and the collection gallery above the turbines are considered to play an essential role in the effectiveness of the facility. This fish pass is one of the few examples of a well-designed fish pass, adapted to native species and well monitored in developing countries.

In Nepal a couple of fish passes exist that were probably derived from the European or North American pool type and vertical slot passes. However, they do not seem to function well due to the chosen design criteria, resulting in the discharge through the pass being too low compared to the river flow and too turbulent. The dam that was under construction in 2001 on the Kali Gandaki River is 44 m high and the Kali Gandaki “A” Hydroelectric Project will generate about 842 gigawatt-hours (GWh) of electric energy per annum. The dam cuts off a river bent of approximately 70 km and the minimum flow rate below the dam will only be of ca. 4 $m^2 s^{-1}$. Together with the dam on the Andhi Khola River, it blocks the migration of important fish species, e.g. *Tor* sp. and *Bagarius*. No fishpass for upstream migration has been incorporated into the project. Instead, “trapping and hauling” of fish at the dam and constructing a hatchery to provide stocking material to stock the river upstream of the dam was preferred. A fish pass for downstream migration has been incorporated. Also the fish passes on the rivers Bagmati, Modi and Trijuga do not seem to function properly.

The construction of major and medium dams and barrages has accelerated in India due to the increased need of water for agriculture, industry and community use. It is noteworthy that over the last forty years almost 200 billion cubic meters of storage has been created, thereby intercepting almost 30 percent of the available surface flow. While providing great benefits for agriculture through irrigation, the water resources projects have concurrently blocked the migration routes of fish leading to considerable reduction in fish catch. The dams modify significantly the historical flow patterns of the rivers and in turn have led to a radical change of the river ecology affecting fish in particular. In addition to an overall loss of fish production, many diadromous species are threatened with extinction because of habitat destruction and obstruction of migration routes at the barriers (P.B. Das pers. comm. 2003).

Bad experience in the past, with catches dropping due to the construction of dams and weirs without or with poorly designed fish passes, has led to the construction of some fish passes in India in more recent years. However, some of these passes have not been effective in the absence of detailed studies of the target species and their swimming capabilities. The economic sustainability of the fishing communities along many large rivers has been affected significantly, with colossal annual losses. With barrages on the main arm of Ganges and its tributaries, even the Dolphin population (rare species) has decreased and isolation of subpopulations makes the species even more vulnerable genetically (P.B. Das pers. comm. 2003).

Data on the performance of fish passes, fish landings, spawning and growth patterns on some of the large Indian rivers, such as Ganges (at Farakka barrage), Yamuna (Hathnikund barrage), Mahanadi (Hirakud Dam and barrage at Cuttack) and Cauveri (Mettur Dam) has been collected by research institutes.

Detailed information on the migratory fish species has been collected by the Central Inland Fisheries Research Institute (CIFRI) before a fish pass was designed at the Farakka barrage, which was built in 1975 on the Ganges River. This information included data on species’ biology and behaviour, their spawning habits, characteristics of migration and swimming performance, number and size of fish passing per hour and, last but not least, the economical value of the fisheries they are supporting. As a result, two fish locks have been constructed but the commercially important Hilsa shad (*Tenualosa ilisha*) has highly suffered from Farakka barrage blocking of almost 1 000 km of its migratory path. Today, the upstream catches do not show a coherent tendency, with only one of four landing sites reporting an increase in catch after the construction of the barrage. No detailed analysis as to the functioning of the fish locks has been available (P.B. Das pers. comm. 2003).

A drastic reduction in fish yield has been noticed due to Salandi Dam, which became operational in 1970 in Orissa State. The annual catch of the main species has fallen from annually 350 tonnes (1950-65) to approximately 25 tonnes (1995-2000) in the same river reach. After a dam was built on the Mahanadi River, fish catch dropped form 800 tonnes to 500 tonnes Two new barrages, built between 1985 and 2000, have been equipped with Denil-type fish passes, which are reported to have increased upstream catches. A study of Beas River has revealed the adverse impact of water abstraction on aquatic life due to the diversion of Beas water to Sutlej by a dam at Pondo. *Tor putitora*, another important species, has been negatively affected by being cut off from important spawning grounds. Where large losses of fish occur at high water discharges that require the excess water to be spilled over a dam, fish passes would be an appropriate means to help fish migrating back into the reservoir.

The two major 100-year old barrages on the Ganges at Haradwar and on the Yamuna at Tajewala have proved detrimental to the migration of *T. putitora* in particular as the old fish pass constructed in the early 1890s did not prove effective. The new barrage on Yamuna, constructed in 1999, was equipped with a Denil-type fish pass, which seems to benefit upstream migration of *T. putitora*. However, in general the new Indian fish passes have only partially mitigated the migration problem. Therefore, a comprehensive solution is to incorporate fish passes at all major barrages for the benefit of the families fishing along the thousands of kilometres of main rivers (P.B. Das pers. comm. 2003).

The idea of the construction of fish passes and “fish friendly structures” (FPFS) has been introduced in Bangladesh in the 1990s and since then four FPFS have been built in the country (Kabir and Sharmin pers. comm. 2003). The primary objectives were to facilitate fish migration and reduce mortality rate of young fish while moving through the FPFS gates. Unfortunately, technical details of the fish passes and FPFS are not available and on this basis it is difficult to assess the structures. The differences between the two are not really clear but appear to lay in the seasonality, the efficiency for different fish sizes and the construction costs. The fish passes seem to be more efficient than the fish friendly regulators in terms of fish migration. The appreciation of efficiency is different in the different stakeholder groups, i.e. whereas fishers do not see any benefit, local officials think that the structures allow free passage. The main problem with both the structures does not seem to be of a technical nature but a management issue. Management committees have been established but do not function. Also, management regulations are missing and the structures have even been misused as fish traps.

Africa

Africa has over 2 000 known species of indigenous freshwater fishes. The construction of dams has multiplied since the 1950s for both irrigation and hydroelectric power generation.

Shad populations are present in North African rivers, namely in Morocco, but existing and some recent fish passes seem not to be adapted to this species. Shad disappeared from the Oum-er-Rbia after the construction of the Sidi-Saïd Dam, equipped with a Denil-type fish pass (Chapuis 1963). The fish pass planned in 1991 on the Garde Dam on the Oued Sebou was neither adapted to shad nor to the dam and was clearly bound to fail.

Apart from shad in North Africa, no anadromous species are known. As noted in Daget, Gaigher and Ssentongo (1988), dams are only likely to hinder potamodrous species such as large *Labeo*, *Barbus*, *Alestes*, *Distichodus* and *Citharinus* which migrate long distances up and down rivers in relation to their breeding cycle and seasonal flooding. The impact of dams is perhaps more obvious in the disappearance of biotopes for some rheophilic species located in areas where there are rapids, gorges or rocky ground, all of which are areas likely to be chosen for dam building.

In South Africa, the need for fish passes has become apparent only in recent years. This country has a low diversity of freshwater fish. In the coastal streams there are only six catadromous species: striped mullet, freshwater mullet and four species of eels (Mallen-Cooper 1996). In the more inland rivers of the Transvaal, there are potamodromous species, mainly cyprinids, with both juveniles and adult migrating upstream. The few existing fish passes (only 7 in 1990, Bok 1990), have been based on existing European and North American designs for salmonids and do not meet the needs of native species.

Australia

In temperate southeastern Australia, there are approximately 66 indigenous freshwater species; over 40 percent of these make large-scale movements or migrations that are essential for the completion of their life histories (Mallen-Cooper and Harris 1990). Coastal streams have many migratory fishes that are catadromous or amphidromous, with both juveniles and adults migrating upstream. In the second major drainage system, the Murray-Darling River system, most migrating species are potamodromous with adults migrating upstream. About 50 fish passes have been recorded (Mallen-Cooper and Harris 1990). Most of them are pool-type fish passes and were judged ineffective because inadequate maintenance and inappropriate design characteristics, i.e. steep slopes, velocities and turbulence were not adapted to native species.

In New South Wales, up to the mid-1980s salmonid pool-type designs (submerged orifice and pool-and-weir) with salmonid design criteria were used. Recent laboratory studies on native fish using experimental vertical-slot fishways were successful. Field studies on these vertical-slot fishways (with reduced head losses between pools and reduced turbulence compared with salmonid fishways) have confirmed effectiveness for native fishes (Mallen Cooper pers. comm. 2000). Rock ramps and nature-like bypass channels with very low slope (1:20 to 1:30) are used on smaller barriers. Their use is still experimental. They have had some initial success in passing fish and assessment in most cases is continuing (Mallen Cooper pers. comm. 2000).

In the state of Queensland, a tropical and subtropical region of Australia, about 22 fish passes were built prior to 1970, most of them on tidal dams (Barry 1990). Early designs were based on fish passes used for salmon and trout in the northern hemisphere. The majority of these fish passes were judged to be ineffective in providing native fish passage, mainly striped mullet (*Mugil cephalus*) and barramundi (*Lates calcarifer*) (Beitz 1997), which support important commercial fisheries.

Under the guidance of a Fish Pass Coordinating Committee, Queensland has begun a programme of fish pass design, construction and monitoring which better reflects the requirements of native fish. A major programme of retrofitting existing fish passes has been launched (Jackson 1997). The actual philosophy in Queensland is to use locks where dam heights exceed 6 metres and vertical slot fish passes elsewhere with 0.08 to 0.15 m drop heights between pools (Beitz pers. comm. 1999).

New Zealand

Of the currently recognised 35 indigenous freshwater fish species in New Zealand, 18 are diadromous. The species that require passage to and from the sea are the three eel species (*Anguilla* spp.), one lamprey (*Geotria australis*), five galaxiids (*Galaxias* spp.), two smelts (*Retropinna* spp.), four bullies (*Gobiomorphus* spp.), the torrentfish (*Cheimarrichthys fosteri*), grey mullet (*Mugil cephalus*) and black flounder (*Rhombosolea retiaria*). There is also one shrimp (*Paratya curvirostris*) which requires passage and numerous marine migrators have been affected by structures built in the lower reaches of waterways. Of the diadromous species, galaxiids (whitebait) and eels support important commercial, recreational and traditional fisheries. In addition to the indigenous species there is at least one species of the introduced salmonids that that do require passage to and from the sea. Other introduced species that have formed land locked populations, notably the introduced brown and rainbow trout, can also undertake extensive migrations within river systems (Boubée pers. comm. 2000).

The Fish Pass Regulation of the year 1947 gave fisheries authorities the right to require a fish pass on any dam or weir built on rivers where trout or salmon did or could exist. No provision was made for passage of indigenous species. Indeed, fisheries managers at that time advocated exclusion of elvers as beneficial to upstream population of introduced trout. By the early 1980s, only around eight fish passes had been built at the 33 or so major power, water and flood control dams scattered around the country. All eight passes had been constructed for salmon, which although introduced, were considered the most economically valuable fish species (Jowett 1987). Only with the introduction of the Freshwater Fisheries Regulation in 1983, did passage of indigenous fish species become a requirement for new structures.

Although several fish passes have been built since the 1980s, numerous migration barriers continue to exist not only at high dams but also at weirs, culverts and floodgates. Upstream passage for climbing native species has been mitigated by placing pipes or ramps lined with gravel or brushes over the barrier (Mitchell 1990, 1995). Although some success has been achieved at high dams, these type of passes have proven to be far more effective at low-head structures. More successful for high structures are catch and haul operations where elvers, climbing galaxiids and bullies are collected via short ramps into holding bins and transported upstream by road. Such operations have been particularly valuable in systems with one or more dam or where passage or access would be limited because of flow diversion (Boubée pers. comm. 2000).

With the increasing success of fish passes and transfer operations, downstream passage, especially of adult eels, now needs to be addressed. So far there are no downstream passage facilities installed at any of the hydropower dams.

Latin America

As noted by Northcote (1998), with possibly some 5000 species of freshwater fishes in South America and probably more than 1 300 in the Amazon Basin (Petrere 1989), the potential for fish passage problems at dams is enormous. Fish communities in the large rivers comprise mainly potamodromous characins and siluroids. Among the characins, prochilodids of the genera *Semaprochilodus* and *Prochilodus* make up a large proportion of the catches. The siluroids include *Pimelodus*, *Brachyplatystoma*, *Pseudoplatystoma* and *Plecostomus*. Fish can migrate distances from 200 km (Welcomme 1985) to more than 2 000 km (Barthem, Lambert de Brito de Ribeiro and Petrere 1991).

Hydroelectric impoundments are seen as potentially the most dangerous human-induced threat to Amazonian fisheries (Bayley and Petrere 1989). In Brazil, Petrere (1989) recorded about 1 100 dams managed by government authorities. Dam construction in the upper reaches of rivers appears to lead to the disappearance of migratory stocks in reservoirs and in the river upstream. Most dams have no facilities for fish passage (Quiros, 1989). He listed for the whole of Latin America only 46 fish passes with another 7 planned or under construction. The Itaipu Dam on the Paraná River was originally built without facilities for upstream migration. Only an experimental fish entrance unit was installed to obtain more precise information on the biology of the migratory species. However, the attracting flow was only 0.3 $m^3 s^{-1}$ when the average flow rate of the river was 11 800 $m^3 s^{-1}$ at times of the experiment (Borghetti *et al.* 1994). A fish pass has now been built covering a differrence in elevation of 120 meters. This pass is more than 7 km long and consists of three different sections, i.e. the lower part of the pass uses the river channel of a small tributary to the Paraná River, the middle section is a pool-type pass and the upper part is built as a by-pass channel. There is one big lake at the outlet of the pool-type section (about half way up the pass) and a small lake two-thirds up the by-pass channel; they can be used as resting “pools” for fish using the pass. Monitoring will show the efficiency of the pass in the years to come.

The first fish passes built in Latin America were pool-and-weir types, used in the northern hemisphere for passing salmonids. More recently, fish locks and mechanical fish lifts based on Russian experience described by Pavlov (1989) have been built for obstacles over 20 m in height.

Very few fish passes have been evaluated and they seem to function with varying degrees of success. Quiros (1989) mentions three ineffective passes in Argentina. Godinho *et al*. (1991) captured in a fish pass 34 of the 41 species present in the region of the Salto do Morais Dam. However, the fish pass seemed selective, there were few individuals of each species and only 2 percent of them reached the upper section of the fish pass. They mentioned another fish pass at Emas Falls on a low dam that seems to be more efficient.

As noted by Clay (1995), experiences from Latin American seem to be following that of other parts of the world, with limited success, because of lack of knowledge of the species involved and lack of application of the criteria needed for good fish pass design.

CONCLUSIONS AND RECOMMENDATIONS

If a new dam or weir is planned and constructed, the project cycle usually consists of six major phases, i.e. the identification phase, the design phase, the project appraisal phase, the construction phase, the operation phase and the decommissioning phase (World Bank 1991a, 1991b, 1991c). In this respect, fisheries interests should be taken into consideration right from the beginning. Bernacsek (2001) has identified specific fisheries management capacity and information base requirements for the six phases of the dam project cycle. For example, during the dam identification phase, basic information in as much detail as possible should be gathered as regards the status of the aquatic environment, fish biodiversity, fish migration, existing fisheries upstream and downstream as well as regarding the likely impacts the dam might have and possible mitigation measures. The key output during the second phase must contain an assessment of the level of impacts on and the risks for fish and fisheries, as well as a statement with regard to the degree of suitability and acceptability - or need for rejection - of the project *from a fisheries point of view*. Where the construction of a dam cannot be avoided care has to be taken that the needs for fisheries management are addressed, *inter alia* through the construction of fish passage facilities (Cowx and Welcomme 1998; Bernacsek 2001).

Fish passes have been developed mainly in North America and Europe for a very limited number of target species, mainly salmonids and clupeids, present in these countries. Today, the design of such passes can be considered relatively well developed for these species. Salmonids and clupeids are the only species for which reliable, quantitative data exists on the effectiveness of passes. In general, data is gathered through monitoring (trapping or video surveillance) or marking/recapture and telemetry experiments. By respecting a certain number of design criteria regarding the pass itself, its location, the position of its intakes and the flow, it is possible to design passes that are relatively effective in terms of percentage of the population able to pass without major delay.

While suitable passes can also be designed for other species, much less data is available on their effectiveness, particularly for potamodromous or catadromous species such as eels. It is often difficult to assess the real efficiency of such passes in so far as the migration needs and the part of the population likely to use the pass are often unknown.

Interrupted upstream fish passage is only one of the aspects of dam-induced problems. Very often, also the downstream migration is rendered difficult or made impossible. In addition, there are indirect effects, e.g. changes in water flow rates, water quality, increase in predation and more particularly the loss or deterioration of upstream or downstream habitat. An accumulation of these factors, especially at high dams or for a series of dams, may compromise the survival of migrating fish populations. This remark is in keeping with the trend in both North America and Europe to decommission dams of limited usefulness or those considered having a major impact on the environment. This is a trend of increasing importance and, for example, in the United States dozens of dams have been removed since 1999 after the breaching of Edwards Dam on Maine’s Kennebec River. In the last years, many more dams have been proposed for removal to restore the native salmon fisheries, e.g. Elwha and Glines Canyon dams, as well as four dams on the lower Snake River. In France, three dams have been destroyed on rivers whose migratory population was the subject of a restoration programme.

In countries where fish pass technology is advanced for a very limited number of species, fish passes may be considered an effective means of mitigation for obstacles that do not drastically modify neither the upstream habitat conditions (by their height or their number in the case of series of dams) nor the water flow and quality.

The situation is very different in other countries, e.g. in particular in South America, Asia and Oceania, where the biology and migratory behaviour, i.e. periods and stages of migration, of many species is not well known or even unknown. There, fish passes must often accommodate species of very different sizes, swimming abilities and migratory behaviour and especially small catadromous species with limited swimming abilities. Very often, fish pass design has been based on American or European experience with salmonids and most frequently with less-than-optimal design criteria, which makes the passes generally unsuitable for the species concerned. The passes are often undersized and not particularly well adapted to the pertaining hydraulic conditions. Also, the attraction aspect of the fish pass entrances has rarely been adequately considered. The lesson learnt is that for such countries, many of which are developing countries, maintaining or restoring free fish passage has, if at all, almost never been given appropriate attention. The effectiveness of such passes has very rarely been assessed and in such conditions it is not surprising that the situation may be considered catastrophic.

When discussing passes in South America, Quiros (1989) noted that the lack of knowledge of the swimming ability and migration behaviour of the native species in developing countries, coupled with the lack of available data on their behaviour, means that it is impossible to establish broad guidelines regarding the most suitable fish pass designs. Therefore, the priority must be to acquire a better knowledge of fish communities, their biology and their migratory behaviour which should enable stakeholders to better define the objectives of a fish pass in a given river and to design more suitable devices.

Suitable technologies should therefore be developed for contexts other than North America or Europe. Countries such as Japan and Australia have become aware of the specific nature of their problems and have undertaken to develop a technology suitable for their own rivers and their own species: two symposia were held in Japan in 1990 and 1995 and two workshops in Australia in 1992 and 1997, which enabled an overview to be drawn up and priorities to be defined such as to conduct well resourced and directed research to determine migratory requirements, to design programmes involving the appropriate mix of biologists and engineers, to make commitments to monitor all new or modified fishways and to adopt a holistic approach identifying fish passage within a whole river rather than past individual barriers. The results obtained already appear encouraging.

As also outlined in the FAO Code of Conduct for Responsible Fisheries (FAO 1995) and the related Technical Guidelines (FAO 1997), a precautionary approach should be adopted, i.e. the fact that knowledge of the migratory behaviour and the swimming capacities of many species is scarce or non-existing must not be an excuse for doing nothing. Doing nothing is, however, unfortunately all-too-often the option that is adopted, as was recently the case of the Petit Sault Dam on the Sinnamary River in French Guiana.

In the absence of good knowledge of the characteristics of the species concerned, the fish passes must be designed to be as versatile as possible. Some passes, such as vertical slot passes with successive pools, are more suitable than others when targeting a vast variety of species because the drop between pools and thus the energy dissipated in each pool can be adapted to the fish size. Selective or highly specific passes, such as Denil passes or mechanical lifts, should be avoided. Also, provisions must be made to allow for modifications of the construction, if necessary, e.g. if indicated by monitoring results. Thus, a comprehensive monitoring programme must be part of any fish passage rehabilitation project and devices to monitor fish passage must be installed. This monitoring process will enable the fish pass to be assessed and the feedback thus obtained may be useful for improving the pass, if necessary, or for designing other fish pass projects in the same regional context.

For high dams, when there are numerous species of poorly-known variable swimming abilities, migratory behaviour and population size, it is best to initially concentrate mitigation efforts on the lower part of the fish pass, i.e. to construct and optimize the fish collection system including the entrance, the complementary attraction flow and a holding pool which can be used to capture fish to subsequently transport them upstream, at least in an initial stage. This was the policy adopted by France in the 1980s for the first large passes for shad, until the fish pass technology had been fully mastered for shad (Travade *et al.* 1998).

Fish pass design involves a multidisciplinary approach. Engineers, biologists and managers must work closely together. Fish passage facilities must be systematically evaluated. It should be remembered that the fish pass technique is empirical in the original meaning of the term, i.e. based on feedback from experience. If one looks at the history of fish pass techniques, it is clear that the most significant progress has been made in countries that systematically assessed the effectiveness of the passes and in which it was required to provide monitoring results. It is the increase in monitoring and the awareness of the need for checks which is at the origin of progress in fish pass technology in countries such as the United States, France and Germany and, more recently, Australia and Japan.

However, one should never lose sight of the limits of the effectiveness of a fish pass even if its design is optimum because even if the obstructed passage can be mitigated, there may exist indirect effects of dams as mentioned above which may prove of major significance. Complementary mitigation measures, e.g. modified flow management at certain times of the year, could prove indispensable for sustainable long-term preservation of migratory fish populations. The mitigation measures to be adopted to protect species from the negative impacts of a dam must thus consider a much wider context than the mere aspect of obstructed fish passage alone.

REFERENCES

Amstrong G.S. 1996. River Thames case study: Blakes weir fish pass, river Kennet. *In* R.H.K. Mann & M.W. Aprahamian eds. *Fish pass technology training course*. Dorset, UK, Environment Agency Publishers. pp. 87-102

America Society of Civil Engineers (ASCE). 1985. *Guidelines for design of intakes for hydroelectric plants*. NewYork, ASCE Publishers. 499 pp.

Bailey P. & Petrere M. 1989. Amazon fisheries: Assessment methods, current status and management options. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium. Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 385-398.

Barry W.M., 1990. Fishways for Queensland coastal streams: An urgent review. *In Proceedings of the International Symposium on Fishways '90.* Gifu, Japan. pp. 231-238

Barthem R.B., Lambert de Brito de Ribeiro M.C. & Petrere M. 1991. Life strategies of some long-distance migratory catfish in relation to hydroelectric dam in the Amazon basin. *Biological Conservation*, 55: 339-345.

Bate K. 1992. *Fishway design guidelines for Pacific salmon. Report of Washington Department of Fish and Wildlife.* 110 pp.

Beach, M.H., 1984. Fish pass design - criteria for the design and approval of fish passes and other structures to facilitate the passage of migratory fishes in rivers. Ministry of Agriculture, Fisheries and Food, Lowestoft. *Fish. Res. Tech. Rep.*, 78: 45.

Beitz E. 1997. Development of fishlocks in the Queensland. *In* A.P. Berghuis, P.E. Long & I.G. Stuart eds. *Second National Fishway Technical Workshop*. Rockhampton, Australia, Fishery Group, Department of Primary Industries Publishers. pp. 125-15.

Bernacsek G.M. 2001. Environmental issues, capacity and information base for management of fisheries affected by dams. *In* G. Marmulla ed. *No. 419. Dams, fish and fisheries: Opportunities, challenges and conflict resolution. FAO Fisheries Technical Paper.* Rome, FAO. 166 pp.

Bok A.H. 1990. The current status of fishway in South Africa and lessons to be learnt. *In Proceedings of the Workshop on the rationale and procedures for the evaluation of the necessity for fishways in South African rivers*. Pretoria, Australia, March 1990. pp. 87-99.

Borghetti J.R., Nogueira V.S., Borghetti N.R. and Canzi C. 1994. The fish ladder at the Itaipu binational hydroelectric complex on the Parana river, Brazil. *Regulated Rivers: Research & Management*, Vol. 9: 127-130.

Cada G. 1998. Fish passage migration at hydroelectric power projects in the United States. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. *Fish migration and fish bypasses*. Fishing News Books, Blackwell Science. pp. 208-219.

Chapuis M. 1963. Des échelles à poissons et du franchissement des barrages par les aloses. *Bulletin Annuel de Pisciculture du Maroc*, pp. 20-23.

Clay C.H. 1995. Design of fishway and other fish facilities, 2nd edition. Boca Raton, Florida, USA, CRC Press Publisher. 248 pp.

Conrad V. & H. Jansen, 1983. *Refinements in design of fishways for small watersheds*. Paper presented at Northeast Fish and Wildlife Conference, Dover, Vermont, USA, 15-18 May. 26 pp.

Cowx I.G. 1998. Fish passage facilities in the UK: Issues, and options for future development. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. *Fish migration and fish bypasses*. London, Fishing News Books, Blackwell Science. pp 220-235.

Cowx I.G. & Welcomme R.L. 1998. Rehabilitation of rivers for fish. European Inland Fisheries Advisory Commission of the United Nations Food and Agriculture Organization. London, Fishing News Books, Blackwell Science. 260 pp.

Daget J., Gaigher I.C. & Sentongo G.W. 1988. Conservation. *In* C. Levêque, M.N. Bruton & G.W. Sentongo eds. Biologie et écologie des poissons d'eau douce Africains. Paris, Editions de l'ORSTOM. pp. 481-491.

DVWK Deutscher Verband für Wasserwirtschaft und Kulturbau, 1996. Fischaufstiegsanlagen - Bemessung, Gestaltung, Funktionskontrolle. *Merkblätter zur Wasserwirtschaft.* Vol. 232: 110.

Elvira B., Nicola G. & Almodovar A. 1998. Impacto de las obras hidraulicas en la ictiofauna. Dispositivos de paso para pesces en las presas de Espana. *Colleccion Technica. Organismo Autonomo Parques Nacionales.* 207 pp.

EPRI. 1994. *Research update on fish protection technologies for water intakes*. Stone and Webster Engineering. Corp. 225 pp.

Euston E.T., Royer D. & Simons C. 1998. American eels and hydro plants: Clues to eel passage. *Hydro Review*, Vol. 174: 94-103.

FAO. 1995. *Code of Conduct for Responsible Fisheries*. Rome. 41 pp.

FAO. 1997. *FAO Technical Guidelines for Responsible Fisheries: Inland fisheries. No. 6.* Rome. 36 pp.

FAO/DVWK. 2002. *Fish passes: Design, dimensions and monitoring*. Rome. 119 pp.

Ferguson J.W., Poe T.P. & Carlson T.J. 1998. The design, development, and evaluation of surface oriented juvenile salmonid bypass systems on the Columbia River, USA. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. *Fish migration and* *fish bypasses*. London, Fishing News Books, Blackwell Science. 281-299.

Francfort J.E., Cad G.F., Dauble D.D., Hunt R.T., Jones D.W., Rinehart B.N., Sommers G.L. & Costello R.J. 1994. Environmental mitigation at hydroelectric projects. Idaho, US Department of Energy Publishers. 303 pp.

Gebler R.J. 1998. Examples of near-natural fish passes in Germany: Drop structure conversions, fish ramps and bypass channels. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. *Fish migration and fish bypasses*. London, Fishing News Books, Blackwell Science. pp. 403-419.

Godinho H.P., Godinho A.L., Formagio P.S. & Torquato V.C. 1991. Fish ladder efficiency in a south-eastern Brazilian river. *Ciencia e Cultura*, Vol. 43: 63-67.

Grande R. 1990. Fish ladder in Norway. *In Proceedings of the International Symposium on Fishways ’90*. Gifu, Japan. pp. 517-522.

Hadderingh R.H., Van Der Stoep J.W. & Hagraken J.M. 1992. Deflecting eels from water inlets of power stations with light. *Irish Fish. Invest*., Vol. 36: 37-41.

Jackson P. 1997. Strategy for fish passage in Queensland. *In* A.P. Berghuis, P.E. Long & I.G. Stuart eds. *Second National Fishway Technical Workshop*. Rockhampton, Australia, Fishery Group, Department of Primary Industries Publishers. pp. 1-7

Jowett I.G. 1987. Fish passage, control devices and spawning channels. *In* P.R. Henriques ed. *Aquatic biology and hydroelectric power development in New Zealand*. Auckland, Oxford University Press. pp. 138-155.

Laine A., Kamula R. & Hooli J. 1993. Fundamental concepts of fish passage in Scandinavian countries. Fish passage policy and technology. *Pro. Symp. Bioeng. Am. Fish. Soc*. Portland, Oregon, September 1993. pp. 81-85.

Larinier M. 1983. Guide pour la conception des dispositifs de franchissement des barrages par les poissons migrateurs. *Bulletin Français de Pêche et Pisciculture, Special Edition*. 39 p.

Larinier M. 1990. Experience in fish passage in France: Fish pass design criteria and downstream migration problems. *In Proceedings of the International Symposium on Fishways ’90*. Gifu, Japan. pp. 65-74.

Larinier M. 1992a. Passes à bassins successifs, prébarrages et rivières artificielles. *Bulletin Français de Pêche et Pisciculture*, Vol. 326/327: 45-72.

Larinier M. 1992b. Les passes à ralentisseurs. *Bulletin Français de Pêche et Pisciculture*, Vol. 326/327: 73-94.

Larinier M. 1998. Upstream and downstream fish passage experience in France. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. *Fish migration and fish bypasses*. London, Fishing News Books, Blackwell Science. pp. 127-145.

Larinier M. & F. Travade 1999. La dévalaison des migrateurs: Problèmes et dispositifs. *Bulletin Français de Pisciculture*, Vol. 353/354: 181-210.

Lonnebjerg N. 1980. Fiskepas af modströmstypen. Meddelser fra Ferskvandsfiskerilab. Fiskeri-og Havundersogelser, Silkeborg, Denmark. 107 pp.

Mallen-Cooper M. 1996. Fishways and freshwater fish migration in Southeastern Australia. University of Technology, Sydney. 377 pp. (doctoral dissertation)

Mallen-Cooper M. & Harris J. 1990. Fishways in mainland Southeastern Australia. *In Proceedings of the International Symposium on Fishways ’90*. pp. 221-230.

Mitchell C. 1990. Fish passes for New Zealand native freshwater fish. *In Proceedings of the International Symposium on Fishways '90*. Gifu, Japan. 239-244.

Mitchell C. 1995. Fish passage problems in New Zealand. *In Proceedings of the International Symposium on Fishways '95*. Gifu, Japan, 33-41.

Monan G., Smith J., Liscom K. & Johnson J. 1970. *Evaluation of upstream passage of adult salmonids through the navigation lock at Bonneville dam during the summer of 1969. 4th Progress Report on Fish. Eng. Res. Prog. 1966-1972*. U.S. Army Corps of Engineers, North Pacific Div. pp. 104-113.

Nakamura S. 1993. A review of fish passage facilities in East Asia. Fish passage policy and technology. *In Proceedings of the Symposium*. Portland, Oregon, USA. pp. 87-94.

Nakamura S. & Yotsukura N. 1987. *On the design of fish ladder for juvenile fish in Japan*. Paper presented at the International Symposium on Design of Hydraulic Structures, Fort Collins, Colorado, USA, 24-27 August. pp. 499-508.

Nakamura S., Mizuno N., Tamai, N. & Ishida R. 1991. An investigation of environmental improvements for fish production in developed Japanese rivers. *Fisheries Bioengineering Symp. 10. American Fisheries Soc. Symp. USA*. pp. 32-41.

Northcote T.G. 1998. Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. Fish migration and fish bypasses. Oxford, UK, Fishing News Books, Blackwell Science. pp. 3-18.

Odeh M. & Orvis C. 1998. Downstream fish passage facilities design considerations and development at hydroelectric projects in the Northeast USA.

Office of Technology Assessment (OTA). 1985. *Fish passage technologies: Protection at hydroelectric facilities. Report OTA-ENV-641*. Washington, DC. 167 pp.

Parasiewicz P., Eberstaller J., Weiss S. & Schmutz S. 1998. Conceptual guidelines for natural-like bypass channels. *In* M. Jungwirth, S. Schmutz & S. Weiss eds. *Fish migration and fish bypasses*. Oxford, UK, Fishing News Books, Blackwell Science. pp. 348-362.

Pavlov D.S., 1989. *Structures assisting the migration of non-salmonid fish. USSE. FAO Fish. Tech. Pap*. No. 308. Rome, FAO. 997 pp.

Petrere M. 1989. River fisheries in Brazil: A review. *Regulated Rivers: Research & Management*, Vol. 4: 1-16.

Philippe L. 1897. *Rapport sur les échelles à poissons*. Ministère de l'Agriculture, Commission des Améliorations Agricoles et Forestières. 27 pp.

Porcher J.P. 1992. Les passes à anguilles. *Bulletin Français de Pêche et Pisciculture*, Vol. 326/327: 134-141.

Quiros R. 1989. Structures assisting the migrations of non-salmonids fish: Latin America, *FAO-COPESCAL Technical Paper* 5. Rome, FAO. 41 pp.

Rajaratnam N. & Katopodis C. 1984. Hydraulics of Denil fishways. Vol. 110: 1219-1233.

Rizzo B. 1969. Fish passage facilities design parameters for Connecticut river dams. Turners Falls Dam. Boston, MA, USA, Bureau of Sport Fisheries and Wildlife. 33 pp.

Travade F. & Larinier M. 1992. Ecluses et ascenseurs à poissons. *Bulletin Français de Pêche et Pisciculture*. Vol. 326/327: 95-110.

Travade F., Larinier M., Boyer-Bernard & S.J. Dartiguelongue, 1998. Performance of four fish pass installations recently built in France. *In* Fish migration and fish bypasses eds. M. Jungwirth, S. Schmitz & S. Weiss. Fishing News Books, Oxford, UK, Blackwell Science Ltd. Publisher: 146-170.

Wan Y. 1990. Design and application of fish passage and protection facilities in China. *In Proceedings of the International Symposium on Fishways '90*. Gifu, Japan. pp. 53-63.

Washburn & Gillis. 1985. Upstream fish passage. Montréal, Canada, Canadian Electrical Association. 34 pp.

Welcomme R.L. 1985. *River Fisheries. FAO Fish. Tech. Pap*. No. 262. Rome, FAO. 330 pp.

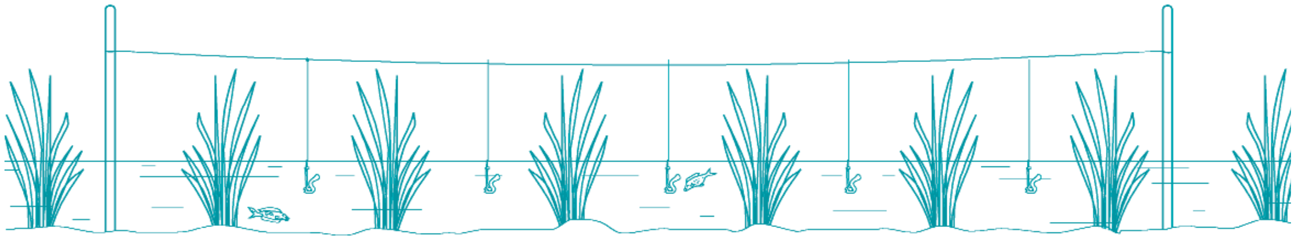
World Bank. 1991a. Environmental *assessment source-book, volume1: Policies, procedures, and cross-sectoral issues, World Bank technical paper No. 139*. Washington, DC, USA. 227 pp.

World Bank. 1991b. Environmental assessment source-book, volume 2: Sectoral guidelines, world bank technical paper No. 140. Washington, DC, USA. 282 pp.

World Bank, 1991c. Environmental assessment source-book, volume 2: Guidelines for environmental assessment of energy and industry projects, World Bank technical paper No. 154. Washington, DC, USA. 237 pp.

Zhili G., Qinhao L. & Keming A. 1990. Layout and performance of Yangtang fishway. *In Proceedings of the International Symposium on Fishways '90*. Gifu, Japan. 283-287.

Ziemer G.L., 1962. Steep pass fishway development. Informational Leaflet of Alaska Department of Fish and Game. 9 pp.



COMMUNITY FISHERIES AND CO-MANAGEMENT ON THE LOWER AMAZON FLOODPLAIN OF BRAZIL

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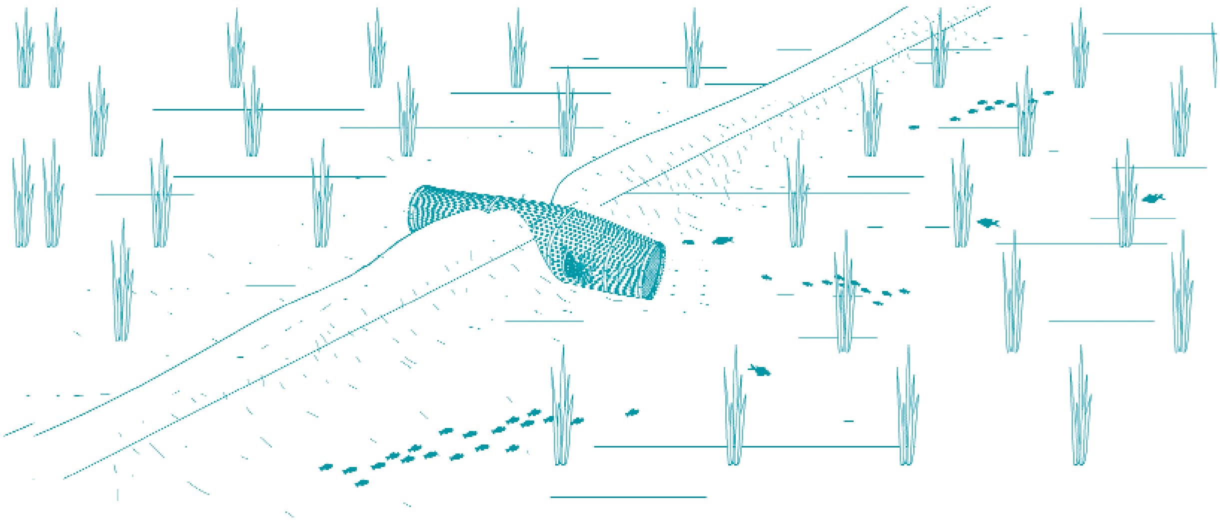


ABSTRACT

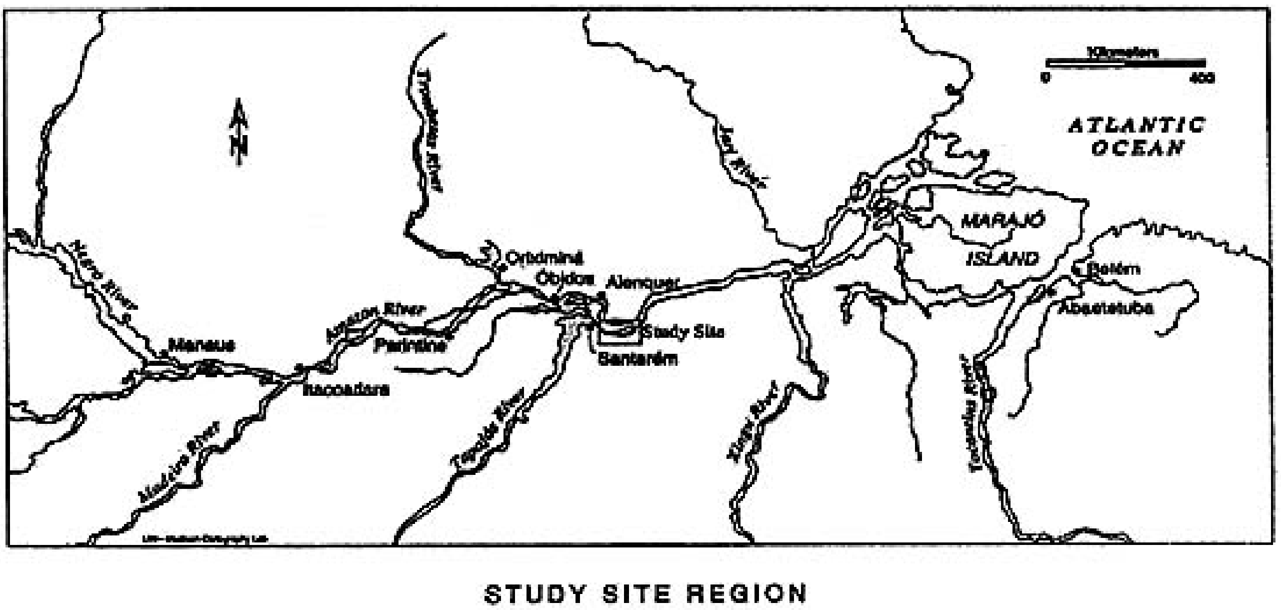
In response to the growth of Amazon commercial fisheries, a loose regional network of community-managed lakes has proliferated throughout the Amazon floodplain system. This approach has been widely perceived as a promising alternative for the sustainable management of floodplain fisheries. Over the last decade, communities, NGOs, grassroots organizations, and IBAMA - the Brazilian environmental agency, have worked together to develop a co-management system for floodplain fisheries based on the legal recognition of community fishing agreements. This paper examines the experience of the Santarém region of the Lower Amazon, the major regional experiment in fisheries co-management. Here, while considerable progress has been made in setting up a functional co-management system, it suffers from serious problems that undermine its effectiveness and threaten its long-term sustainability. Unless communities are permitted to restrict access and charge user fees, it is unlikely that the co-management system will survive once funding for project implementation terminates. There are, however, legal precedents for making the necessary design changes, thereby increasing prospects for the long-term institutional sustainability of the system.

INTRODUCTION

Like many other regional fisheries in the world, fisheries managers in Amazonian Brazil have been experimenting with the implementation of a co-management system since the early 1990s (Castro 2000; Castro and McGrath 2002). The move towards co-management of Amazon fisheries is in part a response to pressure from grassroots movements for community control of floodplain lakes and in part related to changes in environmental management policy at the national level. As elsewhere, adoption of a co-management model is widely regarded as a response to the poor performance of the centralized, top-down management model that has characterized fisheries management in Brazil since its inception (McGrath *et al*. 1999; McGrath 2000). Co-management, by incorporating resource users into the management process, is seen as the most effective way of resolving many of the problems associated with the conventional scientific model of fisheries management, especially those involving resource depletion, conflicts between user groups and development of policies that better address the characteristics of local fisheries (Pinkerton 1989; McGoodwin 1990; Jentoft and McCay 1995).

While the trend towards participatory management is world wide, motives and outcomes can be quite varied. In this context, it is important to distinguish between countries with well-developed institutional structures for resource management and those where resource management institutions are rudimentary or insufficient for maintaining an effective presence in the field. The problem may be quite different in these two contexts. While in the former case increasing user group participation may be an appropriate corrective to the overly centralized approach that often characterizes scientific management (Sen and Nielsen 1996), in the latter case, pressures to increase user group participation may be due to the absence of an effective governmental presence rather than to the poor performance of the scientific management model *per se* (Sunderlin and Gorosope 1997). In these latter cases simply increasing user group participation may be insufficient to improve the effectiveness of local resource management systems.

Over the last ten years a co-management system has evolved in the Lower Amazon floodplain that is a product of both local initiative, government design and efforts of local NGOs and international funding agencies. Though still largely an experimental approach now being tested in a few regions, implementation in these areas has progressed sufficiently so it is possible to trace the main outlines of the emerging system. This paper analyses the experience of the Santarém region of the lower Amazon floodplain, the major Brazilian experiment in fisheries co-management (Figure 1). We describe the process through which community initiatives are being incorporated into an evolving institutional framework for co-management, evaluate progress to date and outline the key



■ **Figure 1.** Lower Amazon region

issues yet to be addressed if this approach is to provide an effective basis for a regional fisheries management policy.

BACKGROUND

While the origins of the current Amazonian experience in co-managing floodplain fisheries can be traced to regional grassroots movements, changes in national policy and even worldwide trends in fisheries management, it is fundamentally the result of local efforts to resolve conflicts and pressures resulting from within the sector itself (Hartmann 1989; McGrath *et al.* 1993; Castro 2000). While nowhere near as well organized, the community lake reserve movement has many parallels with the rubber tapper movement that captured world attention with the assassination of the charismatic rubber tapper leader, Chico Mendes (Allegretti 1995; Schwartzmann 1989). Like the forest people's movement, floodplain communities were motivated by a perceived threat to their resources and way of life resulting from developments in the regional economy; the eclipse of traditional extractive activities by logging and ranching in the case of rubber tappers and the intensification of commercial fisheries in the case of flood plain communities (McGrath *et al*. 1993; Lima 1999; McDaniel 1997). Another common denominator is the strong, though regionally variable, tie to the Catholic Church and Liberation Theology (Lima 1999; Oliveira and Cunha 2002).

Three or four phases can be identified in the emergence of the co-management system: the rise of a modern commercial fishery in the 1960s and 1970s; mobilization of floodplain communities to defend local lakes as part of regional rural labour movements in the 1980s; proliferation of fishing accords as a local strategy within the context of the Amazon wide movement of traditional peoples in the early 1990s; and in the latter half of the decade the effort to integrate these community-based initiatives into a new co-management system for floodplain fisheries.

Rise of Commercial Fisheries

Conflicts between largely agricultural communities and commercial fishers over access to floodplain lakes began early in the development of Amazon commercial fisheries. The introduction of gillnets made of synthetic fibres, diesel engines, ice and fish processing plants led to the transformation of Amazon commercial fisheries from a seasonal activity involving dried salted fish to a year round activity involving fresh and frozen fish (Chapman 1989; McGrath *et al*. 1993; Smith 1985; Veríssimo 1970). With these changes there arose a class of professional, urban-based, commercial fishers know as *geleiros*, who exploited lake fisheries in a steadily expanding radius from major urban centres such as Belém and Manaus (Almeida *et al.* 2001; Goulding 1983). As exploitation of floodplain lakes intensified, conflicts over access to fisheries proliferated. Major conflicts erupted in the Monte Alegre lake system just downstream from Santarém in the mid-sixties and in the Janauacá lake system above Manaus in the early seventies (Hartmann 1989; Junk 1984).

Mobilization of Rural Labour

In the 1980s community opposition to outside commercial fishers was organized and integrated into rural labour movements dedicated to ending two decades of military dictatorship (Leroy 1990; Lima 1999). During this period, experiments with collective fishing agreements emerged in various places along the Amazon River such as Tefé on the Solimões River, Silves below Manaus and Santarém. In the state of Amazonas (Tefé and Silves) the Catholic Church through the efforts of MEB (Movimento Educacional de Base) and the CPT (Comissão Pastoral da Terra) played a major role in organizing communities for managing local fisheries (C.P.T. 1992a, 1992b; Oliveira and Cunha 2002). In the Santarém area FASE (Federação de Órgãos para Assistência Social e Educacional) worked with the municipal Fishermen's Union [*sic*] to organize regional fishers and wrest the Union from the hands of government appointed administrators (Leroy 1990). Here, though, because the Union represents all fishers, support for community agreements was ambivalent and most such agreements were local initiatives with little outside support (McGrath *et al.* 1993; Castro 2000).

Lake Fisheries Accords

The third phase began in the late 1980s with the growth of the people of the forest movement (Povos da Floresta). What distinguishes this phase is the development of a strategic alliance between the rural labour and environmental movements around the proposal for conserving forests through use by traditional populations ((Shwartzmann 1989). The assassination of the rubber tapper leader, Chico Mendes, in 1989 led to a massive outpouring of national and international support for the rubber tappers and traditional Amazon populations in general (Gryzbowski 1989). This support was rapidly translated into major institutional changes including the creation of the first extractive reserves and the establishment within IBAMA of the National Centre for Traditional Populations (CNPT) (Allegretti 1995). At the same time international funding for conservation initiatives involving traditional populations increased enormously.

While the major emphasis of institutional and financial support has been for forest-based initiatives, this period also witnessed the proliferation of experiments in community lake management throughout the floodplain region and the establishment of several major projects to develop the community lake management model as a floodplain equivalent of the extractive reserve (IBAMA 1995); Projeto Várzea-IPAM (Almeida and McGrath 2000) and the Reserva de Desenvolvimento Sustentável Mamirauá (Lima 1999; Gillingham 2001). In the Santarém area the Colônia has taken a leadership role in working with floodplain communities to develop collective agreements for local lake fisheries. The number of such agreements in the region increased rapidly during this period. Two internationally funded projects in Santarém, Projeto Várzea of IPAM (Instituto de Pesquisa Ambiental da Amazônia) with funding from WWF-DFID and Projeto Iara a bilateral project involving the German government (GTZ) and IBAMA, also began to work with the Colônia and community organizations to develop a participatory management system for floodplain fisheries. During the first part of the decade many of the basic elements of the co-management model that IBAMA was later to implement were developed.

Implementing a co-management system

The fourth phase began in the latter half of the decade with the promulgation of a series of measures that step by step began to lay the legal and institutional basis for co-management of floodplain fisheries. These included decentralization of certain powers from the presidency of IBAMA to the regional superintendents, definition of criteria for legalizing fishing accords, definition of an institutional framework for co-management and creation of a category of volunteer community environmental agents. In addition, the Provarzea program of the G-7 Pilot Program for the Conservation of the Amazon Rainforest was finally approved, with the overall objective of developing the regional institutional and policy framework for co-management of floodplain fisheries (IBAMA 2001).

FISHING ACCORDS

One of the striking features of the community lake management movement of the Lower Amazon is that from quite early on it has been based on formal written documents (Castro and McGrath 2003). This reliance on written documents probably reflects the training community leaders received while participating in the activities of the Catholic Church and the rural labour movement. Known locally as “acordos de pesca” these documents typically consist of two parts, a short preamble, which may state the motives and objectives of the agreement and the area and communities covered and a list of the measures that govern fishing activity, define procedures for monitoring and enforcing accords and possibly sanctions for infractions. A list of signatures of those community members who support the accord may also be annexed.

The general objective of fishing accords is to control fishing pressure in local lake systems. They typically seek to achieve this objective indirectly by restricting the type of gear that can be used, storage capacity and or the sale of catch. Few if any accords specify catch limits or minimum size requirements, measures that would be more difficult to enforce. While few accords seek to prohibit commercial fishing entirely, many do seek to contain it. A central concern of floodplain fishers is to maintain the productivity of local fisheries at satisfactory levels with the gear they have. Floodplain fishers typically engage in a number of economic activities, including annual cropping, small animal husbandry and cattle raising and do not have either the time or the resources to compete with full-time commercial fishers.

A second important feature of accords is that in contrast to conventional fisheries management policies that seek to protect fish during the spawning season, most fishing accords seek to restrict fishing effort during the low water season when fish are concentrated in smaller water bodies and vulnerable to overexploitation (Isaac, Rocha and Motta 1993). They believe that the rising water levels that coincide with the spawning season provide species with adequate natural protection from fishing pressure. Typical measures during the low water period include the prohibition of gill nets and in some cases restrictions on the sale of fish outside the community. Flood season restrictions of fishing gear, on the other hand, are quite rare and tend to be site specific.

Surprisingly, given the formal presentation of the document itself, most accords are fairly sketchy on how monitoring and enforcement are to be organized. Few contain instructions on who and how these activities are to be carried out and most of these refer vaguely to community members or leaders. Only the most recent accords provide adequate information on how monitoring and enforcement are to be carried out. Those that do address the question of sanctions frequently specify graduated punishments, progressing from verbal warnings for first offenders to apprehension of gear and registration of complaints with IBAMA for those caught a second or third time. Frequently, gear are either held until the end of the closed season or turned over to the Colônia or IBAMA.

FORMALIZATION OF FISHING ACCORDS

While fishing accords are designed to assert community control over local lake fisheries, they should not be regarded as an attempt to substitute government authority. In fact, from the beginning, local leaders have sought to involve IBAMA and the Colônia in support of their accords. Leaders frequently deposit copies of their signed accords with the Colônia and IBAMA and often turn confiscated gear over to these institutions. They also frequently denounce infractors to IBAMA and actively lobby for IBAMA agents to patrol their lakes. One of IBAMA's first concrete actions in this direction took place in response to conflicts in the Lago Grande de Monte Alegre. This is one of the largest lake systems in the region and has a history of fisheries conflicts dating back to the mid 1960s (Hartmann 1989). In an attempt to resolve the problem, or at least separate the warring parties, IBAMA divided the lake into two zones, a northern zone where gillnets and commercial fishing were prohibited and a southern zone where they are permitted. While this was an isolated action at the time, it was an early effort in what later developed into a much more systematic approach to the problem of local participation in fisheries management (Hartmann 1990).

Over the course of the 1990s, the basic structure of the regional co-management system for floodplain fisheries has been developed. There were two interrelated concerns in this process, institutional and legal. The first has involved community level work to improve the performance of existing community management systems and the second development of the legal measures needed to integrate this system into a new formal policy and institutional framework for the co-management of floodplain fisheries.

As has been noted in other regions, the main problems with community fishing accords were identified as their fragile organizational base, the absence of mechanisms to insure representation of all major stakeholder groups and the lack of an explicit organizational structure for monitoring and enforcement.

While most communities have some form of elected leadership, very few have the capacity to actually organize and implement anything but isolated, short-term activities. Furthermore, with the exception of those areas where the Catholic Church and the Fishers' Union provide a regional organizational framework and leadership, there were no multi-community organizations to serve as the institutional base for fishing agreements. Both these organizations, however, had other priorities, organization of church activities in the first case and more political, union-oriented activities in the second.

A related problem is representation in the process of defining and approving fishing accords. Typically, interested individuals, who may or may not be part of their respective community's elected leadership, initiate the process by inviting members of communities sharing the same lakes to a meeting to discuss creation of the fishing accord. Through a series of such meetings a document is eventually produced that satisfies the participants. Those who are opposed to the idea of a fishing accord or to the specific proposals of those promoting the accord, tend not to participate. Since they do not participate, they do not feel any obligation to comply with its regulations once implemented. Since these people are typically the more commercially oriented fishers in the region, the fishing accord that is eventually created is fatally flawed. Unless there is exceptional resolve on the part of the proponents, it is likely to disintegrate if community members suspect that others are not complying.

To address the combined problems of organizational base and representation, efforts in Santarém focused first on creating intercommunity councils for the major lake systems. Called Regional Fisheries Councils, they are composed of representatives of all the communities sharing a common lake system. These councils were created to take responsibility for organizing the process of defining, approving and implementing fishing accords for their respective lake systems. Through an iterative process in which proposals for a fishing accord are developed at the community level, taken to the Regional Council for discussion and development of a common proposal, evaluated and where necessary amended by participating communities, a definitive version is finally developed and approved by the Regional Council and participating communities. While this process does not guarantee adequate representation, it does insure that all communities have roughly equal representation in developing the regional fishing accord and provides abundant opportunities for anyone to participate in the process.

A third problem area was that of monitoring and enforcement. As noted earlier, most fishing accords did not describe in adequate detail procedures for organizing the monitoring of fishing accords nor for judging those accused of infractions. Monitoring tends to be haphazard with irregular patrols of lakes typically conducted by a few community members while the great majority shirked their responsibilities. While such a system may be adequate for dealing with the occasional incursions of outsiders, it is problematic for dealing with situations where infractors are members of the community. In these latter cases, the informality and lack of representation of patrols and leadership leave those apprehending infractors vulnerable to the charge of bias and favouritism, clouding issues and calling into question the credibility of the whole endeavour. This is especially problematic in Amazonia where people are predisposed to assuming that others are dishonest and prone to favour their friends and relatives. While the structuring of Regional Fisheries Councils helped to inject a significant degree of institutional formality into the process of development and implementation, the absence of a legal basis for the developing system was a problem.

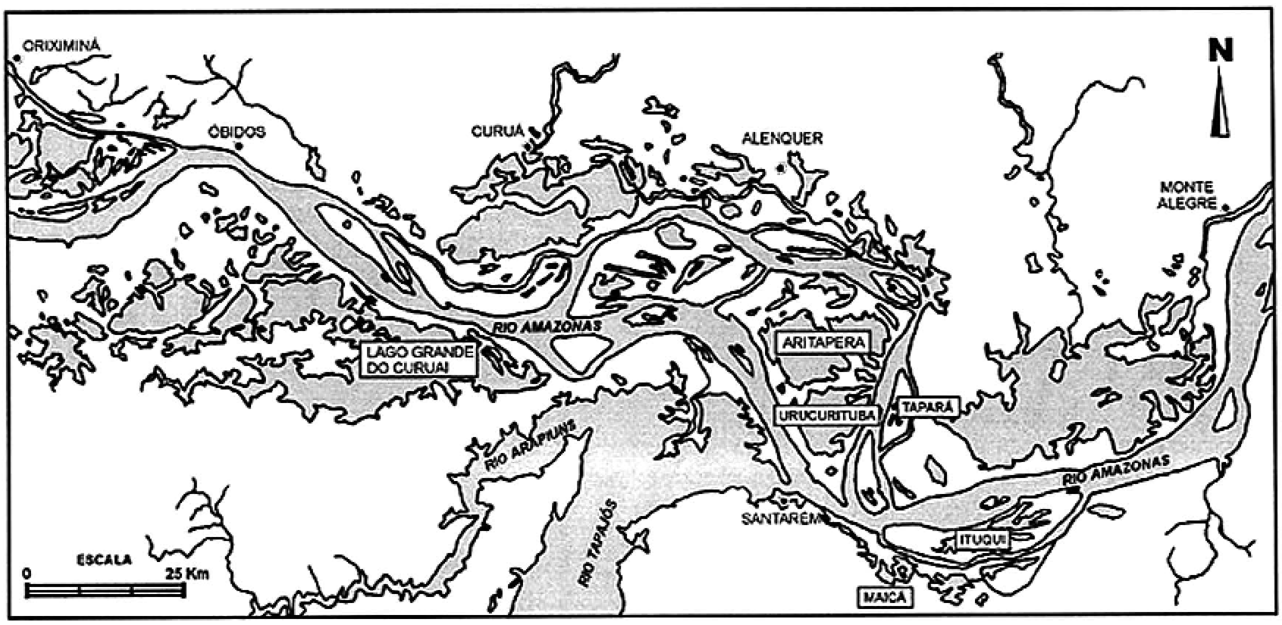
Integration of fishing accords into the formal institutional framework for fisheries management involved several steps whereby IBAMA moved from its initial position that community fishing accords were illegal to one in which they have become a fundamental component of the new co-management system for Amazon fisheries. The first step in this process was the decentralization in 1996 of legal authority to issue complementary administrative laws (*portarias complementares*) from the presidency of IBAMA to the regional superintendents (IBAMA 1996a). This move answered one early objection to legalizing fishing accords, which was that because of the size of the country; IBAMA's national office simply could not operate at such a small scale.

Another problem, though one of less importance to co-management, was that fisheries regulations were defined at the state level. In the case of the Amazon, the five or six Brazilian states of the Amazon basin all had slightly different minimum size requirements for many species, permitted different kinds of gear to be used, protected different species during the spawning season and defined the spawning season slightly differently. This was a constant source of problems, especially for the two states of Pará and Amazonas. Since neither state had much control over the fishery, it was easy for fishers to avoid one state's laws by travelling up or downstream to sell their catch in the other. In 1996 IBAMA issued a law homogenizing fisheries regulations at the basin rather than state level, eliminating many of the contradictions between states (IBAMA 1996b). This measure established the river basin and not the state as the basic unit of management, a move that brought fisheries management in line with the new water resources legislation passed the following year.

That same year an internal memorandum was released specifying criteria and procedures for the legal recognition of community fishing accords, opening the possibility for transforming them into *portarias complementares.* Two criteria are especially relevant, first, the agreement cannot contain provisions for limiting who can fish in the lake and second the agreement must be proposed by an organization that represents all the communities located within the lake system's boundaries and that takes responsibility for implementing the accord once it is approved.

While only an internal memorandum, this document provided the basis for development of regional co-management systems based on community fishing accords. The first fishing accord to be transformed into a *portaria complementar* was that of the Maicá region adjacent to the city of Santarém. This area had a long history of conflict with urban-based canoe fishers that had motivated the communities to seek legal recognition for their fishing accord. Over the next five years Regional Fisheries Councils were set up and fishing accords approved by IBAMA for all seven major lake systems of the municipality (see Figure 2).

Once a fishing accord becomes law, IBAMA is obligated to enforce it. However, merely legalizing the



■ **Figure 2.** Regional Fisheries Councils of the Santarém Region accord does not address the problems that have limited IBAMA's ability to enforce fisheries legislation, namely the lack of personnel, equipment and funds for maintaining an effective presence in the field. To resolve this problem IBAMA created the position of Volunteer Environmental Agent (VEA) (IBAMA 2001a, 2001c). These agents are community members who receive training in environmental legislation and enforcement procedures and are responsible for monitoring local compliance with environmental regulations. They do not have the power to make arrests or confiscate equipment, but only to issue citations, which they subsequently turn over to IBAMA field agents. These agents then take over pursuing the appropriate legal procedures for each case. IBAMA has organized several training courses for VEAs of regions that have legal fishing accords. Each community chooses one or two people to participate in the training. Frequently, although not necessarily, they are the community's representatives on the Regional Fisheries Council.

With the creation and training of the VEAs, the main components of the co-management system are now in place. Regional Fisheries Councils representing all the communities of a given lake system define fishing accords and submit them to the regional IBAMA office. If the accord meets IBAMA's criteria for approval it is forwarded to the national office in Brasília for final review, signed by the President of IBAMA and published in the official government registry as a complementary law valid for one to three years. Once the fishing accord has become law, IBAMA trains VEAs who assume responsibility for monitoring compliance with the accord. When infractors are apprehended, VEAs issue citations and report the incident to IBAMA's enforcement office, which pursues the case as deemed appropriate.

In 1999, the ProVarzea Program of the PPG-7 became operational with a projected duration of five years. ProVarzea (Projeto Manejo dos Recursos Naturais da Várzea) was designed to serve as the vehicle for the development and implementation of a region-wide policy and institutional framework for the co-management of Amazon fisheries (IBAMA 2001b; Kolk 1998). The program consists of three components, a Strategic Research component that investigates eight critical areas for fisheries management, a Promising Initiatives Component that supports individual management projects and a Monitoring and Control Component through which the co-management system is to be implemented. Two pilot regions, Santarém and Parintins, were elected for initial implementation of the co-management system described earlier. In terms of approach to fisheries management, institutional relationship with IBAMA and staff origins, the ProVarzea program represents a scaling up of the German-Brazilian Iara Project in Santarém. Coordination of the program is based in IBAMA's office in Manaus with regional offices in Santarém and Parintins. The program is funded through the G-7 Pilot Program as an IBAMA project and is housed in IBAMA's offices. Provarzea staff members, however, are not employees of IBAMA reinforcing the short-term project character of this initiative.

CO-MANAGEMENT EXPERIENCE TO DATE

Over the last six years the basic structure of the regional co-management system has been constructed in the Santarém area that builds on decades of grass-roots efforts to control pressure on local lake fisheries. There are now seven Regional Fisheries Councils encompassing all the major floodplain lake systems within the municipality. Eight fishing accords have been legalized, six VEA training courses have been held and 98 agents certified representing four of the seven Regional Fisheries Councils. Finally, in January 2003, IBAMA published legal guidelines for formal recognition of fishing accords as the centrepiece of floodplain fisheries management policy (IBAMA 2003). These accomplishments are the result of a major sustained effort involving floodplain communities, Fishers' Unions, NGOs, IBAMA and international funding agencies and environmental organizations. While the resulting co-management system is far from consolidated, it is sufficiently well developed that it is now possible to evaluate performance and identify those aspects of the system that seem to be working and those that are especially problematic. In the following pages we evaluate the co-management system from the perspective of common pool resource theory focusing on transaction costs, access restrictions, enforcement, research and monitoring and institutional sustainability (see Ostrum 1998).

Co-management systems tend to have fairly high transaction costs from the perspective of users when compared to the conventional resource management model (Pereira 2002). This is because users must participate actively in the management process, attending meetings to decide the rules for fishing activity, patrolling lakes and apprehending infractors. In the Amazon case, these costs tend to be quite high for several reasons. Many of the lake systems are quite large, up to 40 km across and few community members have motorized transport. Participation in local management activities, then, demands a considerable time investment in travel to and from inter-community meetings and in patrolling lakes. It also involves small but significant financial expenditures for participants since there are no mechanisms for covering these costs. Finally, enforcement can be very stressful, especially when infractors are neighbours and relatives. This is exacerbated, as we will discuss below, by the fragile institutional status of VEAs.

A second critical problem with the co-management model is the requirement that communities maintain local lake fisheries open to outsiders. While fishing accords can specify how to fish, including what gear may be used, they cannot specify who can fish. Technically, this position is based on the 1934 Water Resources Code (Brasil 1934) that guarantees access to all water bodies for purposes of navigation. However, this interpretation confuses two fundamentally distinct issues: navigational rights and rights of access to the fish in the water. Use in the former case has no effect on the resource while use in the latter reduces the amount available to others. IBAMA officials have also voiced concern over the very real and complex distributional issues that granting closure of individual lakes to local communities would raise, the most pressing of which relates to the demands of urban canoe fishers.

While there are good reasons for insisting on some degree of accessibility for outsiders, the position taken by IBAMA undermines two basic tenets of the theory of collective action: clear definition of the group of users and the right of that group to the fruits of it's own labour without competition from free-riders (Olsen 1967). As it stands now, anyone can fish in the lake and so have access to the benefits, but they do not have to share in the obligations of maintaining the system. Thus, those who invest in managing the lake must compete with all other users to obtain a share of whatever benefits their efforts generate. From a theoretical perspective, this attribute alone is sufficient to ensure the failure of the enterprise (Olsen 1967; Ostrum 1998).

As noted earlier, it is possible to restrict access by imposing gear restrictions and other measures that make it uninteresting for outsiders to travel long distances to fish in the lake. The problem is that these kinds of restrictions also affect the efficiency of local fishing effort and so impose an additional cost on those participating in the accord. Furthermore, the present system contains no mechanisms through which outsiders could share in the cost of maintaining the system. In fact, Fisheries Councils are specifically prohibited from charging user fees, an attribute of the Federal government (IBAMA 2003). By charging such fees, it would be possible to compensate members for the time they invest in management activities. In the absence of a mechanism such as user fees, Fisheries Councils have had to resort to sponsoring events, such as raffles, bingos and football competitions, to raise funds. While this may solve the immediate financial problem of generating resources to cover management costs, it is an exogenous solution divorced from participation in the lake fishery. Thus it tends to separate economic and regulatory interests, making returns from management even more diffuse and difficult to protect from free riders (see Jentofts and McCay 1995).

These logistical and financial difficulties are exacerbated by problems involving enforcement. Existence of efficient mechanisms for punishing infractors and resolving conflicts is another critical aspect of the design of community-based management systems (Ostrum 1998). In the Amazon co-management experiment, the main problems relate to the role of VEAs. On the governmental side of the co-management system, collaboration with IBAMA field agents has been problematic. IBAMA field agents have often shown that they do not take citations brought by VEAs seriously and have occasionally declined to pursue normal procedures in cases the VEAs have brought to their attention. Part of this behaviour can be attributed to the lack of resources to undertake patrols, but, more problematically, it also reflects IBAMA agents' resistance to sharing authority with community members.

VEAs have also had difficulty in their relations with communities. VEAs role was originally conceived as responsible for organizing monitoring and enforcement of fishing accords at the community level, legitimising community involvement and extending IBAMA's enforcement capacity. They were not expected to undertake these activities by themselves. Rather than seeing VEAs as organizers of local co-management activities, however, members of many communities assume that the agents have sole responsibility for patrolling lakes and enforcing rules and that therefore they no longer need to participate. The problem is not just one of sharing the work, but of community solidarity with those responsible for monitoring and enforcing the accord. VEAs must often confront infractors, who may be neighbours or relatives, with little explicit, organized support from their communities.

Because of this lack of support, many VEAs find themselves in a difficult position. There is little they can do on their own since their authority depends on the support they receive from IBAMA and their communities. Infractors see that the citations VEAs have issued are not enforced by IBAMA and feel increasingly confident that they can act with impunity. In a few cases, infractors have taken environmental agents to court and these agents have had to defend themselves with little support from IBAMA. Frustrated and humiliated by their lack of power and support, a number of agents have quit and many others have stopped carrying out monitoring and enforcement activities. Of a total of 98 agents that have been trained thus far in seven regions, only 67, are currently active (Table 1). If we consider only the regions where VEAs have been active for at least a year, the proportion drops to 50 percent and in some regions as low as 36 percent. There is the danger that the ambivalence of government officials, will lead to the demobilization of the community commitment to co-management as local leaders see that little has come of their efforts to enforce local fishing accords. As Acala and Vuse (1994) observe, "it is not enough to have laws and organized communities to apprehend offenders. The process must follow through to conviction and penalty when necessary," if communities are not to lose interest in the co-management system.

Table 1: Accredited and Active VEAs

Region	Accredited	Active	% Accredited
Urucurituba	9	5	56
Aritapera	8	4	50
Maica	12	8	67
Ituqui	14	5	36
Tapara	3	1	33
Lago Grande I	27	19	70
Lago Grande II	25	25	100
Total:	98	67	68
One Year Minimum	46	23	50

Some progress in enforcement is being made, however, in response to pressure from Council representatives and supporting NGOs, IBAMA has increased VEAs police powers. They are now permitted to confiscate gear used by infractors, but are still not permitted to make arrests. IBAMA agents are also being pressured to take VEAs more seriously, pursue citations and prosecute infractors where appropriate. In addition, under the formal umbrella of Provárzea the original group of organizations working with IBAMA is developing new institutional arrangements that seek to address the weaknesses of the present system. The main objective here is to develop an alternative mechanism for enforcing fishing accords. Towards this end, an informal, multi-institutional system for monitoring and enforcement, CIDA, has been organized that brings together the various governmental agencies with policing powers, including the Public Ministry, the Civil Police, the Coast Guard (Capitânia dos Portos) and IBAMA. In addition to meeting local enforcement demands, this kind of institutional collaboration may also help solve a critical problem for the eventual expansion of the Santarém co-management system, the small number of regional IBAMA offices along the Amazon River.

A fourth point is that the developing co-management system is more focused on regulation than management. Regulation consists of the rules and procedures designed for controlling fishing activity. Management includes regulation but is not limited to it. Management is objective oriented and regulations are the means for achieving those objectives. Management involves monitoring and evaluating the status of the fishery as a basis for developing concrete objectives to determine to what extent those objectives are being met once the management system is implemented. User group participation in collecting the information needed to evaluate the status of the fishery and in developing appropriate regulations is a vital part of creating a local sense of ownership with regard to the management system and an understanding of how regulations will contribute to the plan's objectives. This participation is also essential for obtaining concrete indicators of performance through which users can see what impact their efforts are having on the fishery, thereby reinforcing their motivation for managing the fishery.

The process of developing accords does not involve a regular system for collecting information on the status of local fisheries and is based primarily on local views of the status of local fisheries and the kinds of fishing activities that should or should not be permitted. Accords also do not include specific objectives, so it is unclear what the proposed rules are intended to achieve. Without clear objectives, there is no explicit basis for evaluating whether or not the regulations are having the intended effect on local fisheries. Furthermore, accords do not as yet contain provisions for monitoring performance to determine whether they are succeeding in maintaining fishing pressure within sustainable levels. In this sense, it seems that accords are more concerned with making access to fisheries roughly equal for all users than with conserving fish stocks (Castro and McGrath 2003). While development of a system for monitoring the status of lake fisheries is a complex task (Berkes *et al*. 2000), it is essential to the long term viability of the developing co-management system that it move from a concern with regulation to a more comprehensive concern with management of lake fisheries. This is important not just to ensure the sustainability of the fishery, but also to motivate community participation by providing concrete feedback on the performance of the management system.

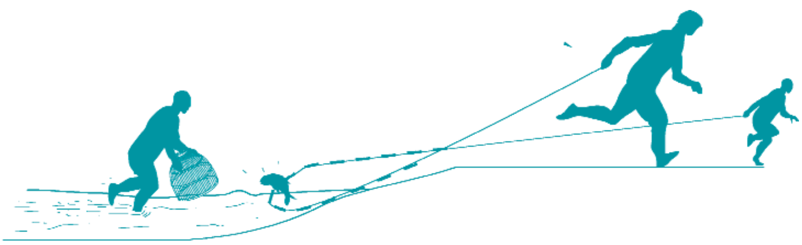
The long-term success of co-management in the Brazilian Amazon will depend on revising regulations to permit definition of a user group with exclusive access to the resource and the right to charge user fees. There are precedents for these changes. The Superintendency of IBAMA for the State of Amazonas, for example, has taken advantage of legislation decentralizing some executive powers to bypass Brasília and issue decrees giving some communities exclusive rights to local lakes. In the State of Pará, the number of commercial fishers on the Tucurui reservoir on the Tocantins River is also restricted (Camargo 2002). In both cases, the community or fisher association controls marketing of the catch.

Following these examples, a concession system could be created in which specific community-based, user group associations, which could include non-community members, are granted exclusive fishing rights to specific lake systems. These associations would be responsible for managing the lake fishery and as associations could charge members a user fee, thereby bypassing constitutional constraints on levying fees. They could also centralize marketing of fish and use that control to obtain additional funds in support of management activities. Also, by strengthening local control over lake systems, such an approach would increase incentives to participate in enforcement and thereby reduce dependence on government support. In addition to contributing to long-term institutional sustainability, this approach could facilitate expansion of the system in regions where IBAMA does not have a permanent presence. Since legal precedents exist for this model, there should be no major legal impediment to implementing such a system on the Amazon floodplain.

CONCLUSION

In conclusion, over the last 10 years considerable progress has been made in the development of a co-management system for Amazon floodplain fisheries that builds on grassroots traditions of community management. The experience is an important example of how diverse groups, communities, fishers' unions, local NGOs, government agencies, international donor agencies and international conservation organizations can work together to develop a new approach to management that supports and legitimises grassroots efforts to defend local resources and livelihoods. The experience also illustrates the capacity of participants to learn from the process and adjust the model to address problems as they arise.

The Santarém experiment also illustrates the difficulties involved in implementing a co-management system where the formal institutional base for fisheries management is minimal. In this regard, one of the main points of this paper is that a critical distinction between First and Third world fisheries management has been neglected in the literature on the development of co-management. Many of the problems identified here can be traced to this confusion. By concentrating on organizing communities and developing policies to support user participation in management, the main problem with the original management system, the absence of an effective governmental presence, has been largely ignored. Design flaws that tend to undermine local participation in the management system have exacerbated this central problem. The result, as the Santarém experience may be illustrating, is a system that is starved for resources and in which the government partner in the co-management system is unable and often unwilling to fulfil its role. This approach is open to the criticism that the whole exercise is little more than a cynical strategy for shifting the cost of fisheries management from the government to the rural poor. In this case, however, relatively straightforward changes in the design of the system could substantially increase the effectiveness and long-term institutional sustainability of the co-management system. It remains to be seen whether IBAMA, the government agency responsible for fisheries management, will be able to make the necessary adjustments.



REFERENCES

Acala A. & Vuse F. 1994. The role of government in coastal resources management. *In* R.S. Pomeroy ed. *Community management and common property of coastal fisheries in Asia and the Pacific: Concepts, methods and experience*. *ICLARM Conf. Proc. 45*. pp. 12-19.

Allegretti M. 1995. Reservas extrativistas: Parâmetros para uma política de desenvolvimento sustentável na Amazônia. *In* R. Arndt ed. *O Destino da Floresta*. Rio de Janeiro, Dumará. pp. 17-47.

Almeida O.T. & McGrath D.G. 2000. Research and intervention for the participatory management of Várzea resources. *Instituto de Pesquisa Ambiental da Amazônia, Santarém*. 24 pp.

Almeida O., McGrath D.G. & Ruffino M.L. 2001. The commercial fisheries of the lower Amazon: An economic analysis. *Fisheries Management and Ecology,* 8: 253-269.

Bayley P. & Petere M. Jr. 1989. Amazon fisheries: Assessment methods, current status and management options. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106.

Berkes F., Mahon R., McConney P., Pollnac R. & Pomeroy P. 2001. Managing small-scale fisheries: Alternative directions & methods. Ottawa, Canada, IDRC.

Brasil. 1934. Código das Águas. Decreto No 24.643 de 17 de julho de 1934.

De Camargo S.A.F. 2002. Pesca profissional, dilemas e conflitos no reservatório da UHE-Tucurui, PA. São Paulo, Brazil, Tese de Doutorado, CAUNESP.

Castro F. de 2000. *Fishing Accords: The political ecology of fishing intensification in the Amazon*. Dissertation Series No. 4, Bloomington, IN, University of Indiana, Center for Studies of Institutions, Population & Environmental Change.

Castro F. & McGrath D.G. 2003. Moving toward sustainability in the local management of floodplain lake fisheries in the Brazilian Amazon. *Human Organization*, 622:123-133

Chapman M. 1989. The political ecology of fisheries depletion in Amazonia. *Environmental Conservation*, 164: 331-337.

C. P.T. 1992a. *Ribeirinhos: Uma estação de luta*. Dossier 1992. Manaus, Comissão Pastoral da Terra, Regional Amazonas e Roraima.

C.P.T. 1992b. *Os ribeirinhos: Preservação dos Lagos, defesa do meio ambiente e a pesca comercial.* Manaus Comissão Pastoral da Terra, Regional Amazonas e Roraima.

Gillingham S. 2001. Social organization and participatory resource management in Brazilian *Ribeirinho* communities: A case study of the Mamirauá Sustainable Development Reserve, Amazonas. *Society and Natural Resource,s* 14: 803-814.

Goulding M. 1983. Amazonian fisheries. *In* E. Moran ed. *The Dilemma of Amazonian Development*. CO, USA, Westview Press. pp. 189-210.

Gryzbowski C. 1989. *O Testamento do Homem da Floresta, Chico Mendes por Ele Mesmo*. Rio de Janeiro, FASE.

Hartmann W. 1989. Conflitos de pesca em águas interiores da Amazônia e tentativas para sua solução. pp. 103-118 *In Pesca Artesanal: Tradição e Modernidade. III. Encontro de Ciências Sociais e o Mar*. Programa de Pesquisa e Conservação de Áreas Úmidas no Brasil. São Paulo.

Hartmann W. 1990. Por uma co-administração de recursos pesqueiros em aguas interiores da Amazônia. O Caso das comunidades ribeirinhas e pesqueiras do Lago Grande de Monte Alegre. *Populações Humanas, Rios e Mares da Amazônia. IV Encontro de Ciências Sociais e o Mar no Brasil*, 6-9 de junho.

IBAMA Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 1995. Projeto IARA - Administração dos Recursos Pesqueiros do Médio Amazonas: Estados do Pará e Amazonas. Coleção Meio Ambiente. Série Estudos de Pesca, 15. IBAMA, 100 pp.

IBAMA Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 1996a. Portaria Nº 7, de 2 de Fevereiro de 1996.

IBAMA Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 1996b. Portaria Nº 8, de 2 de Fevereiro de 1996.

IBAMA Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 2001a. Instruçã Normativa Nº 19 de 5 de Novembro de 2001.

IBAMA Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 2001b. Provárzea: Projeto de Manejo dos Recursos Naturais da Várzea, Programa Piloto para a Conservação das Florestas da Amazônia, Brasília, D.F.

IBAMA Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 2001c. Manual dos agentes ambientais colaboradores. Brasília, D.F.

Isaac V. J., Rocha V. L.C. & Mota S.Q.C. 1993. Considerações Sobre a Legislacão da Piracema e Outras Restriçõoes da Pesca da Região do Médio Amazonas. *In Povos das Águas: Realidade e Perspectiva na Amazônia*. Lourdes F. Gonçalves, Wilma Leitão & Alex F. Mello, eds. pp. 187-212. Belém, Pará, Brazil. Coleção Eduardo Galvão, PR/MCT/CNPq, MPEG.

Junk W. 1984. Ecology, fisheries and fish culture in Amazonia. *In* SIOLI, Harald. *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin*. Boston, MA, USA, Dr. W. Junk Publishers. Vol. 58(1984): 443-476.

Jentoft S. & McCay B. 1995. User participation in fisheries management. *Marine Policy*, 193: 227-246.

Kolk A. 1998. From conflict to cooperation: International policies to protect the Brazilian Amazon. *World Development*, 268: 1481-1493.

Leroy J.P. 1991. *Uma Chama na Amazônia*. Vozes. Rio de Janeiro, Brazil. 213 pp.

Lima D. 1999. Equity, sustainable development and biodiversity preservation: Some questions on the ecological partnership in the Brazilian Amazon. *In* C. Padoch, M. Ayres, M. Pinedo-Vasquez & A. Henderson eds. Conservation and development of Amazonian Varzea. New York: New York Botanical Garden Press. pp. 247-263.

McDaniel J. 1997. Communal fisheries management in the Peruvian Amazon. *Human Organization*, 562: 147-152.

McGoodwin J.R. 1990. *Crisis in the world's fisheries: People, problems, and policies*. Stanford, Stanford University Press. 235 pp.

McGrath D. 2000. Avoiding a tragedy of the commons: Recent developments in the management of Amazonian Fisheries. *In* A. Hall ed. *Amazonia at the Crossroads*. London: Institute of Latin American Studies. pp. 171-197.

McGrath D., Castro F., Futemma C.RT., Amaral B. D. & Calabria, J. 1993. Fisheries and the evolution of resource management on the Lower Amazon Floodplain. *Human Ecology*, 212: 167-95.

McGrath D., Castro F., Camara E. & Futemma C.R.T. 1999. Community management of floodplain lakes and the sustainable development of Amazonian fisheries. *In* C. Padoch, M. Ayres, M. Pinedo-Vasques & A. Henderson eds. *Varzea: Diversity, development, and conservation of Amazonia's whitewater floodplains. Advances in economic botany*, Vol. 13. New York, The New York Botanical Garden Press. pp. 59-82.

Oliveira A.C. & Cunha L.H. 2002. Manejo comunitário de lagos en la planicie inundable de la cuenca media del río Solimões, Estado de Amazonas, Brasil: um modelo de preservaçión en transformación. *In* R.C. Smith & D. Pinedo eds. *El Cuidado de los Bienes Comunes*. Lima, Peru, Instituto de Estudios Peruanos e Instituo del Bien Común. pp. 244-271.

Ostrum E. 1998. A behavioral approach to the rational choice theory of collective action. *American Political Science Review,* Vol. 921: 1-22.

Pereira H. dos Santos. 2002. Economia institucional da co-gestão de recursos pesqueiros na várzea do Rio Amazonas. Provárzea. Manaus, AM, IBAMA.

Pinkerton E. ed. 1992. Translating legal rights into management practice: Overcoming barriers to the exercise of co-management. *Human Organization*, 514: 330-41.

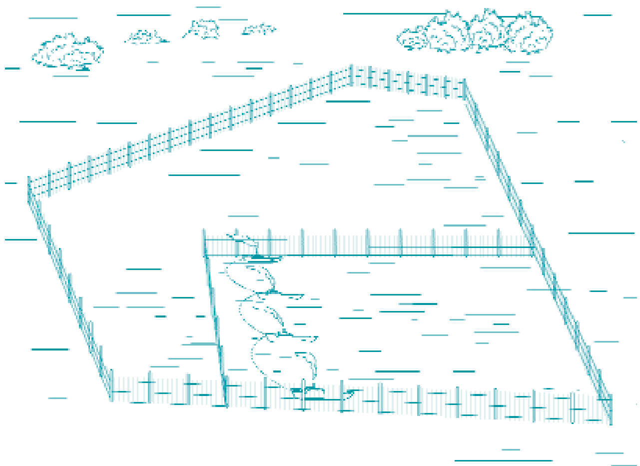
Schwartzman S. 1989. Extractive reserves: The rubber tappers' strategy for sustainable use of the Amazon rainforest. *In* J. Browder ed. *Fragile lands of Latin America: Strategies for sustainable development*. Boulder, CO, USA, Westview Press. pp. 150-165.

Sen S. & Nielsen J.R. 1996. Fisheries co-management: A comparative analysis. *Marine Policy,* 20: 405-418.

Smith N. 1985. The impact of cultural and ecological change on Amazonian fisheries. *Biological Conservation*, 32: 355-373.

Sunderlin W.D.R. & Gorospe M.L.G. 1997. Fishers' organizations and modes of co-management: The case of San Miguel Bay, Philippines. *Human Organization*, 56(3): 333-343.

Veríssimo J. 1970. *A Pesca na Amazônia*. Rio de Janeiro, Universidade Federal do Pará. 195 pp.



IRRIGATION SYSTEMS AND THEIR FISHERIES IN THE ARAL SEA BASIN, CENTRAL ASIA

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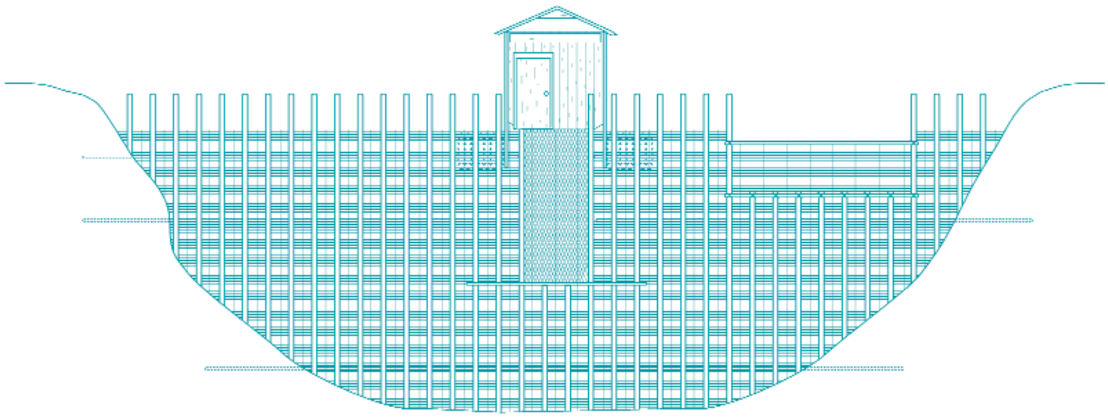


ABSTRACT

In the countries of Central Asia (Kazakhstan, Tajikistan, Kyrgyzstan, Uzbekistan and Turkmenistan) there are over 50 reservoirs that serve irrigation and hydropower production. In the basin of the Syr-Darya there are 19 reservoirs and in the Amu-Darya 36 reservoirs. The irrigation demand is so high that only rarely does any water reach the Aral Sea, resulting in the rapid desiccation of this sea. Irrigation systems require a novel approach to fisheries, as many economically important river fish species are unable to establish themselves in the reservoirs and many perish in the uptakes to irrigation canals. Until the end of the era

of the Soviet Union, in which the countries of Central Asia were included, fisheries management in reservoirs was effective, largely based on introduction of fish species and fish food organisms to the new irrigation systems. Interconnecting river basins with canals led to mixing of fish faunas of the major rivers, such as Amu-Darya and Syr-Darya. Fish faunas became dominated by introduced and immigrant fish species, which also dominated fish catches. With the diversion of water for irrigation, the delta lakes in the Amu-Darya and Syr-Darya also became important fish producing water bodies and the new water bodies established from drainage waters temporarily produced commercial quantities of fish. Since the independence of the countries of Central Asia in 1990, the former centralized management of fisheries has become fragmented, each country being dependent on its own human and material resources. Combined with the effort to dismantle the centrally planned economic system and introduce free market economy, the result has been a rapid decline in both fisheries management and control over fisheries resources. Fisheries law and regulations, dating from the former Soviet Union period, need to be updated and enforced, as today much of the fishing is uncontrolled. As a consequence of the changes, fish have become less available to the broader communities. This presentation concentrates on the fishery problems in two countries of the region: Kazakhstan and Uzbekistan.

INTRODUCTION

Irrigated farming is essential for food production in the countries of Central Asia. In Kazakhstan, prior to transition to the market economy in the last decade of the twentieth century, approximately one third of agricultural products came from irrigated lands, although this represented only 5-6 percent of the farmed area. At the end of the twentieth century in southern Kazakhstan the produce from irrigated farming often represented 2/3 of the total produced in Kazakhstan while over 70 percent of water is used for irrigation.

Uzbekistan, where about 73 percent of the irrigated land is set aside for cotton production, is the fourth largest cotton producer in the world. Uzbekistan has developed a sophisticated irrigation system, which includes reservoirs, irrigation canals, drainage canals and lakes for residual/drainage water.

The large-scale manipulation of the two major rivers, Amu-Darya and Syr-Darya forms the main base of the economy of the five countries of Central Asia. These rivers, situated in the basin of the Aral Sea, are used for irrigation and hydropower production, which have had considerable impact on the aquatic biotic resources, especially on the indigenous fish fauna (e.g. Petr (ed.) 1995; Petr and Mitofanov1998; Petr (ed.) (2003). With the development of fisheries, the highly manipulated water resource environment consisting of reservoirs, canals and water bodies storing drainage water, requires a unique approach to maintain and improve fish production. While in the second half of the twentieth century fisheries management concentrated on enhancing fish stocks through introductions and translocations of fish species and on stocking juveniles produced in hatcheries constructed near most of the reservoirs (Petr and Mitrofanov 1998), the political and economic changes in the 1990s virtually halted this management work. There was a decline in fish production, which only recently is being slowly reversed. This paper reviews the past and present situation and puts forward some measures required for the rehabilitation of fisheries in water bodies serving irrigation in the countries of Central Asia.

GEOGRAPHICAL AREA

Central Asia occupies an area of about 2 million km^2 situated deep in Eurasia. Five countries form this region: Kyrgyzstan (198 500 km^2), Tajikistan (143 100 km^2), Turkmenistan (448 100 km^2), Uzbekistan (447 000 km^2) and the southern part of Kazakhstan. About 70 percent of Central Asia is covered by steppes and deserts and 30 percent by mountains. The basin of the Aral Sea occupies the central part of the region (Figure 1).

catchments constitute a major part of the Aral Sea catchment. Before reaching the sea their water is stored in numerous reservoirs from where it is distributed for irrigation and also used for hydropower production.

The Amu-Darya, 1 440 km long, has an annual water runoff of about 78 km^2. The Syr-Darya has a runoff of 36 km^2 and is 2 140 km long. The rivers receive water largely from the mountains located in

■ **Figure 1.** Location of the Aral Sea Basin

Due to the landlocked location of the region and it being open to the north, the climate is extremely continental, with high aridity; about 20 percent of the region receives less than 100 mm precipitation per year, 90 percent less than 300 mm. Large seasonal and daily fluctuations in temperature are characteristic.

The two large rivers of the Aral Sea basin, the Amu-Darya and Syr-Darya, can only exist because of the presence of high mountains, from which they receive predominantly snow- and ice-melt water. Their

Tajikistan and Kyrgyzstan, with only 10 km^3 originating from the Uzbekistan Mountains, but the water consumption in Uzbekistan far exceeds this amount, being 62-65 km^2 per year. About 85 percent (53-55 km^2) of the water is used in agriculture, 12 percent (6 km^2) in industry and 3 percent (1.7 km^2) as municipal supply. These sectors also generate 28.2 km^3 of return waters (Anon. 2000) with fisheries as a side beneficiary of the available water resources. For the catchment areas in the Aral Sea basin see Table 1 and for the current distribution of population see Table 2.

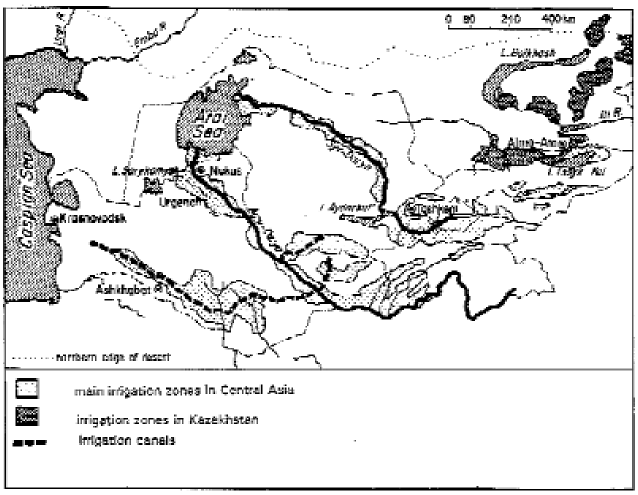
Table 1: Catchment areas in the Aral Sea basin (km²/year)

State	River basinAral		Sea basin	
	Syr-Darya	Amu-Darya	Km^2	Percent
Kazakhstan	2 624	-	2 626	2.1
Kyrgyzstan	27 605	1 604	29 209	25.1
Tajikistan	1 005	59 578	60 583	52.0
Turkmenistan	-	1 549	1 549	1.2
Uzbekistan	6 167	5 056	11 223	9.6
Afghanistan and Iran	-	11 593	11 593	10.0
Total Aral Sea Basin	37 203	79 280	116 483	100

IRRIGATION SYSTEMS AND IRRIGATED AGRICULTURE

Although the Aral Sea basin is mostly covered by deserts, it has had highly developed agriculture since ancient times. This has been possible only through the development of irrigation. For the last 2 000 years, irrigated agriculture has expanded far from rivers, such as in the Fergana Valley and Tashkent and even deep into deserts to form oases, such as Khorezm and Bukhara. Without irrigation those places would still be desert. Today, more than 50 percent of the total irrigated area in Central Asia (4.3 million ha) is located in Uzbekistan, a country located between the Amu-Darya and Syr-Darya. Kostyukovsky (1992) gives an example of the increasing demand for irrigation water in Turkmenistan: in 1900, there were 5 530 km^2 of irrigated land, requiring 3.68 km^3 of water, by 1986 this had risen to 17 830 km^2, which required 16.50 km^3 of water.

Micklin (1991) produced a map of the major irrigation zones in Kazakhstan and Central Asia (Figure 2).



■ **Figure 2.** Major irrigated areas in Central Asia and Kazakhstan (based on Micklin 1991)

The irrigation infrastructure comprises an interconnected system of canals and drainage collectors, with freshwater and drainage (return) water flows. In Uzbekistan there are 28 000 km of main and inter-farm irrigation canals and 168 000 km of on-farm irrigation

Table 2: Distribution of population in the Aral Sea basin (1998)

Country	Population						
	Total			Urban		Rural	
	inhabitants	% of total	inhabitants per km^2	inhabitants	%	inhabitants	%
Kazakhstan*	2 710 000	6.8	7.9	1 219 500	45	1 490 500	55
Kyrgyzstan*	2 540 000	6.4	19.9	685 800	27	1 854 200	73
Tajikistan	6 066 600	15.2	42.0	1 880 646	31	4 185 954	69
Turkmenistan	4 686 800	11.8	9.7	2 109 060	45	2 577 740	55
Uzbekistan	23 867 400	59.8	53.2	9 308 286	39	14 559 114	61
Aral Sea basin	**39 870 800**	**100**	**25.7**	**15 203 292**	**38.1**	**24 667 508**	**61.9**

** Only provinces in the Aral Sea basin are included* canals. Only 5-6 large main canals, with a length of 100-350 km and each with a capacity of 100-300 $m^3 s^{-1}$, are at present of fishery significance. In most canals water flows by gravitation, but pumping is used in two canals, the Karshi main canal and Amu (Darya)-Bukhara main canal. For fisheries only large main drainage collectors with more than 100 km length and water flow rates of 40-100 $m^3 s^{-1}$ each are important. The canals and collectors are not efficient and water losses from irrigation networks are estimated at about 40 km^3 annually. This amount of water would be enough to stabilise the Aral Sea at its current level (Kamilov 2003). Intensive development of irrigation and drainage in the Aral Sea basin has had two major impacts on water quantity and quality in the rivers: a major freshwater uptake for irrigation and generation of polluted return water of elevated salinity. If the salt concentration is too high, the water may be discharged into lakes, some of which have been formed entirely from such water.

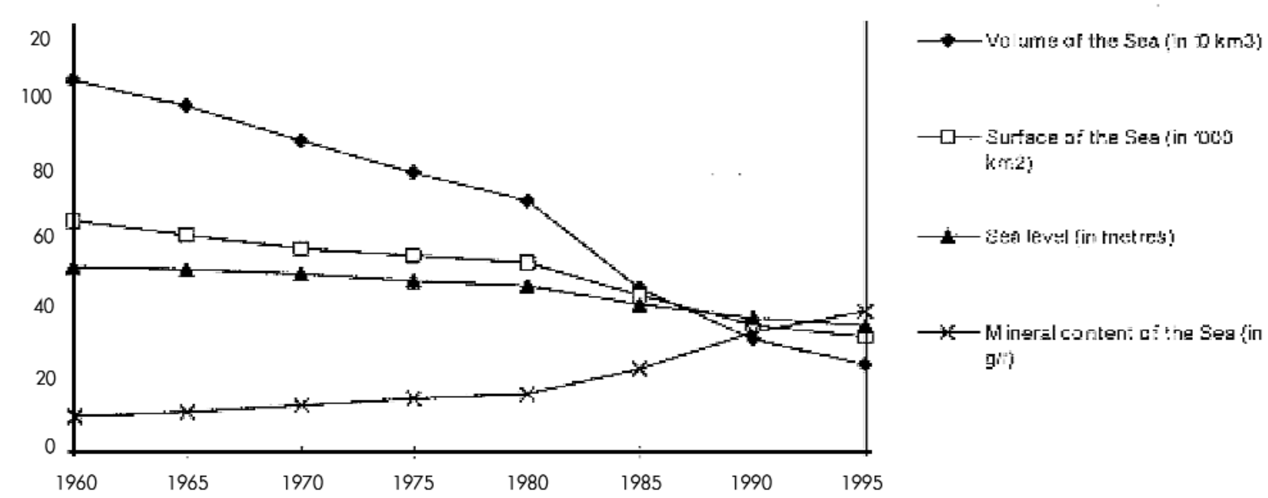
Fresh water of less than 1 g L^{-1} is present only in the upper catchments of the rivers and tributary streams and in the upper parts of the middle courses of major rivers. Further downstream all rivers and associated lakes receive return waters. During the last decades water salinities in rivers ranged from 0.5 to 2.0 g L^{-1}, in reservoirs from 0.5 to 2.5 g L^{-1} and in lakes formed from residual waters and in natural lakes receiving such waters then were from 3 to 20 g L^{-1}.

The shortage of water resources leads to the use of return waters for irrigation. This has resulted in degradation of flora and fauna and in pollution of surface water resources as they contain elevated concentrations of salts, fertilizers, herbicides, other harmful chemicals and bacteria than water present in unpolluted rivers.

During the last decades, all natural lakes have been impacted by large-scale irrigation development. Some lakes have dried up; others have been used for residual water storage. In the middle and lower courses of Uzbekistan rivers there are practically no natural lakes left whose water quality and quantity would not be affected by salinity and by the irregular discharges of drainage water.

In Uzbekistan all four major rivers, Syr-Darya, Zarafshan, Kashka-Darya and Amu-Darya and their tributaries have been regulated and have storage reservoirs (Kamilov and Urchinov 1995) the major purpose of which is to keep sufficient amount of water of required quality for irrigation use. Only these large rivers and some of their tributaries have fisheries importance. Inter-connecting a number of river systems by canals has formed one vast network through which fish species formerly specific for one catchment now disperse into other catchments.

The major impact of water diversion for irrigated agriculture has been well documented for the Aral Sea. While during the first half of the twentieth century water uptake for irrigation did not upset the water balance of the Aral Sea, since the 1960s the flow redistribution has caused irreparable damage to the whole ecosystem. Irrigation has changed the water regime in the whole of the Aral Sea basin and the Aral Sea itself. Uzbekistan shares the Aral Sea with Kazakhstan. In 1960, the Aral Sea had an area of about 68 000 km^2 and a volume of 1 061 km^3 (Micklin 1988). Before 1960, the Syr-Darya and Amu-Darya rivers annually discharged into the Aral Sea about 56 km^3 of water and a further 8 km^3 came in the form of precipitation and as ground water flow. The mean annual evaporation from the sea surface was 63 km^3. The water level of the Aral Sea was about 53 m above sea level (a.s.l.). As a result of the intensive uptake of water for irrigation until the 1990s, the annual water runoff reaching the Amu-Darya and Syr-Darya river deltas was reduced to 5 km^3 and in some years the rivers virtually stopped flowing into the sea. By 1992 the Aral Sea water level had dropped to 37 m a.s.l., the surface area was reduced to 34 100 km^2, salinity reached 34-37 g L^{-1} as compared with 9-10 g L^{-1} in the 1960s. Today the seacoast is 60-80 km from the original coastline (Kamilov 2003). The changes in the Aral Sea over the period 1960 – 1985 are shown in Figure 3.



■ **Figure 3.** Changes in the Aral Sea from 1960 to 1985

RESERVOIRS AND LAKES

There are about 60 reservoirs with a total volume of 61.6 km^3 in the countries of Central Asia, constructed in the basins of all large rivers. In the basins of the two major rivers, Amu-Darya and Syr-Darya, there are 55 reservoirs, of which 36 in the Amu-Darya basin and 19 in the Syr-Darya basin. There are 22 reservoirs in Uzbekistan, 13 in Turkmenistan, 8 in Tajikistan, 6 in Kyrgyzstan and two in Kazakhstan. The total water surface of reservoirs with fisheries importance is 3 310 km^2 (Table 3) (Nikitin 1991).

Table 3: Reservoirs of fisheries importance in the Aral Sea basin

River basin	Number of reservoirs	Area km^2	Volume Km^3
Syr-Darya	22	1 850	34.5
Amu-Darya	17	1 460	23.3

Under the arid conditions of Central Asia the average evaporation rate is twice that of precipitation. This leads to salinization of water and soils. The long-term average salinities of reservoirs in the montane and foothill zones above 500 m altitude range from 223 to 527 mg L^{-1}, with maximum salinities reached during winter and spring, before floods. In lowland reservoirs the salt concentration ranges from 550 to 1 200 mg L^{-1}, with a maximum of 1 700 mg L^{-1} reached during the autumn-winter period (Nikolaenko 1988). Nikolaenko (1988) compiled information on average salinities of 13 reservoirs of Central Asia (Table 4) that shows that by the mid-1980s, salinities exceeded the value of 1g L^{-1} in four out of 13 reservoirs. Water quality in the reservoirs of Central Asia started deteriorating in 1974 when drainage waters with high concentrations of sulphates, chlorides, manganese and sodium were diverted back into rivers.

Table 4: Mean salinity values (mg/L) in 13 reservoirs situated in Central Asia (from Nikolaenko 1988)

Reservoir	Years	Salinity
Charvak	1917-1980	223.1
Ortotokai	1958-1961	291.8
Tuyabuguz	1968-1980	304.8
Kattakurgan	1970-1980	417.4
Jizak	1969-1970	527.4
Yuzhno-Surkhan	1970-1980	551.2
Chimkurgan	1974-1980	581.2
Pachkamar	1969-1976	866.2
Uchkyzyl	1973-1980	908.8
Kairakkun	1968-1980	1062.5
Tyuyamuyun	1983	1069.5
Kuyumazar	1973-1980	1135.6
Chardara	1966-1976	1202.0

While water with salinity over 1 mg L^{-1} is considered unsuitable for the usual crops, less is known about salinity levels that are harmful to the native fish of arid and semiarid climates and especially to the young. Antagonistic interactions between the agriculture and fisheries sectors arise from the application of pesticides and herbicides, which can be harmful to aquatic living organisms. Agrochemicals used against pests or for defoliation, such as in cotton production, contribute to serious water quality problems and represent a hazard to fish and the end consumers – birds and man. Where drainage and wash waters are diverted in desert depressions without an outflow, or into swamps, salinity and agrochemical concentrations may gradually reach unacceptable levels, making the fish unsuitable for human consumption. Many large lakes with saline water, such as Sarykamysh (3 300 km^2) and Dengizkul (260 km^2), formed along the Amu-Darya.

A number of natural lakes and of those artificially created for residual water storage have been important for fisheries. Those of importance for fisheries cover about 7 000 km^2, a surface area of about twice that of all reservoirs. Most of the lakes function for many years. They do not experience major seasonal changes. After the demise of fisheries in the Aral Sea, the Aydar-Arnasai lake system and the lakes of the Amu-Darya delta are the major water bodies in this category supporting fisheries in Uzbekistan. Due to the current problem of harmonizing the use of the Syr-Darya among the riparian countries, the Aydar-Arnasai system is now receiving large volumes of water and as a result of that it now covers more than 4 000 km^2, which makes it the largest artificial lake in the region.

In the 1960s, the delta of the Amu-Darya had some 40 lakes with a total water surface of 1 000 km^2, now there are only some 20 lakes, but they have a total water surface of 1 150 km^2. The increase in area is a direct result of the restoration of the main lakes and appearance of new isolated ones on the dried Aral seabed. These water bodies are maintained almost completely by collector-drainage waters.

FISH FAUNA

Prior to large-scale irrigation efforts the indigenous fish fauna in the Aral Sea catchment rivers and lakes was little affected by human activities. Kamilov and Urchinov (1995) listed 84 species of fish for Uzbekistan, including those that were rare and those that were introduced. The ichthyofauna has undergone major changes as a result of water regulation and introductions of fish species from outside the Aral Sea basin (Kamilov 1973; Kamilov *et al*. 1994). By blocking the migratory path of fish, dams have a major impact on fish species that require suitable spawning and/or nursery and feeding grounds. Dams on the Amu-Darya and Syr-Darya have blocked the migratory path of fish, such as Aral barbel (*Barbus brachycephalus* (Kessler), shovelnose (*Pseudosca-phirhynchus kaufmanni* Bogdanow), spiny sturgeon (*Acipenser nudiventris* Lovetzky), Aral trout (*Salmo trutta aralensis* Berg) and pike asp (*Aspiolucius esocinus* (Kessler), which are all now threatened with extinction (Pavlovskaya 1995).

The most recent information on the fish fauna is provided by Kamilov (2003). Species considered extinct or rare because they have been unable to adapt to the new environment include the endemic shovelnoses (*Pseudoscaphirhynchus kaufmani*, Bogd.), *P. hermani* (Kessler), *P. fedtschenkoi* (Kessler), ostroluchka (*Capoetobrama kuschakewitschi*, Kessler), minnows (*Alburnoides bipunctatus* (Filippi), *A. taeniatus* (Kessler), *A. oblongus* (Bulgakov) and Zarafshan dace *Leuciscus lehmanni* (Brandt). Spiny sturgeon and Aral barbel disappeared because dams blocked their spawning migrations. Some species such as gudgeons (*Neogobius fluviatilis* (Pallas), *N. melanostomus* (Pallas), *Proterorhinus marmoratus* (Pallas) and Baltic herring (*Clupea harengus membras* L.), introduced in the Aral Sea became established for a while, but later on disappeared as a result of increasing salinity and other changes in the Aral Sea environment. During the period 1960-1990 a number of fish species from outside the region were introduced in a number of irrigation water bodies of Central Asia. Pikeperch and bream were released into reservoirs and lakes of the rivers Zarafshan, Kashka-Darya and the middle courses of the Syr-Darya and Amu-Darya. Silver carp (*Hypophthalmichthys molitrix* (Valenciennes), grass carp (*Ctenopharyngodon idella* (Valenciennes), bighead carp (*Aristichthys nobilis* (Richardson) and snakehead (*Channa argus warpachowskii* (Berg), introduced from the Far East, were stocked in fish farms in the Tashkent area and from there the hatchery-produced stocking material was regularly stocked into lakes and reservoirs. Three species of buffalo (*Ictiobus cyprinellus* (Valenciennes), *I. bubalis* (Rafinesque), *I. niger* (Rafinesque) and channel catfish (*Ictalurus punctatus* (Rafinesque) were also introduced into fish farms but they did not enter rivers, except the last species which entered the Syr-Darya. Rainbow trout (*Oncorhynchus mykiss* (Richardson), Sevan trout (*Salmo ischchan issykogegarkuni* Kessler), peled (*Coregonus peled* (Gmelin) and lake herring (*Coregonus sardinella* Val.) were released into Charvak reservoir in the Tashkent area where they are now established.

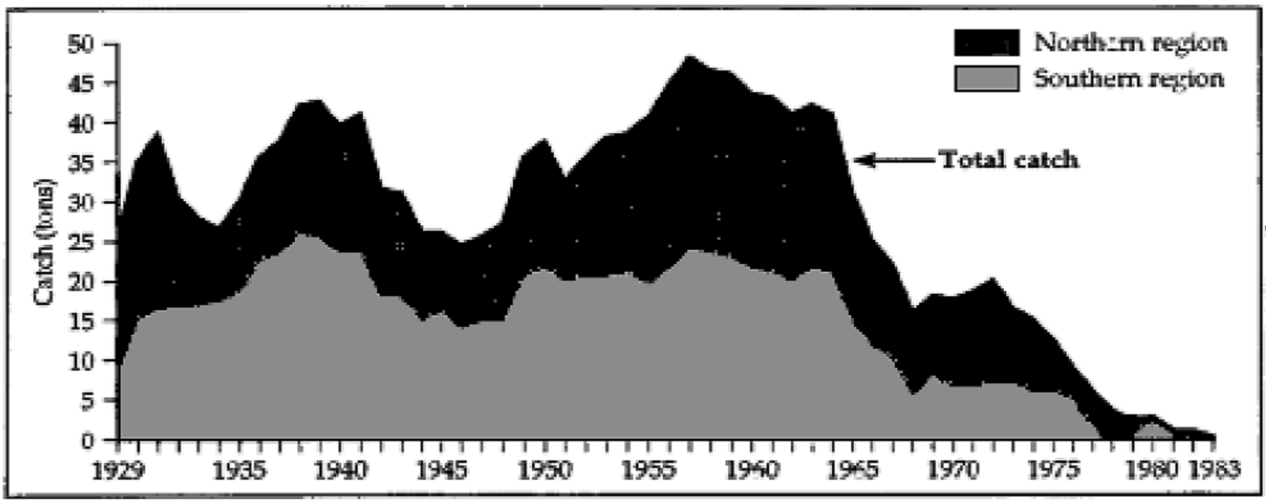
Many species spread throughout the basin via the connecting major canals. Some species started to breed in both the irrigation and drainage canals. Fish stocks in canals were not managed. In the 1970s-1980s management concentrated on stocking fingerlings and one-year-old marketable fish, the stocking material for which was produced in fish farms. Silver carp, grass carp, common carp and bighead carp were regularly stocked in reservoirs and lakes for residual water storage. This resulted in fish yields increasing by 5-15 kg ha^{-1}. After 1991 stocking continued only in the Aydar-Arnasai lake system and several other large water bodies.

FISHERIES

Until 1960 the fishing concentrated on the inshore waters of the Aral Sea and the deltas of the major inflowing rivers. In 1958 fish catches reached a maximum close to 50 000 tonnes (Figure 4). The major fish species captured were common carp (*Cyprinus carpio* L.), bream (*Abramis brama* Berg), barbel (*Barbus brachycephalus* (Kessler), roach (*Rutilus rutilus aralensis* Berg) and shemaya (*Chalcalburnus chalcoides aralensis* Berg). Less common were wels (*Silurus glanis* L.), pike (*Esox lucius* L.), asp (*Aspius aspius* Kessler), sturgeon (*Acipenser nudiventris* Lovetzky), and pikeperch (*Stizostedon lucioperca* (L.). In the 1960s only one small fish farm and one hatchery existed near Tashkent. In those days the fisheries were government-owned, but several fisheries cooperatives also operated on the Aral Sea. During the 1960s-1970s, fish catches decreased sharply. In 1983, the last year of the Aral Sea fishery, only 53 tonnes were caught. As a result of the Aral Sea desiccation and increased salinity to 14 g L^{-1} (the salinity in 1983), there has been no fishing in the Aral Sea since 1983. Today's fish yields in lakes and reservoirs in the Aral Sea catchment range from 1.2 to 209 kg ha^{-1} (Anon. 1990, 1998, 2001).

Fisheries in Uzbekistan had to find new sources of fresh fish. During the 1970s fishing fleets were transferred from the Aral Sea to Lake Sarykamysh and the Aydar-Arnasai lake system. During this period up to 6 000 tonnes of fish were caught annually in these lakes. While in 1964 the catch in Aydar-Arnasai lakes was only 26 tonnes, in 1971 it was 512 tonnes and a maximum of 4 200 tonnes was captured in 1988, corresponding to a yield of approximately 25 kg ha^{-1}. Sarykamysh eventually lost its fishery value due to an increase in salinity, which now reaches 20 g L^{-1} in some areas.

While most irrigation reservoirs have good water quality, they also have some limitations, such as unseasonal water level drawdown which conflicts with fish reproduction. This requires regular stocking of hatchery-produced juvenile fish. Another problem is the absence of any structures, which would prevent fish from entering irrigation canals and fields where they perish. Thus, in the lower Amu-Darya up to 90 percent of larvae and fry entering canals die on irrigated fields (Pavlovskaya 1995). But large connecting canals can be beneficial for fish distribution. For example fish larvae and fry of the middle course of the Amu-Darya migrate through the Amu-Bukhara Main Canal into Tudakul reservoir where they contribute to maintaining fish stocks in this reservoir.



■ **Figure 4.** Fisheries in the Aral Sea zone (Zholdasova *et al.* 1996)

By the end of the 1980s, the annual volume of drainage water in the basin of the Aral Sea reached about 33 km^3, which was about 60 percent of the total river discharge into the Aral Sea. This volume included 17 km^3 in the basin of the Amu-Darya, 13 km^3 in the Syr-Darya and 3 km^3 in the Zarafshan and Kashka-Darya. Part of the 33 km^3 was returned into rivers and 10-13 km^3 was diverted into depressions where this water eventually created Lake Sarykamysh (3 000 km^2), the Aydar-Arnasai lake system (at present more then 4 000 km^2) and a number of smaller lakes. For a while lakes for residual water storage were more preferred for capture fishery than reservoirs as they behaved like lakes, i.e. their water level was not affected by drawdowns.

Reservoir capture fisheries and those established in water bodies which have formed from drainage and wash water could not replace the quantity of fish lost from the Aral Sea. The Uzbekistan Ministry of Fisheries had to do the best possible to develop fisheries in the new water bodies, whatever the constraints to fish production arising from their management for irrigated agriculture. The Government of Uzbekistan and the former All-union Ministry of Fisheries developed a large-scale development programme of pond fish culture and fisheries in inland water bodies. That programme included creation of new fish farms and fishing enterprises in all regions of Uzbekistan, testing and implementation of new technologies, establishment of research centres, specialist training, etc. The well-managed fish farms all functioned well between 1970 and 1990. The total annual fish production in Uzbekistan ranged from 24 to 33 thousand tonnes per year. From this 7-8 thousand tonnes came from capture fisheries and 18-23 thousand tonnes from fishpond culture. Besides the capture and culture, the fisheries organisations also dealt with fish transport, storage and marketing of about 60-70 thousand tons of marine fish imported from other regions of the former USSR. This comprehensive fishery programme was possible under the very centralized system, where the fisheries were under the USSR Ministry of Fisheries, which was assisted by the appropriate Uzbekistan authorities.

IMPACT OF INDEPENDENCE ON FISHERIES IN WATER BODIES OF IRRIGATION SYSTEMS

After the countries of Central Asia gained independence at the beginning of the 1990s, there has been a decline in agriculture production. For example in Kazakhstan, over a period of five years the cultivated irrigated lands were reduced by 880 000 ha, i.e. 43.4 percent. The existing structures have been deteriorating due to the almost complete absence of government financial support. This reflects the deterioration of the overall economic situation in agriculture. Almost one million hectares of irrigated land are now out of production, there has been an increase in poor practices of water use and construction and rehabilitation have been suspended. The deterioration of irrigation systems has had also a negative impact on fish production from water bodies serving irrigation.

Prior to independence, Uzbekistan was implementing a large-scale comprehensive programme of fish production for all types of inland water bodies. Special attention was paid to education, research, planning, water and fish quality monitoring and other issues. State-owned fishing companies were established at all large reservoirs and lakes for return water storage. Hatcheries for producing stocking material were constructed in all parts of Uzbekistan. By the 1980s up to 7 000 tonnes of fish per year were harvested from reservoirs and lakes. All fish farms were state owned, financed by the government and functioned within the structure of the Ministry of Fisheries. They regularly reported on their fish production. The positive aspect of the former centrally planned economies of some countries in the Region was that they had well-organized research and collection of statistics obtained through regular monitoring of fish stocks, so that the impacts of introductions, stocking and catches could be evaluated and management strategies adjusted. Centralised statistics provided the longest series of data for a number of irrigation reservoirs in the former Soviet Union, including Central Asia (Karpova, Petr and Isaev 1996) and these were used for further assessment, evaluation and as examples of the level of efficiency of the applied enhancement measures. They also showed the failures resulting from some introductions.

Independence resulted in fragmentation of the formerly regional system of water resource management in the Aral Sea basin. For example, the government of Uzbekistan privatised all state-owned fish farms and capture fisheries enterprises and starting in 1994 it stopped providing financial support. Fishers found themselves in the new and unfamiliar conditions of a market economy. The overall economic crisis and the loss of economic links with producers of equipment in the former USSR have also adversely affected fisheries.

At present water resources in the basin of the Aral Sea are regulated from five centres, one in each country of Central Asia. This has already caused a number of problems. For example, during the period 1991-2001 huge amounts of Syr-Darya water had to be discharged from the Chardara reservoir in Kazakhstan into the Aydar-Arnasai lake system in Uzbekistan. Aydar-Arnasai has no outflow, therefore the water cannot be reused and accumulates in this depression and has become a water body of fisheries importance.

Over the last ten years fishing equipment in Uzbekistan has much deteriorated. The number of fishing boats, nets and seines dropped. By the end of the 1990s there were only 20 fishing boats with 130 horsepower engines, 40 boats with 20 to 60 horsepower engines and 250 other types of motorised boats. All fisheries companies together had only 5 000 gillnets and 36 beach seines, which were worn out. Tables 5 and 6 give information on reservoir lake and river capture fisheries for selected years. After a major decline in catches, which reached the lowest value in 1996, there has been a slow recovery. Nevertheless, fish production dropped to one third and large-scale fishing in Uzbekistan reservoirs such as Charvak, Chimkurgan and several others virtually stopped or was significantly reduced, as for example in Tudakul reservoir, where the reported fish catches dropped from 700 tonnes in the early 1990s to 250 tonnes in the late 1990s.

Fish production in ponds in Uzbekistan decreased on the average from 3 000 kg to 850 kg per ha. Education and training of specialists also stopped and the research network came to an almost complete standstill (Kamilov 2003). The main limitation in aquaculture has been the absence of formulated fish feed. In 1995, the total fish production was 5 600 tonnes. Table 5 shows aquaculture production in Uzbekistan prior to and after gaining independence, with the lowest production being in 1996. The trend is the same as for the capture fisheries. This has been followed by a slow recovery. Of the 20 existing fish farms established along the irrigation network in Uzbekistan, 12 have fresh water and 8 contain drainage water with a salinity of 5-6 g L^{-1} (Table 6).

Table 5: Capture fisheries and aquaculture in Uzbekistan (in thousand tonnes) (from Kamilov 2003)

Year	Capture fisheries			Aquaculture	Total
	Lakes#	Reservoirs	Rivers		
1980s##	5.5	1.0	0.5	23.0	30.0
1994	2.0	0.8	0.3	14.6	17.7
1996	1.2	0.3	0	5.0	6.5
1999	3.1	0.4	0	5.6	9.1
2000	2.7	0.3	0	6.2	9.2

- lakes used for residual water storage
- average for a decade

Table 6: Aquaculture production (thousand tonnes) in Uzbekistan by type of water (from Kamilov 2003)

Year	Fish farms with fresh water	Fish farms with saline water	Total
1990	13.2	7.6	20.8
1993	12.8	6.1	18.9
1996	3.8	1.2	5.0
1999	4.1	1.5	5.6

Today, Uzbekistan has no national programme or specific fishery development projects supported by the government or international assistance. Private initiative focuses only on exploitation of rich fish stocks in the Aydar-Arnasai system using small fishing teams. The fishery potential of water bodies of the irrigation system of Uzbekistan is largely unexploited.

An example of problems facing fisheries managers of irrigation reservoirs is reported from Chardara reservoir in Kazakhstan by Ismukhanov and Mukhamedzhanov (2003). This reservoir was constructed for irrigation and hydropower production in 1965 on the middle course of the Syr-Darya. Like a majority of irrigation reservoirs in southern Kazakhstan, Chardara is filled in the autumn-winter period (October-March) and drawdown takes place in spring and summer (April-September). Seasonal fluctuations of the water level reach up to 11 m. During the spring and summer the drawdown reduces the reservoir surface to only 15 000-20 000 ha, which is a quarter or less of the water surface area of the full reservoir. At the same time the water volume is reduced 10-12 times. Such considerable seasonal changes in the volume and the surface area are mainly due to the irrigation water uptake. Water for irrigation enters Kyzylkum Canal, but some water is also used for power generation.

The most important factors influencing fish stock formation in Chardara reservoir is the hydrological regime, which is determined by water uses other than fisheries. Reduction of the surface area and depth leads to the reduction in the number of spawning areas and to a high mortality of the spawn during the spring breeding period (1 April – 20 May). In summer months fish may die due to low concentrations of dissolved oxygen resulting from cyanobacteria blooms. Reservoir drawdown also considerably reduces the habitat of benthic organisms and changes their species representation. Benthic invertebrates are an important food source for some fish species. By autumn, with the drop in water temperature, the situation worsens, especially for plankton. There is also a loss of valuable fish species such as zander, roach and bream due to the fry being carried out into the Kyzylkum Canal. In May the maximum number of fish fry are washed out, with an estimated loss of 1 million per day.

Following the independence of Kazakhstan in 1992, there was a change in the pattern of use of the reservoir. The upper part of Chardara reservoir was now located in Uzbekistan. In 1992-2000 high discharges of the Syr-Darya from February to April led to water spilling over the Chardara spillway as well as over the Arnasai emergency spillway. Large quantities of fish fry and fish of all age groups were washed out. The outflow of 800-1 600 $m^3 s^{-1}$ over the emergency spillway resulted in great losses of fish. It is estimated that during those two months, from 1992 to 2000, annual losses of fry of valuable fish species reached 18 to 64 billion. Taking into consideration that the commercial fishing pressure has not changed during the last ten years and the impact of other factors has not changed either, one can assume that the loss of fry and larger fish during floods was responsible for the sharp drop in catches of commercial fish species, from 2 040 tonnes in 1992, to 216 tonnes in 1999. Another problem has been caused by pollution with pesticides, causing fish mortalities. More recently concentrations of pesticides and herbicides have been declining as a result of the reduced use of these agrochemicals.

Measures to reduce the rate of fish loss and increase the stocks of valuable commercial fish species in Chardara include: reconstruction of the Kyzylkum sluice of the Kyzylkum irrigation canal uptake and construction of a fish protection device on the Arnasai emergency spillway. A new reservoir (Koksarai) is being constructed 120 km distant from Chardara reservoir to store floodwaters which now end in the Arnasai depression. Other measures include limits on the catch or even closing of the fishery and intensive stocking of the reservoir with fish species of high value. An attempt to protect common carp by closing the carp fishery during the period 1997-2000 failed because of lack of enforcement. Low value fish species need to be controlled by intensive fishing to reduce the pressure on fish food organisms. This would make them available for higher value fish species. To increase the stocks of silver carp it is recommended to stock reservoirs every year with 250 000 two-year-old fish, which is 3-4 times the current stocking rate. This should result in a sustainable annual harvest of 100-120 tonnes of silver carp.

FISH PRODUCTION POTENTIAL IN THE AMU-DARYA AND SYR-DARYA CATCHMENTS

There is good development potential for both capture fisheries and aquaculture, especially in Uzbekistan, Kazakhstan and Turkmenistan. However, successful development will depend on a number of conditions, which at present still need to be established. Between 1996 and 2001, with the help of foreign assistance, in Uzbekistan two project proposals were formulated for the development of fisheries on fish farms: a project for a model aquaculture farm using semi-intensive technology and a fish farm sturgeon production project. Both projects are pending, mainly because of lack of funds on the Uzbek side and because of insufficient experience of Uzbek fishery specialists in implementing such projects (Umarov 2003).

There has also been lack of continuity in some successful projects, such as one for using irrigation systems for fish production in the Golodnaya and Karshy steppes.

Many fish hatcheries in Uzbekistan and Kazakhstan are still functioning, including the breeding and production of fish fry and fingerlings of cyprinids. They have sufficient capacity to provide potential farmers with the required quantities of fry, fingerlings and yearlings for increasing fish production (Kamilov 2003; Ismukhanov and Mukhamedzhanov 2003). The major constraint is the high cost of fish feed.

Uzbekistan has a good transportation and industrial infrastructure, large rural population and diversified agriculture. This creates favourable social and economic conditions for development of fish production in irrigation water bodies. There is no reason why the current shortage of fish in Central Asian countries couldn't be overcome by intensified fish production. All countries in the Aral Sea basin have favourable climates and abundant water resources. In Uzbekistan there is also an optimal density of population and available labour force and good access to markets, especially in larger towns. The lowland water bodies are suitable for the development of fisheries based on warmwater Chinese carps, i.e. silver, bighead and grass carp and common carp. The mountain and foothill storage reservoirs could produce cold-water fish such as rainbow trout, Issyk-Kul (Sevan) salmon and whitefish (*Coregonus* spp). It would be profitable to use the existing ponds, now in private ownership, for creation of fish farms. With a model of a profitable small fish farm, farmers of Uzbekistan could then combine pond fish culture with the traditional farm crop production. This would appear to be an efficient way of boosting the fish production in the country.

While a new management approach is required, some of the knowledge on reservoir fish and fisheries can be adapted from similar situations where a river was dammed for hydropower electricity production. In addition to introductions, some reservoirs have been regularly stocked with fingerlings produced in hatcheries. This, in the past, resulted in a sustainable fish production in a number of reservoirs in Uzbekistan, Turkmenistan and Kazakhstan, with the highest yield of 30.9 kg ha^{-1} achieved in one reservoir, where the potential sustainable yield was estimated at 78 kg ha^{-1}, if regularly stocked with silver, grass and common carps.

Fisheries managers have a number of options for fishery development in irrigation systems. Most options are a response to the impacts caused by the manipulation of the water resource for purposes other than fisheries. Irrigation systems are subject not only to rainfall and evaporation rates, but also ambient air temperature, which determines the amount of snow- and ice-melt from glaciers. Agriculture practices such as selection of crops are not static and may change from year to year and with them the amount of water and timing of the demand required for achieving the best crop. Furthermore, there is the use of agrochemicals, which may differ from year to year. Thus, fisheries managers, while having an overall master plan, may also need contingency plans, as fisheries in irrigation systems are subordinated to other demands for water. An example is when there is a sudden release of water from an upper reservoir. In the Kazakhstan Chardara reservoir on the Syr-Darya, fish fry, fingerlings and young fish are sometimes washed out due to a sudden surge of water released from a neighbouring country; there is a need for installing fish protection devices to prevent such losses. As the government usually under funds the fishery sector in countries of Central Asia, this may place a limit on what fisheries managers can do.

Long-term research on several reservoirs has indicated that the major reasons for the low fish production in some reservoirs are: poor utilisation of the natural fish food, poor spawning conditions and nursery habitats and vacant niches not yet occupied by economically important fish species. In some reservoirs aquatic plants are under used, or benthos is used by fish species of low value.

Let's now have a look at fisheries management options for irrigation canals and lakes established from drainage/return waters.

Irrigation canals

The rate of water flow in the major irrigation canals usually ranges from 40 to 300 $m^3\ s^{-1}$, with a water velocity between 0.4 to 2.0 m s^{-1}. A minimum flow of 5 $m^3\ s^{-1}$ in some major canals may be maintained even when the canal is not in use. Where rivers carry a high sediment load, a sedimentation reservoir may be constructed at the head of the canal. While the average concentration of sediments at the intake of water from the Amu-Darya into Karakum canal is 3.7 mg L^{-1}, corresponding to a transparency of less than 40 cm, after the water leaves the sedimentation reservoir its transparency is much higher. But as the distance from the reservoir increases, the transparency gets gradually reduced due to the erosion of the canal sides. Apart from current velocity and water transparency, water salinity is also important for fish. In the Amu-Darya irrigation canals salinity ranges from 118 to 1

304 mg L^{-1} (Ergashev 1989), increasing towards the canal tail reach and final distributaries.

Fish with pelagic eggs, such as Aral barbel, razor fish, the introduced Chinese carps and white Amur bream (*Parabramis pekinensis* Basilewsky) have been doing well in slow flowing large canals and side storage reservoirs, such as those alongside the Karakum canal in Turkmenistan. Introduced fish are well established in the Karakum canal and breed there. In a number of irrigation canals grass carp has greatly assisted in controlling aquatic plants. Grass carp is also known to contribute to the eutrophication of those irrigation canals with dual purpose, i.e. irrigation and as a source of drinking water. Its use for control of aquatic macrophytes, therefore, has to be carefully planned, especially in deserts, where other sources of water are not available.

Lakes established from or receiving drainage waters

Where drains collecting residual irrigation water and wash water do not re-enter a river and/or a terminal lake, as required when the salinity of the drainage water exceeds 1 mg/L, the water may be diverted to a depression, where it creates a new water body. Pavlovskaya (1995) estimated the number of drainage collecting depressions in the Aral Sea catchment at 2 341, covering 7 066 km^2 surface area. More than one third of drainage water collecting depressions and water bodies are in the Syr-Darya River basin. Twenty-four percent of such water bodies, with a total area of 52 percent of the total are concentrated in the Amu-Darya River basin with the largest, Lake Sarykamysh, exceeding over 3 000 km^2 in Uzbekistan and Turkmenistan. Kamilov and Urchinov (1995) and Pavlovskaya (1995) provided figures for fish catches for five drainage lakes.

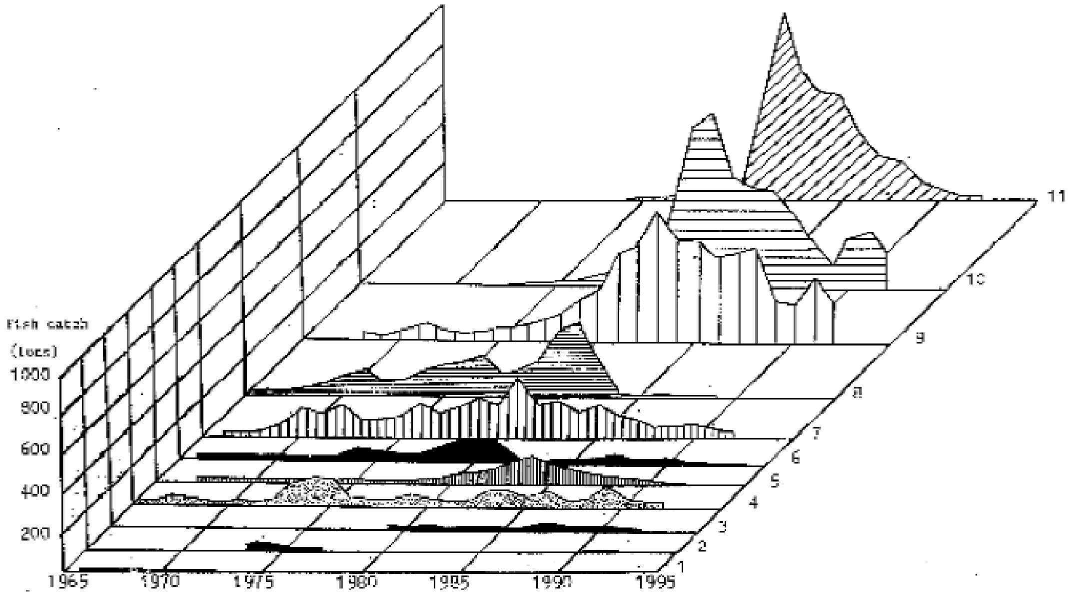
In Sarykamysh the fishery started in 1966 and the maximum annual catch of 2 500 tonnes was recorded during the 1981-5 period, with yields ranging from 4 to 8 kg/ha. The fishery virtually stopped in 1988 as fishing became unprofitable due to the large distance between the water body and the fish processing plant and also because of the poor quality of fish (Pavlovskaya 1995, Figure 3). The fishery focused on Aral barbel and common carp and due to the lack of enforcement of regulatory measures, the stocks of these two species became overexploited. This was accompanied by an increase in the less valuable pikeperch and razorfish, but even those species could not tolerate salinities over 10 g/L.

The Lake Sarykamysh experience has provided a number of lessons on the impact of a rapidly changing aquatic environment on indigenous and introduced fish and their fisheries. Sarykamysh shows the instability of lakes established by drainage water from irrigated agriculture in desert conditions with a high evaporation rate. Instability of especially the limnological environment is inherent in such lakes, which are subject to a gradual increase in salinity. Freshwater fish are stressed as the salinity affects the fertilisation and hatching of eggs and retards growth of fish. Studies have shown that the ratio of predatory to prey fish increases, largely due to the increase in the number of pikeperch, which is the most salinity-resistant commercial fish species in the Aral Sea catchment. In Sarykamysh bream, pikeperch and razorfish were the most adaptable and productive fish under the increasing water salinity. Eventually, pikeperch represented 27 percent of the total fish stocks (Sanin and Shaporenko 1991) but this was followed by their decline.

The experience with Sarykamysh has shown that water bodies with increasing salinity need a dynamic approach to environmental and fishery management if they are to continue producing fish. Breeding fish in hatcheries and stocking fingerlings may perhaps compensate the deteriorating spawning conditions resulting from increasing salinity. Other species, such as those of estuarine character, which tolerate large water salinity differences, could also be tested. A major problem is the increasing load of pesticides and other toxic substances applied in agriculture. Alternative solutions should be found that would lower agrochemical application levels and biological control should be introduced where possible (Petr and

Mitrofanov 1998). A certain decrease in the use of agrochemicals has taken place since countries of Central Asia entered the transition period from centrally planned economy to market-oriented economy.

of water used is for irrigation. It is estimated that in the year 2010, 45 percent of the total global food production will come from irrigated lands. The irrigation demand ranges from the extreme of the total diversion



■ **Figure 5.** The dynamics of food fish catches in Sarykamysh (1965-1995) (Pavlovskaya 1995)

DISCUSSION

The arid zone of Asia extends from the Mediterranean to the Pacific, including the following countries: Turkey, Syria, Iraq, Iran, Southern Russia, Afghanistan, five countries of Central Asia, i.e. Turkmenistan, Uzbekistan, Kazakhstan, Kyrgyzstan and Tajikistan, Outer Mongolia, Pakistan, India and China. In all of them most food crops are produced using irrigated agriculture and many of the water bodies used for irrigation have harvestable fish stocks. In Central Asia, over 80 percent of the total water use is for irrigated agriculture. In Pakistan 78 percent of the arable land depends on irrigation as compared with 100 percent in Egypt, 33 percent in all Asia, 21 percent in the Near East and Northern Africa, 8.5 percent in Latin America and 2.7 percent in Sub-Sahara Africa. In 1987, in 93 developing countries of the world, a total of 164.7 million ha of land was irrigated. This was expected to increase to 220 million ha by year 2000 (FAO 1993). In developing countries over 70 percent of water of some rivers for irrigation, to partial diversions and use, with the consequence of various degrees of flow diminution downstream of water abstraction.

Storing water for irrigation and hydropower production requires construction of dams. The impact on fish stocks of damming rivers is well known: in reservoirs the number of riverine fish species diminishes and are replaced by fish species with a preference for standing waters, subject to their presence in the catchment. The retention time of water in irrigation canals is often a limiting factor on their use by fish. Residual water bodies have a high rate of evaporation under desert and semi-desert conditions and fish there face elevated salinity levels, as well as high concentrations of agrochemicals which may be used in the irrigated crop production. While all this represents formidable obstacles for the fish, careful management of some irrigation water bodies is capable of replacing the losses in fish production due to damming rivers.

In the Aral Sea basin, government policy for the near future should first of all concentrate on the rehabilitation of irrigation systems, but at the same time decisions should be made on how to optimally use water and land resources. This would allow the maintenance of the existing lands under irrigation.

In Central Asia, Uzbekistan is the largest water user with the least potential to generate water resources. It faces water deficit and therefore is applying much effort to solving the problems of transboundary water resources management. Old principles of water management, which were applied to the whole region prior to independence and gave priority to irrigated agriculture are no longer valid, as power generation has become the priority in the now independent countries located in the upper watershed area (Kyrgyzstan and Tajikistan). This leads to a conflict of interests between upstream and downstream countries.

To replace the loss of the Aral Sea fish through a better use of the existing water bodies of irrigation systems is a major task. Without close collaboration among the countries of the region, including consultations and transfer of experience, it will be difficult to achieve such a goal.

With the rising demand for fish in arid countries of Asia the need for a better management of water resources in irrigation systems is evident. Co-management and community-based management of irrigation water bodies could be applied under the new privatisation policy and market-oriented economies emerging in Central Asia. Maintaining and monitoring the fishery by a small group would facilitate exclusion of outsiders, often illegal fishers. Government policy makers may consider delegating the management responsibility to collective or private groups, which then should receive government support through credit, training, scientific and extension assistance.

Due to lack of access to oceans, as well as the demise of the Aral Sea fisheries, Kamilov (2003) believes that the future of Uzbekistan's fisheries lies in aquaculture and enhanced capture fisheries. Extensive pond aquaculture is the most important sector of the fisheries industry, providing 60 percent of today's total fish production. About 20 companies own hatcheries, which induce-breed and farm fish, mainly silver carp, bighead carp and grass carp, with common carp reproduced both artificially and naturally. The fish are grown to market size on farms. In the 1990s the total area of ponds reached 10 400 ha, with sizes of the individual ponds ranging from 10 to 150 ha. Small-scale aquaculture could be developed in reservoirs, canals and lakes, with participation of villagers and local administration. Once the credit mechanism is fully understood, with the help of the local administration the new small-scale aquaculture ventures should be easy to implement.

Constraints

Umarov (2003) identified a number of constraints in using water bodies of irrigation systems for fish production. These do not necessarily apply to all countries sharing the river catchments as Umarov based this account on the experience from Uzbekistan where these include:

Institutional constraints: Absence of governmental and non-governmental institutional structures to promote the use of irrigation systems for fish production. Legislation ensuring the rights of private fish farmers to a guaranteed water supply within special limits and to trade in fish may be lacking.

Economic constraints: Lack of or minimal government financial support and private investments into fisheries. No special credit lines.

Technical constraints: Priorities for water use, i.e. irrigation demand and hydropower production, often do not allow maintaining optimal water supply for fish spawning and in nursery grounds. Lack of protecting devices preventing young fish from being discharged with irrigation water onto irrigated fields; lack of corridors between water bodies including floodplains, river reaches and canals, to make possible the migration of fish and fish fry from and to places of spawning, reproduction and other types of existence; unsuitability or absence of fish passes.

Ecological constraints: water pollution in irrigation systems, including increased salinities and toxicity.

Social and cultural constraints: Low level of public awareness that the irrigation network can be used for fish production. Shortage of fisheries experts and of fisheries training programmes.

The following constraints may be difficult to address, at least initially. These constraints may also apply to other countries of Central Asia in the Aral Sea basin, especially in Amu-Darya and Syr-Darya catchments:

- Lack of economic and technological models for the development of private fisheries in irrigation systems;
- Lack of financial support for scientific and applied research in this direction;
- Lack of experience in obtaining credits for establishment of fish farms and in attracting foreign participation for private ventures;
- Lack of international assistance for the development of fish production.

Fisheries development perspectives

Fisheries development in the Amu-Darya and Syr-Darya river basins has a good potential, given the favourable climatic conditions prevailing in this geographical area. The socio-economic frame also supports this, with abundance of labour. The rapid population growth also means increasing demand for food and the further development and expansion of fisheries is one of the ways to go. In Central Asia and mainly in the catchments of the Syr-Darya and Amu-Darya Rivers, it is estimated that the fish yield potential of lakes, rivers and reservoirs is about 100 kg ha^{-1} $year^{-1}$. This could provide 200 000 tonnes of fish annually to the markets. Uzbekistan of all countries in the region has the greatest potential for using irrigation systems for fish production (Umarov 2003). The development of fisheries in reservoirs serving irrigation will provide employment and contribute to the diversification of food supply. Development of aquaculture in irrigation systems would further increase fish supply to markets.

The transition from the centrally planed economy to market economy has not been a smooth one. Even after more than 10 years fisheries face great difficulties, especially in form of easy credits without which the industry cannot be kick-started. Even maintenance of the existing facilities has proved to be costly, as much of the former government support has evaporated. The decline now seems to have been halted, but the recovery process is extremely slow. With shortage of private funds a valuable resource is being wasted.

Due to the regional interdependence of all five countries on the same water resources, there is also a need for regional cooperation. At present no regional network exists to deal specifically with the use of irrigation systems for fish production. The Interstate Coordination Water Commission (ICWC), based in Tashkent, Uzbekistan, could take this up. This Commission already deals with other aspects of regional cooperation of water resources of the Aral Sea basin (Umarov 2003). The top level management organisations from the five countries of the Aral Sea basin are represented by the ministers at the quarterly meetings of the ICWC which discuss the current situation related to water distribution and use and formulate water strategy for the forthcoming period. The ICWC consists of three permanent executive bodies: Basin Water Organizations (BWO), Amu-Darya and Syr-Darya and the Scientific Information Centre (SIC) of ICWC. BWOs Amu-Darya and Syr-Darya are in charge of the operational monitoring of the water limits set by ICWC and operation of interstate reservoirs and hydrostructures. The SIC ICWC is in charge of technical policy and manages a regional information database on regional water resources.

The ICWC is now also paying attention to the interests of other water resource users including fisheries. It aims at overcoming administrative barriers and tries to involve the general public and private sector, non-governmental organizations and water users in the integrated water resources management both at national and regional levels (Dukhovny and Kindler 1999). Umarov (2003) believes that the available institutional framework for water management at the regional level and the possibility of regular contacts with governments, related ministries and the general public make ICWC the most suitable structure for information support and development of a regional network involving the use of irrigation systems for fish production.

Umarov (2003) formulated a number of recommendations for better use of irrigation systems for fish production in Uzbekistan, a country that is using water resources of both the Amu-Darya and Syr-Darya rivers. He has grouped the measures needed for the rehabilitation of fisheries and further progress in this direction as follows:

Institutional aspects

- Taking into account the institutional integrity of agriculture and water management, there is a need to establish within the Ministry of Agriculture and Water Resources of Uzbekistan a department for the use of irrigation systems for fish production;
- Favourable conditions should be created for involving the personnel operating and maintaining irrigation systems in fish production; this would provide them with additional income and also solve the problem of rapid employee turnover;
- A system of public awareness through mass media needs to be established;
- A legislative base, setting out the rights and duties of fish producers and protecting their interests, needs to be established.

The following institutional framework for fish production is proposed:

- Department of Fisheries under the aegis of the Ministry of Agriculture and Water Resources;
- Agricultural research organisation;
- Aquaculture associations.

Economic aspects

The on-going reforms in agriculture and water management are gradually establishing favourable conditions for private small-scale pond aquaculture. Private fish farmers could be then incorporated in the Associations of Farmers and Water-users.

Technical, training and research aspects

Regular releases of water are needed to prevent salinisation of water bodies with good water quality and to prevent increase in salinity of water bodies which are already saline.

- Fish protection devices need to be constructed on intake structures;
- Subsequent or simultaneous water use for several purposes should be encouraged, for instance combining irrigation and drainage with fisheries;
- Irregular and untimely water releases and flood waters should be harvested in the best possible way for fish production; fish producers should be provided with seasonal flows required for biological functioning of fish;
- An experimental research centre for development of fishery technologies for use in irrigation systems should be established; the centre would also monitor global development and trends, identify the most appropriate technologies and adapt them for the local geographical, social and economic conditions;
- Selected technologies should be tested in pilot projects, with the objective of applying them throughout Uzbekistan and in other countries of Central Asia;
- Regular training courses in aquaculture are needed. The ICWC Training Centre, Tashkent, Uzbekistan, could run these.

Many of the above recommendations are relevant to the other countries of Central Asia where freshwater fisheries need to be rehabilitated and developed in irrigation water bodies.

REFERENCES

Anon. 1990. Socio-economic problems of Aral and Priaralye. Fan, Tashkent. (In Russian)

Anon. 1998. Biodiversity conservation. national strategy and action plan. Tashkent.

Anon. 2000. *Water resources, Aral problem and environment*. Tashkent, Uzbekistan, Tashkent State University. (In Russian)

Anon. 2001. Assessment of the social-economic damage under the influence of the Aral sea level lowering. INTAS/RFBR-1733 Project. Final Report. Tashkent.

Dukhovny V. & Kindler J. 1999. Developing regional collaboration to manage the Aral Sea Basin water under international and inter-sectoral competition - water sector capacity building: concepts and instruments. Rotterdam, Brookfield A.A. Balkema.

FAO 1993. World agriculture toward 2000. Rome.

Ismukhanov K. & Mukhamedzhanov V. 2003. The use of irrigation systems for sustainable production of agricultural and fish production in the Republic of Kazakhstan. *FAO Fisheries Technical Paper*. No. 430. (forthcoming)

Kamilov B. 2003. The use of irrigation systems for sustainable fish production: Uzbekistan. *FAO Fisheries Technical paper*. No. 430. (forthcoming)

Kamilov G.K. 1973. *Fishes in Uzbekistan Reservoirs*. Fan, Tashkent. 234 pp. (In Russian)

Kamilov G.K., Karimov B., Khakberdiev B., Salikhov T., Kamilov B., Pridatkina N.V., Abdullaeva L., Taraskin A., Al Madjid Z., Yuldashev M., Nazarov M. & Gerasimova O. 1994. *Uzbekistan water bodies and their importance for fisheries, vol 1 & 2*. Tashkent, Uzbekistan, Tashkent State University. (In Russian)

Kamilov G.K. & Urchinov Zh. U. 1995. Fish and fisheries in Uzbekistan under the impact of irrigated agriculture. *FAO Fisheries Circular No. 894.* Rome, FAO. pp. 10-41.

Karpova E.I., Petr T. & Isaev A.I. 1996. Reservoir fisheries in the countries of the Commonwealth of Independent States. *FAO Fisheries Circular No. 915*. Rome, FAO. 131 pp.

Kostyukovsky V.L. 1992. Dynamics of Turkmenistan lowlands in conditions of natural and man-induced changes. *Vodnye Resursy*, No. 4: 85-92. (In Russian)

Micklin P. 1988. Desiccation of the Aral Sea: A water management disaster in the Soviet Union. *Science*, 241: 1170-1176.

Micklin P.P. 1991. *The water management crisis in Soviet Central Asia. The Carl Beck Papers in Russian and East European Studies No. 905*. University of Pittsburg Center for Russian and East European Studies. 124 pp.

Nikitin A.M. 1991. *Reservoirs of Central Asia*. Leningrad, Gidrometeoizdat. 165 pp. (In Russian)

Nikolaenko V.A. 1988. Classification of water in reservoirs of Central Asia based on their chemical composition and their evaluation for irrigation use. *Vodnye Resursy*, No. 2: 115-121. (In Russian)

Pavlovskaya L.P. 1995. Fishery in the lower Amu-Darya under the impact of irrigated agriculture. *FAO Fisheries Circular.* No. 894. Rome, FAO. pp. 42-57.

Petr T. ed. 1995. Inland fisheries under the impact of irrigated agriculture: Central Asia. *FAO Fisheries Circular No. 894*. Rome, FAO. 62 pp.

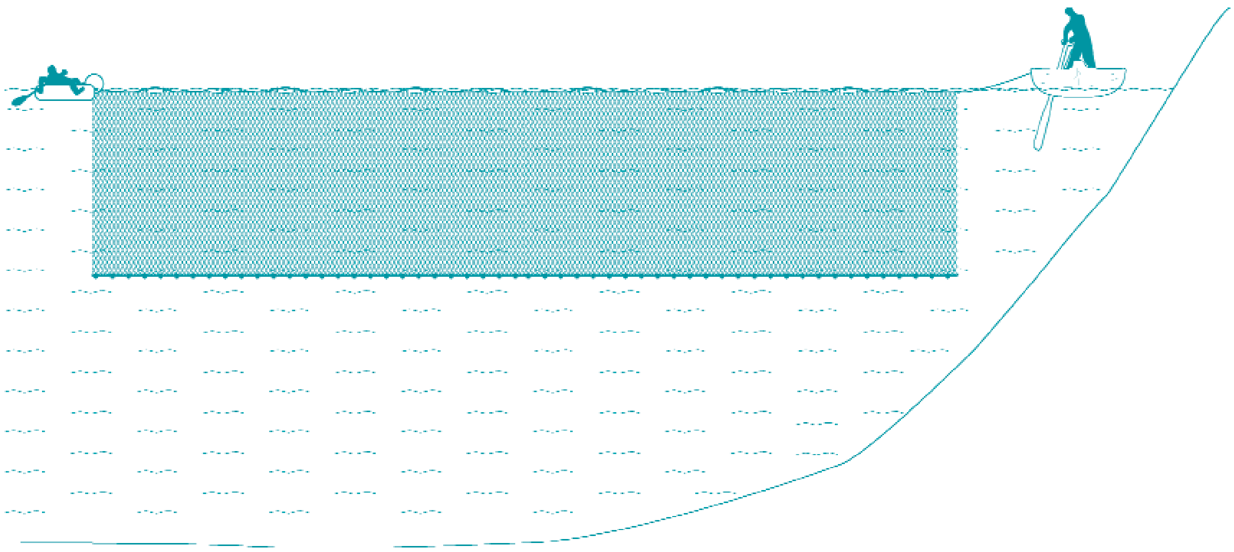
Petr T. ed. 2003. Fisheries in irrigation systems of arid Asia. *FAO Fisheries Technical Paper* No. 430. Rome, FAO. (forthcoming)

Petr T. & Mitrofanov V.P. 1998. The impact on fish stocks of river regulation in Central Asia & Kazakhstan. *Lakes & Reservoirs: Research and Management*, 3: 143-164.

Sanin M.V. & Shaporenko S.I. 1991. On the use of drainage waters for fisheries. *Vodnye Resursy,* No. 4: 147-152. (In Russian)

Umarov P. 2003. Uzbekistan irrigation systems and their management potential for fisheries in regional context. *FAO Fisheries Technical Paper* No. 430. (forthcoming)

Zholdasova M. et al. 1996. Biological bases of fishery development in the water bodies of the southern Aral Sea region. Ecological Research and Monitoring of the Aral Sea deltas: 213-33. UNESCO.



DETERMINISM OF FISH ASSEMBLAGE STRUCTURE IN NEOTROPICAL FLOODPLAIN LAKES: INFLUENCE OF INTERNAL AND LANDSCAPE LAKE CONDITIONS

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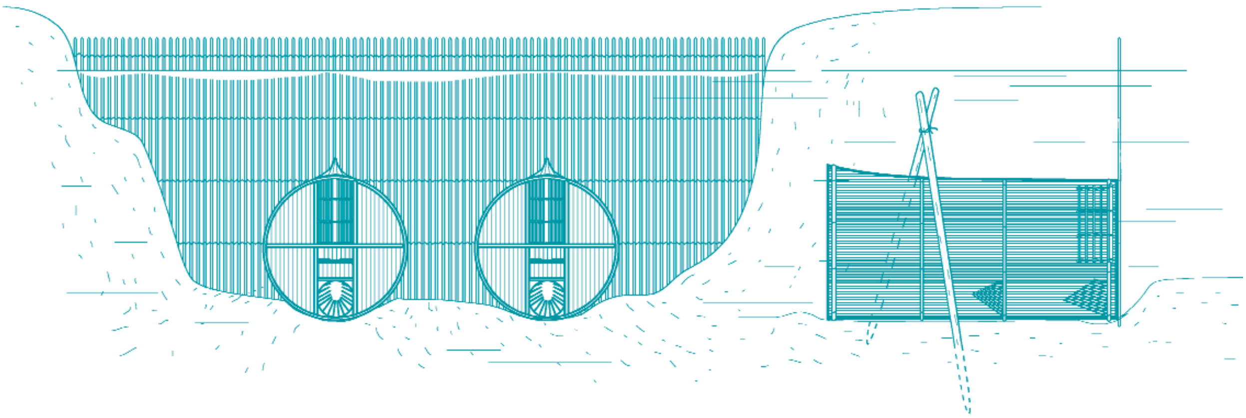


ABSTRACT

In the neotropics, seasonal flooding renders the floodplain an open system in which many fish species can disperse freely. Consequently, it has been suggested that fish assemblage structure in floodplain lakes is largely stochastic. However, recent studies concluded that fish assemblage structure could be determined mostly by local environmental factors. The present work tested 1) the predictability of fish assemblage structure in lakes of the Mamoré River floodplain, Bolivia, in relation to environmental conditions and 2) the general prediction that fish assemblages are structured following the piscivory-transparency-morphometry (PTM) model originally developed for the Orinoco River. Fish species abundances were quantified in eight lakes of the Mamoré River floodplain, positioned along a spatial gradient of distance to the main river, through five high-water and four low-water surveys. We found strong relationships between fish assemblage structure and abiotic variables. Spatial variation in fish assemblage structure was stronger than temporal variation. Consistent with predictions of the PTM model, relative abundances of siluriforms and gymnotiforms declined in clearer and deeper water, whereas relative abundances of characiforms and clupeiforms increased, as expected from knowledge on the sensory capabilities of these taxa. Partitioning of variation showed that although internal variables, especially transparency and water depth, play an important role in structuring fish assemblages, landscape variables, specifically temporal variability of water quality and connectivity, also influenced assemblage structure. These results support the notion of hierarchical control of assemblage structure. Landscape variables seem to operate as a primary filter that differentially limits local movement and migration as a function of lake connectivity. A secondary filter reflecting internal processes appears to exert stronger control in well-connected lakes where the migration filter might be weak. At the ordinal level, the distribution of clupeids, gymnotiforms and siluriforms appeared to be shaped by both landscape and internal variables. In contrast, that of characiforms did not seem limited by landscape variables.

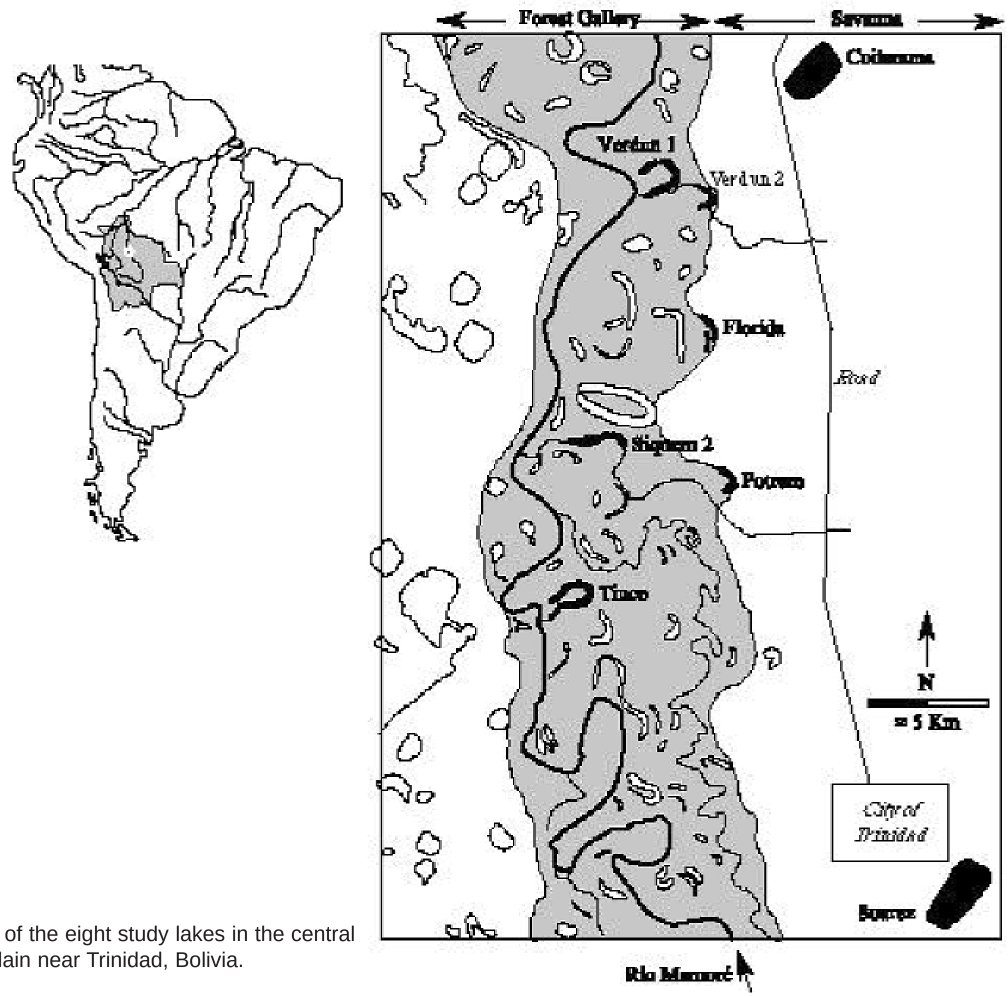
INTRODUCTION

The structure of fish assemblages is influenced by environmental variations at multiple spatial and temporal scales. Assemblage patterns should therefore be evaluated with respect to the relative contribution of small-scale, local and larger-scale, regional, ecological processes (Angermeier and Winston 1998). Specifically, environmental influences acting at different scales can be viewed as hierarchical filters that control species presence or abundance (Tonn *et al.* 1990). Species should be influenced differentially as a function of their adaptations to abiotic and biotic selective forces. Abiotic conditions may be influential at all spatial scales, although biotic interactions are likely to operate only at the local scale (Tonn *et al*. 1990; Keddy 1992). Patterns of control in fish assemblages differ among systems. For example, in Mediterranean streams, variation in fish assemblage structure is mostly explained by large-scale factors (stream size and catchment position) rather than by microhabitat and biotic interactions (Magalhães, Batalha and Collares-Pereira 2002). In small temperate lakes, piscivory and both local and larger-scale environmental variables (water depth, surface area, isolation) influence the structure of fish assemblages (Tonn *et al*. 1990). Finally, in neotropical floodplain lakes of the Orinoco River, the piscivory-transparency-morphometry model (PTM) proposed by Rodríguez and Lewis (1997) indicates that species distribution and abundance is tightly linked to lake water transparency, which is in turn controlled by lake morphometry. A similar pattern was found in the Araguaia River floodplain, Brazil (Tejerina-Garro, Fortin and Rodriguez 1998).

In most neotropical floodplains, the annual flood cycle of the river is predictable and exhibits marked seasonal fluctuations in water level that constitute one of the main ecological characteristics of floodplain waterbodies (Junk, Bayley and Sparks 1989). Floodplain lakes are mainly isolated during the dry season, but during the wet season, lake interconnections and forest flooding give fish access to a broad range of habitats. Consequently, the alternation of dry and wet seasons produces major change in patterns of fish abundance and distribution (Lowe-McConnell 1975; Rodríguez and Lewis 1994).

At the floodplain scale, environmental conditions at any given moment and seasonal change in those conditions are spatially heterogeneous. Young oxbow lakes are located near the river channel and retain a channel-like morphology. Over many years, floodplain lakes undergo morphological change and become shallower as a consequence of sediment deposition, colonization by vegetation and flooding attenuation (Amoros *et al.* 1987). This dynamic physical process is accentuated as the main channel moves away from the lake. Thus, one could expect orderly changes in fish assemblage structure along an age or distance gradient to the main river channel, a relationship driven by changes in lake morphometry, intensity of the flood effect and degree of connection with the main river channel along the gradient. However, Rodríguez and Lewis (1997) and Tejerina-Garro *et al.* (1998) found no influence of landscape variables on structure of fish assemblages and concluded that assemblage structure was determined mostly by internal variables operating locally.

We conducted, over a two-year period, a survey of the structure of fish assemblages in eight lakes of the Mamoré River floodplain, Bolivia, that were positioned along a sharp spatial gradient of landscape conditions. The present work tested: 1) the predictability of fish assemblage structure in the Mamoré River floodplain in relation to both internal descriptors and lake-type categories reflecting landscape conditions and 2) the general prediction that fish assemblages are structured following the PTM model originally developed for the Orinoco River floodplain (Rodríguez and Lewis 1997).



■ **Figure 1.** Location of the eight study lakes in the central Mamore River floodplain near Trinidad, Bolivia.

MATERIALS AND METHODS

STUDY AREA

The Mamoré River is one of the main tributaries of the Madeira River, a major affluent of the Amazon (Figure 1). The Mamoré River drains the southern Bolivian Andes and a vast savannah plain broken by forest gallery. Local climatic conditions are marked by the alternation of a wet (October – March) and a dry season (April – September). A large annual

Table 1: Environmental characteristics (landscape and internal variables) of eight lakes of the Mamoré floodplain. Means (ranges) of internal variables are given for the dry and wet seasons.

	Season	Coitarama	Suarez	Florida	Potrero	Siquero	Verdun 2	Tiuco	Verdun 1
Supra-lake variables									
Lake-type / Position		Savannah	Savannah	Edge	Edge	Forest	Forest	Mamoré	Mamoré
Estimated age (year)		>100	>100	>100	>100	>20	>20	<20	<20
Distance Mamoré (km)		5	6	4.5	4	1.3	1.2	0.1	0.15
Connectivity		isolated	isolated	temporary/ forest	temporary/ channel	temporary/ channel	temporary/ channel	permanent	permanent
Lake Perimeter		8.08	10.99	4.11	3.4	6.13	4.06	9.94	8.81
Lake area		3.43	4.2	0.28	0.39	0.67	0.37	1.19	1.01
Lake shape		1.23	1.51	2.2	1.55	2.11	1.88	2.57	2.48
Temporal variation (CVPCA)		-1.35	-0.84	1.5	1.53	-0.35	0.64	-0.61	-0.11
Whole-lake variables									
Temperature (é C)	Dry	27.7	28.8	25.9	25.9	29.1	27.7	27.7	28.4
		(26.7-29.3)	(26.8-32.9)	(20.3-31.6)	(19.4-32)	(28.8-29.4)	(26.7-28.6)	(24.6-29.6)	(26.8-30.3)
	Wet	28.4	28	27.6	27.2	28.3	27.7	28.7	28.5
		(24.4-31.1)	(24.1-30.5)	(26.4-28.7)	(23.1-30.6)	(25.7-30.2)	(27.4-28.3)	(26.8-32)	(28.1-29.2)
Water depth (m)	Dry	1.5	1.2	0.7	0.6	4.4	0.9	8.7	4.9
		(1.5-1.5)	(1.1-1.3)	(0.6-0.8)	(0.4-1)	(2.3-6.4)	(0.7-1.2)	(6.1-11.6)	(3.4-6.5)
	Wet	1.7	1.4	2.4	1.5	6.4	5.6	11.9	10.5
		(1.6-1.8)	(1.3-1.5)	(0.6-4.6)	(0.5-3.7)	(3.5-8.5)	(3.6-8.1)	(9.2-17)	(9.5-11.7)
Secchi transparency (cm)	Dry	36	13.8	8.3	12.5	19.1	19.3	77.6	33.2
		(27.3-43.3)	(10-23.3)	(8.3-8.3)	(5-29)	(9.7-25)	(14.7-24)	(48.7-139)	(22.7-48.3)
	Wet	42.2	38.5	40.6	29.1	45.4	64.6	73.2	63.8
		(35.7-51.3)	(31-49)	(13.3-68)	(8.7-76)	(31-60)	(46.7-80)	(41.3-106)	(27-85)
pH	Dry	6.8	6.9	5.5	6	6.9	6.6	7.8	7.2
		(6.6-7)	(6.7-7.4)	(5.4-5.5)	(5.7-6.5)	(6.8-7)	(6.1-7.2)	(7.2-8.7)	(6.9-7.7)
	Wet	6.5	6.6	6.5	6.1	6.4	6.5	7.1	6.7
		(6.4-6.7)	(6.3-6.8)	(6.3-6.7)	(5.5-6.8)	(5.9-6.7)	(6.4-6.6)	(6.8-7.5)	(6.4-7.1)
Conductivity (micros/s)	Dry	17	20	90	49	86	74	228	150
		(16-19)	(16-24)	(73-107)	(39-55)	(66-97)	(42-105)	(160-277)	(103-237)
	Wet	16	19	65	36	43	70	139	97
		(15-18)	(14-26)	(56-76)	(27-60)	(30-76)	(51-91)	(85-158)	(73-113)

flood, potentially extending over ca. 150 000 km^2 (Denevan 1980), generally occurs at the end of the wet season (December – April) and can last as long as three or four months (Loubens, Lauzanne and Le Guennec 1992).

The study area is situated in the central part of the Mamoré River floodplain (14°30' - 14°52'S; 64°51'- 65°01'W) near the city of Trinidad. Eight lakes were studied that correspond to four different ecological lake-types (Figure 1, Table 1): six are oxbow lakes situated in the forest gallery at varying distances from the Mamoré River; the remaining two are savannah lakes:

- Mamoré: Lakes Tiuco and Verdun 1, situated near the Mamoré River, were formed about 10 years ago and have a morphology similar to that of the river channel. They are permanently connected to the Mamoré River by way of a short channel (< 100 m).

- Forest: Lakes Siquero and Verdun 2, situated in the middle of the forested floodplain, were formed more than 20 years ago. They are temporarily connected to the Mamoré River by way of a small tributary that drains the savannah and the floodplain. The tributary is over 1 km long and runs through one or two other lakes before reaching the Mamoré River.

- Edge: Lakes Potrero and Florida, situated at the forested floodplain edge, were formed more than 50 years ago (according to local people). Lake Florida was connected to the Mamoré River only by floodwater. Lake Potrero was connected indirectly to the Mamoré River by way of a short channel that converged with a small temporary tributary. Both lakes are more than 4 km distant from the Mamoré River.

- Savannah: The last two lakes, Coitarama and Suarez, were situated in the savannah adjacent to the floodplain. They were estimated to have formed more than 100 years ago. In years with a typical hydrologic cycle, they are isolated year-round, but they likely connect with the Mamoré River in years with exceptionally high water level.

Lakes close to the river may be subject to flooding by whitewater drained by the Mamoré River (Loubens *et al*. 1992; Ibañez 2000) and are largely influenced by annual water level fluctuations. Local rainwater feeds lakes remote from the river, the savannah and edge lake types, which therefore have characteristics, intermediate between white and blackwaters.

Fish sampling and environmental measurements

Fish were sampled using thirteen gillnets with a wide range of mesh sizes (25 m long by 2 m high; mesh sizes: 10, 15, 20, 25, 30, 35, 40, 50, 60, 70, 80, 90 and 110 mm). Sampling was conducted during five periods of wet season (March 1998, March 1999, May 1999, March 2000, May 2000) and four periods of dry season (July 1998, October 1998, September 1999, December 1999). For each sampling (lake-period combination), gillnets were left in place for two hours in the evening (17:00-19:00) and two hours in the morning (5:00-7:00). Gillnets were placed perpendicular to the shore at approximately the same locations throughout the study.

Captured fishes were fixed in buffered formaldehyde (4 percent) and later preserved in buffered ethanol (75 percent). In the laboratory, fish were identified to species, or only to genus when taxonomic knowledge was inadequate for reliable specific identification, by reference to voucher specimens left by a previous taxonomic research project (Lauzanne and Loubens 1985; Lauzanne, Loubens and Le Guennec 1991) at the Trinidad fish collection (CIRA-UTB), the Museo Nacional de Historia Natural, La Paz and the Musée National d'Histoire Naturelle, Paris.

Environmental variables were assigned to two categories. Eight variables characterizing lake internal conditions in individual lakes: temperature, water depth, transparency, conductivity, pH, lake area, perimeter and shape (calculated as Perimeter/(4šArea)$^{0.5}$). Three variables correspond to landscape conditions (features external to the lake) that may influence internal biotic and abiotic processes and that are related to the position of the lake in the floodplain: connection type, distance to the main river channel and temporal variability of water quality. On each sampling occasion, five internal variables: temperature, water depth, transparency (Secchi disk), conductivity (electronic conductimeter WTW model LF31) and pH (colorimetric pH meter HACH), were measured at three points (referenced by GPS) in the deepest area of the lake. Temporal variability of water quality was quantified by means of coefficients of variation (CV) of the five landscape variables. Lake scores on the first axis of a PCA on the covariance matrix of the five CVs were used as an overall measure of temporal variation (CVPCA). Lake area, shape, perimeter and distance to the main channel were estimated from a photographic image (ERS satellite; pixel resolution 12.6 m).

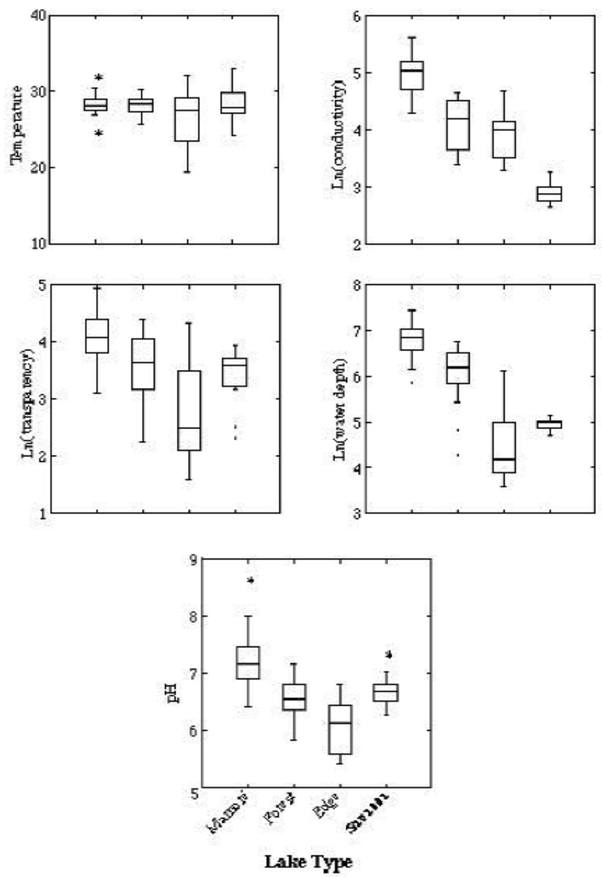
STATISTICAL ANALYSES

Species represented by <5 individuals and <3 occurrences were excluded from the analysis (103 species were conserved of a total of 140). Given that fishing effort was constant, catch per unit effort (CPUE) was calculated for each species and sampling occasion as the total number of individuals captured in all gillnets. Transformations were performed as required to better conform to statistical assumptions. CPUE data were transformed as ln (X+1) or, for proportions, as arcsin ($p^{0.5}$). The environmental variables Secchi transparency, water depth and conductivity were log-transformed.

Multivariate relationships between assemblage structure and environmental variables were quantified by canonical correspondence analysis (CCA), (Ter Braak 1986); (programme CANOCO, version 4), a direct ordination technique based on chi-square distances for the species data. Inclusion of predictor variables was based on a forward selection procedure with cutoff *p* value = 0.05. Statistical significance of species-environment relationships in the CCA was obtained by means of Monte Carlo tests implemented in CANOCO (1 000 permutations).

The variation-partitioning method of Borcard, Legendre and Drapeau (1992) was used to determine the fraction of the variation in the species matrix that could be explained by the landscape variables (pure "spatial" effect), the internal variables (pure "environmental" effect) and a "shared" effect of landscape and internal variables (variation explained jointly by spatial and environmental variables), as well as the fraction of variation not explained by these three components ("unexplained"). The variation is partitioned by dividing the inertia (sum of all eigenvalues) of constrained (partial) CCAs of the species matrix by the total inertia of a correspondence analysis of the species matrix (Borcard *et al.* 1992).

Partitioning of variation was also used to examine further the pure "spatial" component. First, the effect of the significant environmental variables was partialled out, leaving only the "pure" spatial variation and the unexplained variation. Then, forward selection was used to determine which landscape variables contributed significantly to explaining the "pure" spatial variation.



■ ***Figure 2.*** *Boxplot of internal variables (pH, temperature, conductivity, water depth, Secchi transparency), by lake type. Lake types are ordered along the horizontal axis according to their distance to the Mamore River channel.*

As a test of the general prediction of the PTM model, scatterplots were used to depict the relationships between relative abundance of major taxa (CPUE proportion; arcsine transformed) and transparency (Rodríguez and Lewis 1997).

RESULTS

TEMPORAL AND SPATIAL VARIATION OF LAKE INTERNAL CONDITIONS

Variation in water depth, Secchi transparency and conductivity showed clear temporal and spatial structure (Figure 2, Table 1). Savannah lakes, showed very limited variation in water depth both within and between wet and dry periods (range 20 cm); for the other (oxbow) lakes, environmental variation generally increased with distance to the river (Figure 2). Depth of oxbow lakes also diminished with increasing distance to the river, reflecting the temporal evolution of lake morphology along a gradient ranging from recently abandoned river channel to total dry-out.

Temporal variability of Secchi transparency and conductivity showed spatial patterns similar to that for water depth, as did the composite measure of temporal variability based on five environmental variables (CVPCA, Table 1). The six oxbow lakes were generally deeper, clearer and had lower conductivity during the wet season than during the dry season, contrasting with savannah lakes, which showed more limited seasonal variation (Table 1). pH, conductivity, Secchi transparency and water depth generally decreased systematically with the increasing distance to the river; however, the savannah lakes, although further from the river than oxbow lakes, had high pH and Secchi transparency relative to their distance from the river.

FISH ASSEMBLAGE STRUCTURE

A total of 38 292 fish, distributed among 140 species, were caught (Table 2). The 103 species selected for quantitative analysis represented more than 99.8 percent of the total number of individuals. A few very abundant species accounted for more than half of the catch: the small tetra *Moenkhausia dichroura* (30.7 percent), the armored catfish *Hypoptopoma joberti* (9.5 percent), the curimatid *Potamorhina latior* (5.4 percent), the characid "sardines" *Triportheus*

Table 2: List of 140 fish species captured in eight lakes of the Mamoré floodplain. Occurrence, total number of individuals captured, and relative abundance are given for each species, by lake type.

Order, *Family*						Relative Abundance (%) of analysed species	
Species, Authority	pisci.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Beloniformes							
Belonidae							
Potamorrhaphis cf. eigenmanni Miranda-Ribeiro, 1915		3	3	- -	- -	- -	- -
Characiformes				***88.61***	***64.53***	***39.48***	***59.04***
Acestrorhynchidae							
Acestrorhynchus spp.	š	387	26	1.93	0.29	0.19	0.35
Anostomidae							
Leporinus friderici friderici (Bloch, 1794)		86	24	0.30	0.16	0.14	0.19
Leporinus trifasciatus Steindachner, 1876		1	1	- -	- -	- -	- -
Rhytiodus microlepis Kner, 1858		107	13	0.04	1.10	0.31	0.37
Schizodon fasciatus Spix & Agassiz, 1829		154	33	0.48	0.68	0.11	0.46

Order, Family **Species, Authority**	pisci.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Relative Abundance (%) of analysed species Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Characidae							
Agoniates cf. anchovia Eigenmann, 1914	š	9	3	0.00	0.00	0.01	0.10
Aphyocharax anisitsi Eigenmann & Kennedy, 1903		338	3	0.02	8.78	0.00	0.00
Brycon cf. cephalus (Gé nther, 1869)		3	2	- -	- -	- -	- -
Charax gibbosus (Linnaeus, 1758)	š	19	11	0.03	0.26	0.02	0.03
Roeboides affinis (Gé nther, 1868)	š	968	42	4.00	2.07	0.49	2.00
Roeboides biserialis (Garman, 1890)	š	11	3	0.00	0.16	0.00	0.06
Roeboides myersii Gill, 1870	š	277	31	0.76	1.02	0.65	0.59
Piabucus melanostomus Holmberg, 1891		3	1	- -	- -	- -	- -
Astyanax abramis (Jenyns, 1842)		2	2	- -	- -	- -	- -
Astyanax bimaculatus (Linnaeus, 1758)		48	10	0.19	0.42	0.00	0.00
Ctenobrycon spilurus (Valenciennes, 1850)		183	19	0.13	3.48	0.23	0.06
Gymnocorymbus ternetzi (Boulenger, 1895)		2	2	- -	- -	- -	- -
Hemigrammus sp.		4	1	- -	- -	- -	- -
Markiana nigripinnis (Perugia, 1891)		35	10	0.17	0.05	0.03	0.00
Moenkhausia dichroura (Kner, 1858)		11748	43	61.26	12.47	4.74	3.80
Parecbasis cyclolepis Eigenmann, 1914		431	17	0.00	1.41	2.19	2.19
Phenacogaster sp.		4	2	- -	- -	- -	- -
Triportheus albus Cope, 1872		1336	35	0.29	0.92	2.19	13.46
Triportheus angulatus (Spix & Agassiz, 1829)		1831	48	4.48	7.44	2.17	7.37
Triportheus culter (Cope, 1872)		3	1	- -	- -	- -	- -
Triportheus sp.		4	3	- -	- -	- -	- -
Colossoma macropomum (Cuvier, 1818)		35	11	0.08	0.45	0.01	0.05
Metynnis hypsauchen (Mé ller & Troschel, 1844)		13	8	0.04	0.03	0.05	0.00
Metynnis maculatus (Kner, 1858)		30	8	0.17	0.00	0.00	0.00
Myleus tiete (Eigenmann & Norris, 1900)		3	3	- -	- -	- -	- -
Mylossoma aureum (Agassiz, 1829)		32	10	0.02	0.00	0.06	0.28
Mylossoma duriventre (Cuvier, 1818)		157	19	0.06	0.18	0.66	1.00
Piaractus brachypomus (Cuvier, 1818)		4	4	- -	- -	- -	- -
Pygocentrus nattereri Kner, 1858	š	397	39	0.46	4.06	1.35	0.46
Serrasalmus compressus Jé gu, Leé o & Santos, 1991	š	21	16	0.07	0.05	0.04	0.04
Serrasalmus eigenmanni Norman, 1929	š	115	21	0.61	0.03	0.08	0.01
Serrasalmus elongatus Kner, 1858	š	23	14	0.01	0.03	0.06	0.19
Serrasalmus hollandi Eigenmann, 1915	š	372	45	0.35	1.68	1.29	1.61
Serrasalmus rhombeus (Linnaeus, 1766)	š	474	42	0.68	0.37	1.50	2.60
Serrasalmus spilopleura Kner, 1858	š	37	12	0.20	0.05	0.01	0.00
Poptella compressa (Gé nther, 1864)		235	20	1.29	0.08	0.08	0.03
Stethaprion crenatum Eigenmann, 1916		163	14	0.06	0.26	1.45	0.06
Tetragonopterus argenteus Cuvier, 1816	7	4	0.01	0.00	0.04	0.01	

Order, Family Species, Authority	pisci.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Relative Abundance (%) of analysed species Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Curimatidae							
Curimata sp.		27	8	0.15	0.00	0.00	0.03
Curimatella alburna (Mé ller & Troschel, 1844)		1069	27	5.81	0.16	0.31	0.46
Curimatella dorsalis (Eigenmann & Eigenmann, 1889)		55	3	0.21	0.00	0.20	0.00
Curimatella immaculata (Ferné ndez-Yé pez, 1948)		38	5	0.00	0.00	0.01	0.48
Curimatella meyeri (Steindachner, 1882)		131	17	0.51	0.08	0.41	0.03
Curimatella sp.		431	7	2.48	0.00	0.00	0.05
Potamorhina altamazonica (Cope, 1878)		135	31	0.04	0.81	0.49	0.66
Potamorhina latior (Spix & Agassiz, 1829)		2058	34	0.05	9.59	7.54	12.52
Psectrogaster amazonica Eigenmann & Eigenmann, 1889		95	7	0.07	1.91	0.11	0.00
Psectrogaster curviventris Eigenmann & Kennedy, 1903		119	15	0.18	0.10	0.56	0.40
Psectrogaster rutiloides (Kner, 1858)		395	25	0.08	1.81	1.70	1.96
Psectrogaster sp.		2	2	- -	- -	- -	- -
Steindachnerina sp.		14	5	0.00	0.05	0.00	0.15
Cynodontidae							
Cynodon gibbus Spix & Agassiz, 1829	š	29	8	0.02	0.13	0.20	0.01
Hydrolycus scomberoides (Cuvier, 1816)	š	65	17	0.01	0.37	0.33	0.24
Rhaphiodon vulpinus Spix & Agassiz, 1829	š	69	23	0.00	0.08	0.30 0.	49
Erythrinidae							
Hoplerythrinus unitaeniatus (Agassiz, 1829)		1	1	- -	- -	- -	- -
Hoplias malabaricus (Bloch, 1794)	š	100	18	0.29	0.76	0.18	0.05
Gasteropelecidae							
Thoracocharax stellatus (Kner, 1858)		20	9	0.00	0.03	0.17	0.04
Hemiodontidae							
Anodus elongatus Agassiz, 1829		938	28	0.01	0.37	6.61	3.85
Lebiasinidae							
Pyrrhulina vittata Regan, 1912		1	1	- -	- -	- -	- -
Prochilodontidae							
Prochilodus nigricans Spix & Agassiz, 1829		133	28	0.50	0.31	0.19	0.22
Clupeiformes				***3.15***	***1.65***	***14.08***	***11.90***
Clupeidae							
Pellona castelnaeana Valenciennes, 1847	š	187	24	0.26	0.00	0.20	1.60
Pellona flavipinnis (Valenciennes, 1836)	š	968	42	2.89	1.39	0.88	4.31

Order, *Family* Species, Authority	pisci.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Relative Abundance (%) of analysed species Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Engraulidae							
Anchoviella cf. carrikeri Fowler, 1940		2	1	- -	- -	- -	- -
Engraulidae sp.		1701	28	0.00	0.26	13.00	5.99
Gymnotiformes				***0.58***	***5.87***	***1.10***	***0.36***
Apteronotidae							
Adontosternarchus sachsi		73	10	0.00	0.08	0.69	0.06
Apteronotus albifrons (Linnaeus, 1766)		9	5	0.05	0.00	0.00	0.00
Sternarchorhynchus sp.		2	2	- -	- -	- -	- -
Gymnotidae							
Gymnotus carapo Linnaeus, 1758		4	3	- -	- -	- -	- -
Hypopomidae							
Brachyhypopomus cf. brevirostris (Steindachner, 1868)		15	5	0.03	0.08	0.05	0.01
Rhamphichthyidae							
Rhamphichthys rostratus (Linnaeus, 1766)		19	9	0.05	0.13	0.02	0.04
Sternopygidae							
Distocyclus conirostris (Eigenmann & Allen, 1942)		1	1	- -	- -	- -	- -
Eigenmannia humboldtii (Steindachner, 1878)		52	9	0.04	0.92	0.05	0.06
Eigenmannia virescens (Valenciennes, 1842)		259	28	0.35	4.35	0.22	0.14
Sternopygus macrurus (Bloch & Schneider, 1801)		29	16	0.05	0.31	0.06	0.04
Perciformes				***0.35***	***3.09***	***0.52***	***3.65***
Cichlidae							
Astronotus crassipinnis (Heckel, 1840)		2	1	- -	- -	- -	- -
Chaetobranchopsis orbicularis (Steindachner, 1875)		3	3	- -	- -	- -	- -
Chaetobranchus flavescens Heckel, 1840		2	2	- -	- -	- -	- -
Aequidens sp.		1	1	- -	- -	- -	- -
Crenicichla sp.		1	1	- -	- -	- -	- -
Cichla monoculus Spix & Agassiz, 1831	š	19	12	0.09	0.00	0.00	0.04
Crenicichla cf. semicincta Steindachner, 1892		3	3	- -	- -	- -	- -
Satanoperca jurupari (Heckel, 1840)		4	3	- -	- -	- -	- -
Sciaenidae							
Pachypops trifilis (Mé ller & Troschel, 1848)		1	1	- -	- -	- -	- -
Plagioscion squamosissimus (Heckel, 1840)	š	492	38	0.26 3	.09	0.52	3.61
Pleuronectiformes							
Achiridae							
Achirus achirus (Linnaeus, 1758)		1	1	- -	- -	- -	- -

Order, Family Species, Authority	pisci.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
						Relative Abundance (%) of analysed species	
Rajiformes							
Potamotrygonidae							
Potamotrygon cf. motoro (Mé ller & Henle, 1841)		17	11	0.05	0.16	0.01	0.01
Siluriformes				***7.26***	***24.71***	***44.81***	***25.04***
Ageneiosidae							
Ageneiosus inermis (Linnaeus, 1766)	š	72	16	0.00	0.08	0.59	0.17
Ageneiosus brevis Steindachner, 1881		384	9	0.00	0.24	3.94	0.04
Ageneiosus sp.	š	14	5	0.00	0.00	0.13	0.03
Ageneiosus ucayalensis Castelnau, 1855		11	1	- -	- -	- -	- -
Tympanopleura sp.	š	246	15	0.00	0.10	1.95	0.75
Aspredinidae							
Bunocephalus sp.		1	1	- -	- -	- -	- -
Auchenipteridae							
Auchenipterus nuchalis (Spix & Agassiz, 1829)		289	21	0.00	0.29	1.73	1.48
Centromochlus sp.		144	15	0.00	0.00	0.38	1.39
Entomocorus benjamini Eigenmann, 1917		307	22	0.39	5.42	0.16	0.23
Epapterus dispilurus Cope, 1878		124	15	0.00	0.42	0.98	0.21
Trachelyopterus striatulus (Steindachner, 1877)		68	17	0.12	1.13	0.02	0.03
Tatia aulopygia (Kner, 1858)		1	1	- -	- -	- -	- -
Callichthyidae							
Brochis splendens (Castelnau, 1855)		44	3	0.00	0.00	0.46	0.01
Corydoras sp.		64	4	0.00	0.00	0.59	0.10
Dianema longibarbis Cope, 1872		5	4	0.00	0.05	0.02	0.00
Hoplosternum littorale (Hancock, 1828)		3	1	- -	- -	- -	- -
Megalechis thoracata (Valenciennes, 1840)		17	6	0.01	0.10	0.13	0.00
Doradidae							
Anadoras weddellii (Castelnau, 1855)		19	4	0.00	0.45	0.02	0.00
Astrodoras asterifrons (Kner, 1853)		1	1	- -	- -	- -	- -
Doras sp.		178	22	0.02	1.28	1.08	0.30
Opsodoras sp.		120	9	0.00	0.00	1.00	0.33
Platydoras costatus (Linnaeus, 1758)		10	5	0.06	0.00	0.00	0.00
Oxydoras niger (Valenciennes, 1821)		30	13	0.05	0.42	0.00	0.06
Pterodoras granulosus (Valenciennes, 1821)		4	4	- -	- -	- -	- -
Trachydoras paraguayensis (Eigenmann & Ward, 1907)		114	17	0.09	1.62	0.19	0.23

Order, Family / Species, Authority	pisci.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Relative Abundance (%) of analysed species Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Heptapteridae							
Pimelodella spp.		720	30	3.88	0.58	0.20	0.15
Loricariidae							
Hypoptopoma joberti (Vaillant, 1880)		3644	29	0.01	3.35	25.76	13.97
Hypostomus sp.		18	11	0.05	0.05	0.01	0.08
Pterygoplichthys sp.		129	27	0.22	2.04	0.13	0.01
Hemiodontichthys acipenserinus (Kner, 1853)		15	11	0.02	0.26	0.01	0.00
Rineloricaria cf. lanceolata (Gé nther, 1868)		7	5	0.01	0.03	0.03	0.03
Sturisoma nigrirostrum Fowler, 1940		107	10	0.00	0.03	0.86	0.32
Loricaria cf. simillima Regan, 1904		119	16	0.47	0.05	0.07	0.37
Loricariichthys maculatus (Bloch, 1794)		164	34	0.51	0.97	0.21	0.24
Pseudohemiodon laticeps (Regan, 1904)		43	9	0.06	0.00	0.19	0.19
Ancistrus sp.		7	6	0.00	0.00	0.04	0.04
Pimelodidae							
Hemisorubim platyrhynchos (Valenciennes, 1840)	š	8	7	0.01	0.03	0.01	0.05
Leiarius marmoratus (Gill, 1870)		1	1	- -	- -	- -	- -
Phractocephalus hemioliopterus (Bloch & Schneider, 1801)		1	1	- -	- -	- -	- -
Pimelodina flavipinnis Steindachner, 1876		1	1	- -	- -	- -	- -
Pimelodus gr. maculatus-blochi		479	40	1.16	4.03	0.54	0.95
Pinirampus pirinampu (Spix & Agassiz, 1829)	š	*46*	*16*	*0.00*	*0.03*	*0.35*	*0.15*
Pseudoplatystoma fasciatum (Linnaeus, 1766)	š	*28*	*15*	*0.03*	*0.13*	*0.10*	*0.10*
Pseudoplatystoma tigrinum (Valenciennes, 1840)	š	*24*	*11*	*0.01*	*0.39*	*0.01*	*0.09*
Sorubim lima (Bloch & Schneider, 1801)	š	*196*	*19*	*0.01*	*0.58*	*1.08*	*0.91*
Hypophthalmus edentatus Spix & Agassiz, 1829		*109*	*33*	*0.05*	*0.37*	*0.36*	*0.67*
Hypophthalmus marginatus Valenciennes, 1840		*166*	*23*	*0.01*	*0.18*	*1.06*	*0.75*
Calophysus macropterus (Lichtenstein, 1819)	š	*84*	*17*	*0.00*	*0.00*	*0.41*	*0.58*
Total catch number and relative abundance of piscivores (30 species)		***5757***		***13.0***	***17.2***	***12.9***	***21.2***

angulatus and *T. albus* (respectively 4.8 percent and 3.5 percent) and an unidentified species of anchovy, Engraulidae sp. (4.5 percent). Seventeen species had abundances exceeding 1 percent of the total catch (Table 2).

The proportions of individual species, major orders and piscivores differed among lake-types (Table 2). Characiforms dominated savannah lake assemblages (88.6 percent) whereas siluriforms dominated forest lakes (44.8 percent) and were relatively uncommon in the savannah lakes (7.3 percent). Clupeiforms were common in forest and Mamoré lakes.

Gymnotiforms were mostly captured in floodplain edge lakes. Similarly, relative abundance of most species differed among lake-types (Table 2). As an example of extreme patterns, the relative abundance of *M. dichroura* increased from the Mamoré lakes to the savannah lakes and the relative abundance of *T. albus* declined along the same gradient. Other species colonized preferentially one lake-type, such as *Aphyocharax anisisti*, which was present almost exclusively in floodplain edge lakes and *Anodus elongatus* and Engraulidae sp., which were captured mostly in forest and Mamoré lakes.

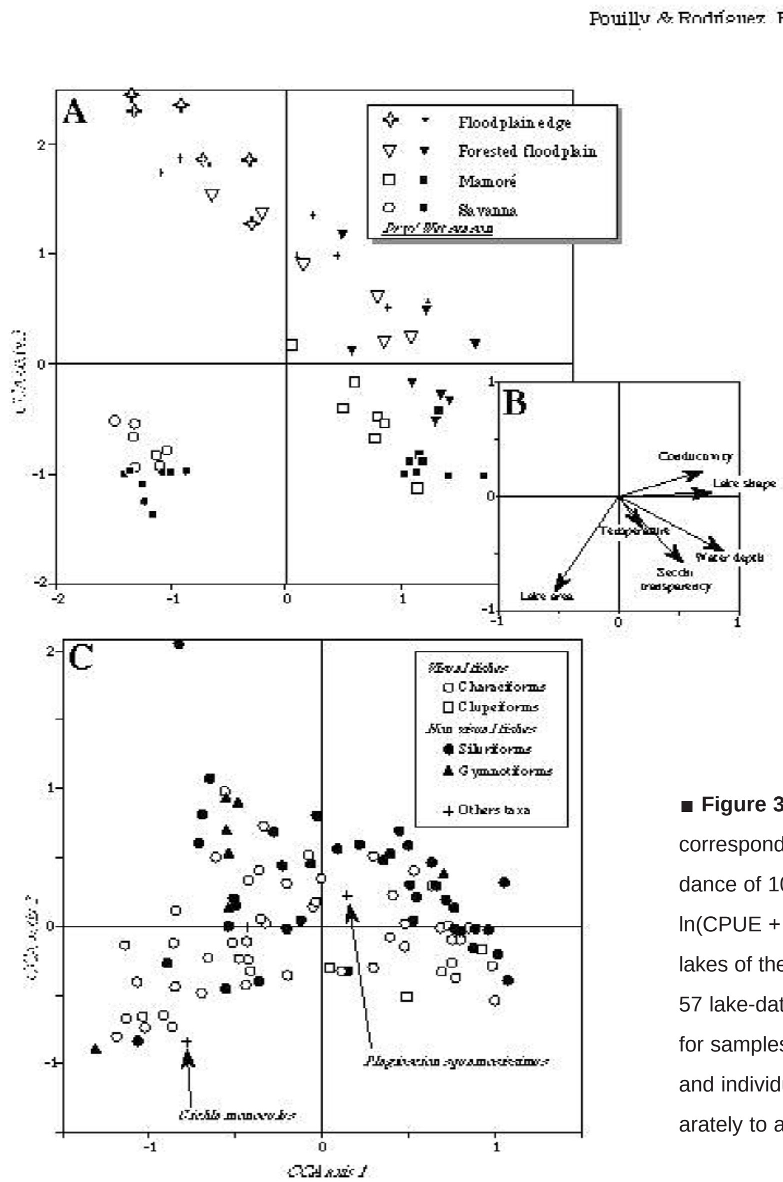
Relationships between assemblage structure and environmental conditions

Six environmental variables (conductivity, shape, water depth, Secchi transparency, temperature and lake area) were retained among the eight internal variables by the forward selection procedure in the CCA analysis. The CCA revealed a significant overall relationship between species CPUE and environmental internal variables (n = 57 lake-date combinations; $p < 0.001$), with the first three canonical axes jointly explaining 80.8 percent of the variation in the species-environment relationship (respectively 50.8, 20.4 and 9.7 percent; Table 3).

The CCA ordination shows a segregation of lake-types (spatial effect) on the first two axes (Figure 3). The temporal effect (dry vs. wet season) is reflected in a systematic shift in sample positions that is consistent across lake-types, but small relative to overall variation among samples. Savannah lakes were grouped in the lower left part of the CCA graph and differed markedly from the oxbow lakes in assemblage structure as well as in area, shape and conductivity. Savannah lakes also showed limited seasonal variation relative to oxbow lakes. Samples from oxbow lakes were concentrated in an elliptical cluster aligned with gradients in Secchi transparency and water depth. The

Table 3: Results of canonical correspondence analysis (CCA) linking abundance of 103 fish species transformed as ln(CPUE + 1), to six internal variables in eight lakes of the central Mamoré floodplain (n = 57 lake-date combinations). Monte Carlo tests for significance of first canonical axis and for all axes together: $p < 0.001$ (n = 1,000 permutations).

	Axis1	Axix2	Axis3
Eigenvalue	0.382	0.154	0.073
Cumulative% of explained variance of species-Env.relation	50.76	71.16	80.83
Species-Env. correlation (r)	0.951	0.915	0.811
Canonical coefficients			
Temperature	0.058	-0.062	0.098
Water depth	0.924	-0.304	-0.678
Secchi transparency	-0.038	-0.280	1.220
Conductivity	-0.145	0.256	-0.134
Area	-0.556	-0.761	-0.532
Shape	0.019	-0.209	-0.348
Correlations of environmental variables with ordination axes			
Temperature	0.171	-0.236	-0.048
Water depth	0.823	-0.433	-0.082
Secchi transparency	0.502	-0.523	0.457
Conductivity	0.658	0.196	-0.226
Area	-0.505	-0.759	-0.123
Shape	0.723	0.028	-0.309



■ **Figure 3.** Graphical output of canonical correspondence analysis (CCA) linking abundance of 103 fish species, transformed as ln(CPUE + 1), to six internal variables in eight lakes of the central Mamoré floodplain (n = 57 lake-date combinations). Ordination plots for samples (A), environmental variables (B), and individual species (C) are presented separately to avoid cluttering.

cluster spanned from dry season samples of floodplain edge lakes (upper left portion of the plot) to wet season samples of Mamoré lakes (lower right).

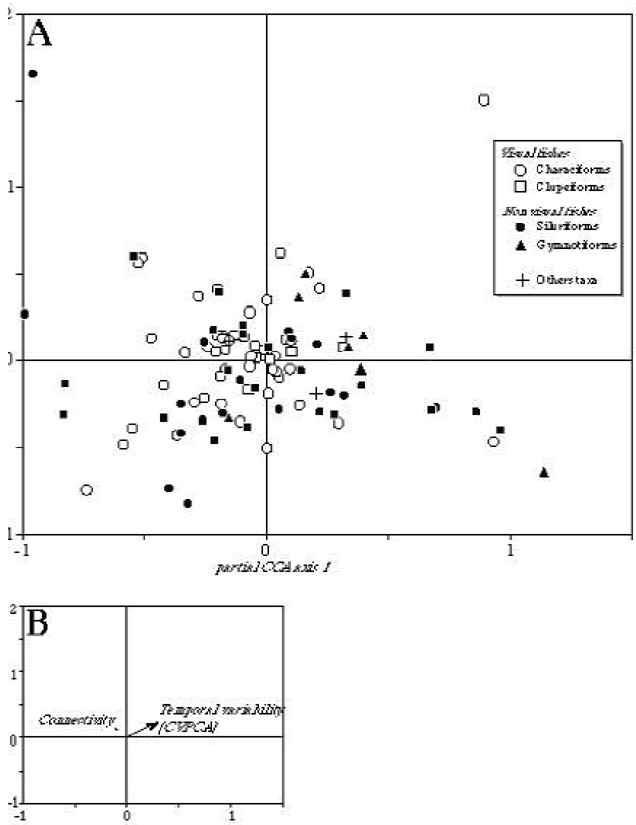
Species points in the ordination plot correspond approximately to the mode of their distributions along the environmental gradients (Ter Braak 1986). Patterns of distribution at the ordinal level can be broadly characterized as follows. The savannah lake samples were dominated mostly by characiform species that were not well represented in the oxbow lakes. All other species were associated mainly with the transparency-water depth gradient (TWD gradient): species found in more turbid and shallow conditions were located in the upper left portion of the ordination plot, whereas species found in clearer and deeper conditions were located in the lower right portion of the plot. Characiform species were evenly distributed between the two portions of the TWD gradient and the savannah lakes samples. Siluriform species were almost absent from the savannah lakes (only 4 of 39 species were present), but were distributed more or less uniformly along the TWD gradient. Gymnotiforms were most abundant in turbid, shallow waters. In contrast, the three clupeiform species had highest abundance in clearer, deeper waters.

Variation partitioning

Table 4: Partitioning of variation in abundance of 103 fish species, transformed as ln(CPUE + 1), at two spatial scales (landscape and internal). The total inertia (sum of eigenvalues) is partitioned into four fractions, three of which correspond to explained variance (landscape, internal, shared), and an unexplained fraction.

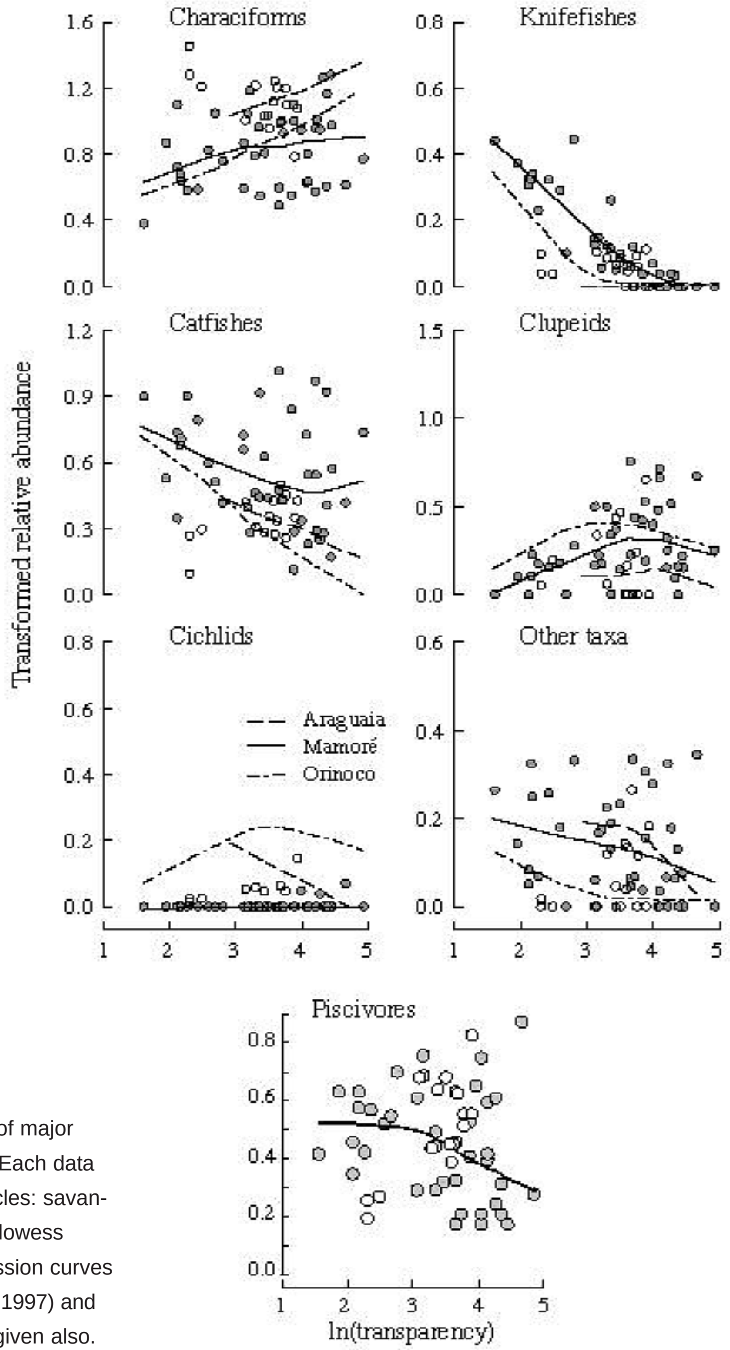
	Inertia	% of total variation explained	partitioning of explained variation (%)
1) Total variation (CA fish)	2.39		
2) CCA Fish vs Whole-lake	0.754	31.5	
3) CCA Fish vs Supra-lake	0.572	23.9	
4) Partial CCA Fish vs Whole-lake/Supr-lake	0.398	16.7	
5) Partial CCA Fish vs Supra-lake/Whole-lake	0.216	9.0	
6) Total explained variation (2+5=3+4)	0.970	40.6	
Unexplained variation (1-6)	1.42	59.4	
Whole-leke variables effect (4)	0.398		41.0
Supra-lake variables effect (5)	0.216		22.3
Shared effect (2-3=3-4)	0.356		36.7

In principle, partitioning of variation could be used to estimate the relative contribution not only of the two spatial scales, but of seasonal change as well. However, to simplify the interpretation and because CCA results showed that in the study system seasonal variation was very limited relative to spatial variation, partitioning of variation was conducted only between the two spatial scales. Landscape and internal variables jointly explained 40.6 percent of variation of the species matrix (Table 4). The unexplained variation corresponds to stochastic fluctuations as well as other biotic or abiotic effects not included in the analysis. The explained variation was partitioned into three components: 41 percent corresponded to internal variables, 22.3 percent to landscape variables and 36.7 percent to a shared influence of both types of variables.



■ **Figure 4.** Graphical output of partial canonical correspondence analysis (CCA) linking abundance of 103 fish species, transformed as ln(CPUE + 1), to two landscape variables in eight lakes of the central Mamoré floodplain (n = 57 lake-date combinations). The effect of the six significant internal variables was partialled out. Ordination biplots are given separately for individual species and environmental variables. Nocon = connectivity, CVPCA = temporal stability of internal variables (see text).

In the partial CCA that controlled for internal variables, two landscape variables were retained by the forward selection procedure: the overall measure of temporal variation, CVPCA ($p < 0.001$) and a binary variable indicating the presence or absence of a connection to the main river channel, NOCON ($p = 0.003$) (Figure 4). However, the position of the connectivity variable very near the origin of the ordination plot relative to the overall dispersion, suggests that the effect of connectivity was not large. Furthermore, there was no obvious pattern relating connectivity to the distribution of major taxa on the plot. In contrast, the distributions of gymnotiforms and characiforms were associated with variable CVPCA even after the effect of internal variables had been removed; the former were associated with fluctuating conditions whereas the latter were associated with more stable conditions (Figure 4).



■ **Figure 5.** Arcsine-transformed relative abundance of major taxa and piscivores in relation to water transparency. Each data point represents one lake-date combination (open circles: savannah lakes; filled circles: oxbow lakes). Solid lines are lowess regression curves for the oxbow lakes. Lowess regression curves for similar data from the Orinoco (Rodréguez & Lewis 1997) and Araguaia (Tejerina-Garro *et al.* 1998) floodplains are given also.

Applicability of the PTM model to the Mamoré floodplain

Variation of relative abundance of major orders along the gradient of transparency in the Mamoré oxbow lakes appeared broadly similar to those for the Araguaia and Orinoco floodplains (Figure 5). Secchi transparency was strongly associated with the abundance of clupeiforms (positive relationship) and gymnotiforms (negative relationship). Characiforms had highest relative abundance in clearer lakes, whereas siluriforms had highest relative abundance in more turbid lakes, but the relationships appeared weaker (with broader scatter) for these two groups in the Mamoré than in the Araguaia and Orinoco floodplains.

Characiforms were common and siluriforms uncommon in savannah lakes (15 samples) relative to oxbow lakes (42 samples). Fish assemblages in savannah lakes do not respond to the same environmental gradients as in oxbow lakes, e.g. abundance trends for characiforms and siluriforms in relation to transparency are neutral or opposite those in oxbow lakes and the Orinoco and Araguaia floodplains.

DISCUSSION

The results revealed strong relationships between fish assemblage structure and abiotic environmental features in eight lakes of the Mamoré floodplain. Fish assemblages were structured primarily along a marked spatial gradient correlated with internal and landscape variables. Spatial variation was stronger than temporal variation, as evidenced by large differences between lake-types relative to seasonal differences within lake types. Consequently, temporal variation was not interpreted on the basis of differences between dry and wet seasons, but remained indirectly included by way of the landscape variable CVPCA, an indicator of the amplitude of seasonal fluctuations in each lake. Ordination results showed major effects of water transparency and water depth on fish assemblage structure and less marked effects of pH, conductivity and temperature. In contrast to studies in other river systems, fish assemblage structure in the Mamoré floodplain, surveyed during wet and dry seasons, also seemed to be influenced by landscape variables.

Structural complexity and hydrological dynamics of the floodplain provide a broad range of habitat conditions that support high fish diversity (Welcomme 1985; Lowe-McConnell 1987). Seasonal connectivity renders the floodplain an open system in which many species can disperse. Consequently, assemblage structure in lakes can change seasonally and yearly as a function of variation in ecological conditions and reproductive success of species. Several studies have failed to link patterns of fish distribution to lake characteristics in neotropical floodplains (Bonetto Cordiviola de Yuan and Pignalberi 1970; Cordiviola de Yuan 1980; Lowe-McConnell 1987; Saint-Paul *et al.* 2000) and the assemblages have often been viewed as stochastic, mainly because of their strong interannual variability (Lowe-McConnell 1964; Cordiviola de Yuan 1980; Goulding. Carvalho and Ferreira 1988; Merona and Bittencourt 1993). However, differences between fish assemblages of white and black water lakes have been reported (Marlier 1968; Rodríguez and Lewis 1994; Saint-Paul *et al.* 2000) and fish assemblage structure in neotropical floodplains has been interpreted in relation to water quality variables that reflect instantaneous and local conditions, such as temperature, pH and oxygen concentration (Kramer *et al.* 1978; Junk, Soares and Carvalho 1983; Welcomme 1985; Goulding *et al*. 1988; Henderson and Crampton 1997). Welcomme (1985) suggested that lake morphometry plays a role in structuring fish assemblages, as exemplified by influence of lake size and bottom type on fish species composition and body size. Two recent studies that examined the effects of water quality, lake morphometry and landscape-level features (distance to main river channel, connectivity, forest cover) on fish assemblages of the Orinoco (Venezuela) and Araguaia (Brazil) floodplains, found that assemblage structure was associated mostly with two internal variables, water transparency and lake depth (Rodríguez and Lewis 1997; Tejerina-Garro *et al*. 1998).

Both studies concluded that fish assemblage structure during the dry season was controlled primarily by internal variables, with no detectable influence of landscape variables. Because of high variability in the inter-annual hydrologic conditions and high potential connectivity between the lakes, it might be expected that the spatial position of lakes does not play a major role in assemblage structure. Given that many fish can migrate, fish could be assumed to colonize lakes according to internal conditions, with little influence of lake position on the floodplain. However, lakes of the Mamoré floodplain are spatially structured at both internal and landscape levels, countering the previous assumption. Although flooding and dispersal could potentially lead to homogenisation of fish assemblages across the floodplain, the gradual evolution of lakes along the successional gradient determined by their spatial position relative to the Mamoré River (and related landscape variables) results in spatial heterogeneity of internal attributes and assemblage structure (relative abundances of major taxa and piscivores).

A salient result was the marked difference in fish assemblages and environmental conditions between savannah lakes and oxbow lakes, which indicates that the savannah lakes are not subject to the same ecological and physical dynamics as the oxbow lakes. Savannah lakes are large, shallow isolated lakes characterized by high stability of internal conditions. Except for their low conductivity, they have water quality characteristics comparable to those of oxbow lakes. Fish assemblages in savannah lakes changed relatively little between seasons. In contrast to oxbow lakes, savannah lakes yielded few siluriforms and gymnotiforms and characiforms were dominant. Because savannah lakes remain isolated for long periods of time, local species extinction may not be compensated by colonization as readily as in lakes with higher connectivity. As a consequence, species abundance and survival in isolated lakes may depend more on ecological attributes conferring local adaptation than on replenishment by recurrent movement or colonization events. Several characiform species seemed adapted to these conditions.

CCA showed that oxbow lakes were arranged along successional gradient of internal conditions, especially transparency and water depth. Mamoré lakes were deeper and clearer; lakes at the annual floodplain edge were more turbid and shallower. Oxbow lakes of the Mamoré floodplain are subject to annual isolation and flooding. These lakes may favour species able to respond to contrasting habitat conditions by moving or adopting ecological strategies. Several previous studies have suggested that exchanges of fish among lakes and the main river channel during the wet season lead to stochastic reassortment of species among the lakes. In contrast, species distributions showed clear patterns for clupeiforms, which were associated with more transparent and deeper lakes near to the Mamoré River and gymnotiforms, which were mostly associated with more turbid, shallower lakes at the forested floodplain edge. However, no clear pattern was apparent in the oxbow lakes for characiform and siluriform species, which were distributed more or less evenly along the lake gradient.

CCA provides modal positions of individual species on the lake-type and TWD gradient. However, the ordination plot for species distributions is not robust to random fluctuation in the position of rare species and, more generally, does not weigh species in relation to their abundances. In contrast, the relation between relative abundance of major taxa and water transparency integrates abundance over species, so that rare species do not unduly influence the analysis.

The results for major taxa in the Mamoré River floodplain appeared concordant with predictions of the piscivory-transparency-morphometry (PTM) model, originally developed for floodplain lakes of the Orinoco River (Rodríguez and Lewis 1997) and subsequently tested in the Araguaia River floodplain (Tejerina-Garro *et al*. 1998) (Figure 4). In the present study, an interaction of sampling methodology with water transparency could have influenced patterns of relative abundance. Although species that are not visually oriented might have equal probability of capture in clear and turbid lakes, visually oriented fishes might be able to detect gillnets more readily in clear water and thus be more vulnerable to capture in turbid water (K. Winemiller pers. comm.). However, predictions of the PTM model seem robust and general, because similar results were obtained in three different floodplain systems (Orinoco, Araguaia, Mamoré) sampled with different gears (electrofishing, minnow traps and gillnets and gillnets respectively). A general pattern arising from the comparison of results from these three systems is that relative abundances of siluriforms and gymnotiforms decline with increasing water clarity, whereas relative abundances of characiforms and clupeiforms increase. These results are consistent with the interpretation that differences in sensory capabilities (whether prevailing sensory modes are visual vs. chemical, tactile, or auditory) strongly influence species distributions along a gradient of water transparency (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998).

Similar to earlier findings, in the Mamoré floodplain some apparent exceptions can be explained by specific adaptations (Rodríguez and Lewis 1997). For example, several of the characiforms that are common in turbid waters are surface specialists (*Triportheus*, *Hydrolycus*, *Cynodon*) (Goulding 1980) or have lateral line adaptations to turbid environments (*Roeboides*) (Sazima 1983). Cichlids are visually oriented fishes that are mostly associated with transparent waters. They are poorly represented in the Mamoré and only the distribution of *Cichla monoculus* was included in our analysis (Table 2). Although *C. monoculus* had few occurrences, all individuals were captured in relatively transparent waters in the savannah and Mamoré lake samples. This result agrees with Rodríguez and Lewis' (1997) observation that cichlids had a unimodal distribution peaking in relatively clear lakes and is also consistent with the PTM interpretation. Interestingly, the relative abundance of "other taxa" in the Orinoco (mostly *Plagioscion*, *Achirus* and *Potamorrhaphis*), Araguaia (*Osteoglossum*, *Plagioscion*) and Mamoré (*Plagioscion*, *Potamotrygon*) floodplains declines with increasing transparency, suggesting that generally these taxa are most abundant in turbid waters.

In the Orinoco floodplain, piscivorous species, with the exception of *Acestrorhynchus*, showed decreasing abundance or unimodal (*Cichla* and *Boulengerella*) distributions in relation to transparency (Rodríguez and Lewis 1997). A similar result applies in the Mamoré floodplain, where the relative abundance of the most abundant piscivores remains relatively constant around 20 percent in turbid waters (Secchi depth <20 cm), but then declines progressively to < 5 percent as water transparency increases beyond 20 cm (Figure 5). This 20 cm threshold is also apparent in the Orinoco floodplain for predators and knifefishes (Figures 2 and 3 in Rodríguez and Lewis 1997). There may thus exist a threshold for visual search at that transparency level that drives an ecological switch in foraging modes (and perhaps in predator avoidance tactics as well). Many piscivores seem well adapted for foraging in low transparency conditions and even species morphologically adapted for visual hunting have developed special strategies for foraging in turbid waters (e.g. cynodontids, *Roeboides*; Rodríguez and Lewis 1997).

The two Mamoré savannah lakes did not conform to the PTM model. Although intermediate in transparency, they supported relatively few siluriforms and gymnotiforms. This lack of support for the PTM model might be attributed to the lack of connection of these lakes with the rest of the system during the annual flood. Savannah lakes probably do not undergo the seasonal cycle of recolonization followed by culling of vulnerable prey by piscivores as postulated by the PTM model. This result suggests that siluriforms and gymnotiforms may require, in addition to a favourable optical environment, ecological conditions such as seasonal access to the lakes from the river. By way of comparison, "morichal" lakes in Venezuela are adjacent to the floodplain, but have no seasonal connections to floodwater. Morichal lakes are small, highly transparent lakes of low conductivity within formations of the palm *Mauritia flexuosa* and fed mainly by seepage. Similar to Mamoré savannah lakes, morichal lakes are generally dominated by characiforms and have low relative abundance of siluriforms and gymnotiforms.

Partitioning of variation showed that although internal variables, especially transparency and water depth, play an important role in structuring fish assemblages, landscape variables such as distance to the river, connectivity and environmental variability also influenced assemblage structure. Because the measured internal variables do not completely characterize landscape conditions and conversely, the landscape variables do not fully account for variation in internal features, the two sets of variables are complementary. The Mamoré findings support the notion of hierarchical control of assemblage structure, similar to the sequence of "filters" proposed by Tonn *et al*. (1990).

Landscape variables (likely distance from the river channel and its corollary, flood period) operate as a primary filter that differentially limits dispersion to the savannah lakes, possibly affecting siluriforms more strongly than characiforms. Internal processes appear to exert stronger control in the oxbow lakes, where the colonization filter might be weak. Landscape filters also may play a role in the distribution of clupeiforms and gymnotiforms, both of which were mostly associated with specific lake-types, but in this case internal variables can be invoked to interpret species distributions. In contrast, landscape filters may not operate for siluriforms and characiforms in oxbow lakes; these species appeared more influenced by internal variables, especially transparency. Because of marked differences in connectivity between savannah and oxbow lakes, colonization or migration may be the processes most likely affected by landscape differences in this system.

Other processes, however, such as tolerance to environmental fluctuation (as quantified by CV) may be affected as well. The savannah lakes present relatively stable conditions, whereas among the oxbow lakes environmental variability increases with distance to the Mamoré River. The floodplain edge lakes had the lowest stability and also had extreme low values for water depth (<0.5 m in the samples; some lakes can dry out entirely at the end of the dry season in years with low rainfall). Changes in fish assemblage structure along an environmental gradient of harshness-stability determined by periodic hypoxia were described for bog lakes in northern Wisconsin, USA (Rahel 1984); a similar gradient driven by periodic hypoxia and dessication was found for oxbow lakes in Texas, United States (Winemiller *et al.* 2000).

In the Mamoré floodplain, the relatively large proportion of variation (36.7 percent; Table 4) associated with the "shared" component in the CCA indicated that effects of lake type and lake internal environmental conditions are partly confounded, as is likely the case in other floodplain systems. Although the influence of landscape conditions on assemblage structure is partly mediated through their relationship to internal features such as transparency and depth, which in the Mamoré floodplain vary predictably with lake position, landscape variables also contributed to the "pure" spatial component of variation in assemblage structure, which was unrelated to the measured environmental variables and accounted for 22.3 percent of total variation (Table 4). The partial CCA that examined the "pure" spatial component shed additional light on the role of landscape conditions, by showing that gymnotiforms were associated with fluctuating environmental conditions whereas characiforms were associated with more stable environmental conditions (Figure 4). None of the other major taxa showed a patterned distribution on the partial CCA plot. Although interpretable in principle on the basis of life-history strategies (r-K continuum, generalist-specialist, bet-hedging) at the ordinal level, these results do not mesh smoothly with previous categorizations of Neotropical fishes.

An analysis of patterns of covariation of ten life-history traits for 71 fish species in the Venezuelan llanos revealed a strong phylogenetic effect on life history strategies (Winemiller 1989). In that study, gymnotiforms were classed as "seasonal" (characterized by synchronized reproduction during the early wet season, high fecundity, absence of parental care, breeding migrations); cichlids were mostly "equilibrium" (parental care and aseasonal reproduction); characiforms were mostly "seasonal" with some "opportunistic" (rapid colonization, early maturation, continuous reproduction, small clutches); finally, siluriform species were split between the “seasonal” and “equilibrium” categories. Winemiller (1989) noted specific instances of fishes with divergent strategies in an environment that should favour only one of the strategies and suggested differential species trophic adaptations, perceived variation in resource abundance and predation pressure. If this explanation applies broadly, information on trophic linkages may complement that on abiotic environmental fluctuations when interpreting life history adaptations of fish species to spatial heterogeneity in the floodplain.

In conclusion, internal variables are linked to processes that modify assemblage structure via biotic and abiotic interactions within individual lakes, whereas landscape variables reflect processes related mostly to movement of fish among lakes and habitat selection based on large-scale landscape features. At the ordinal level, clupeids, gymnotiforms and siluriforms had distributions that may be controlled by both internal and landscape variables. In contrast, the distribution of characiform did not seem limited by the landscape variables. In the Mamoré River floodplain, characiforms seemed to have the greatest potential for colonization, as reflected by their distribution across all lake-types. Siluriforms were more spatially restricted, possibly in relation to their migratory requirements. Gymnotiforms and clupeids had the lowest potential for colonization, as inferred from their limited spatial distributions in this relatively open system.

ACKNOWLEDGMENTS

This work was part of the BIOBAB project (Aquatic Biodiversity in the Bolivian Amazon Basin) developed by IRD, La Paz University and Trinidad University. Takayuki Yunoki and Alfredo Parada, from Trinidad University and Jean Louis Menou, from IRD, helped with logistics, fieldwork and identification of specimens. We also thank Luis Torres (Trinidad University) for his helpful participation in the BIOBAB project. Kirk Winemiller (Texas A&M University) kindly reviewed the manuscript and provided helpful comments.

REFERENCES

Amoros C., Roux A. L., Reygrobellet J. L., Bravard J.P. & Pautou, G. 1987. A method for applied ecological studies of fluvial hydrosystems. *Regulated Rivers: Research & Management*, 1: 17-36.

Angermeier P.L. & Winston M.R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, 79: 911-927.

Bonnetto A., Cordiviola de Yuan E. & Pignalberi C. 1970. Nuevos datos sobre poblaciones de peces en ambientes leníticos permanentes del Paraná medio. *Physis*, 30: 141-154.

Borcard D., Legendre P. & Drapeau P. 1992. Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045-1055.

Cordiviola de Yuan E. 1980. Campaña limnológica Keratella I en el río Paraná medio: Taxocenoses de peces de ambientes leníticos. *Ecology Argentina*, 4: 103-113.

Denevan W.M. 1966. The aboriginal cultural geography of the llanos de Moxos of Bolivia. Berkeley, CA, USA, University of Califronia Press.

Goulding, M. 1980. *The fishes and the forest. Exploration in Amazon natural history*. Berkeley, CA, USA, University of California Press.

Goulding M., Carvalho M.L. & Ferreira E.G. 1988. *Rio Negro: Rich life in poor water*. The Hague, SBP Publishing Company.

Henderson P.A. & Crampton G.R. 1997. A comparison of fish diversity and abundance between nutrient-rich and nutrient-poor lakes in the Upper Amazon. *Journal of Tropical Ecology*, 13: 175-198.

Ibañez C. 2000. *Composición de la comunidad de zooplancton en ocho lagunas de la planicie de inundación del Río Mamoré*. Tesis de Licenciatura, La Paz University.

Junk W.J., Soares G.M. & Carvalho F.M. 1983. Distribution of fish species in a lake of the Amazon river floodplain near Manaus Lago Camaleão, with special reference to extreme oxygen conditions. *Amazoniana*, 7: 397-431.

Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 110-127.

Keddy P.A. 1992. Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science,* 3: 157-163.

Kramer D.L., Lindsey C.C., Moodie G.E.E. & Stevens E.D. 1978. The fishes and the aquatic environment of the Central Amazon Basin, with particular reference to respiratory patterns. *Canadian Journal of Zoology*, 56: 717-729.

Lauzanne L. & Loubens G. 1985. *Peces del rio Mamoré*. Travaux et Documents No. 192. Paris, ORSTOM.

Lauzanne L., Loubens G. & Le Guennec B. 1991. Liste commentée des poissons de l'Amazonie bolivienne. *Revue d'Hydrobiologie Tropicale*, 24: 61-76.

Loubens G., Lauzanne L. & Le Guennec B. 1992. Les milieux aquatiques de la région de Trinidad Béni, Amazonie bolivienne. *Revue d'Hydrobiologie Tropicale*, 25: 3-21.

Lowe-McConnell R.H. 1964. The fishes of the Rupununi savannah district of British Guiana, South America. Part 1. Ecological groupings of the fish species and the effects of the seasonal cycle on the fish. *Journal of the Linnean Society Zoology*, 45: 103-144.

Lowe-McConnell R.H. 1975. *Fish communities in tropical freshwaters*. London, Longman. 337 pp.

Lowe-McConnell R.H. 1987. *Ecological studies in tropical fish communities*. Tropical Biology Series. Cambridge, Cambridge University Press.

Magalhães M.F., Batalha D.C. & Collares-Pereira M.J. 2002. Gradients in stream fish assemblages across a Mediterranean landscape: Contributions of environmental factors and spatial structure. *Freshwater Biology*, 47: 1015-1031.

Marlier G. 1968. Etudes sur les lacs de l'Amazonie centrale. III- Les poissons du lac Redondo et leur régime alimentaire ; les chaines trophiques du lac Redondo; les poissons du rio Prêto da Eva. *Cadernos Amazonia INPA, Manaus,* 11: 21-57.

Merona, B. de & Bittencourt M.M. 1993. Les peuplements de poissons du Lago do Rei, un lac d'inondation d'Amazonie central: Description générale. *Amazoniana*, 12: 415-441.

Rahel F.J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. *Ecology*, 65: 1276-1289.

Rodríguez M.A. & Lewis W.M. Jr. 1994. Regulation and stability in fish assemblages of neotropical floodplain lakes. *Oecologia*, 99: 166-180.

Rodríguez M.A. & Lewis W.M. Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, 67: 109-128.

Saint-Paul U., Zuanon J., Villacorta Correa M.A., Garcia M., Fabré N. N., Berger U. & Junk W.J. 2000. Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes*, 57: 235-250.

Sazima I. 1983. Scale-eating in characoids and other fishes. *Environmental Biology of Fishes*, 9: 87-101.

Tejerina-Garro F. L., Fortin R. & Rodríguez M.A. 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. *Environmental Biology of Fishes* 51: 399-410.

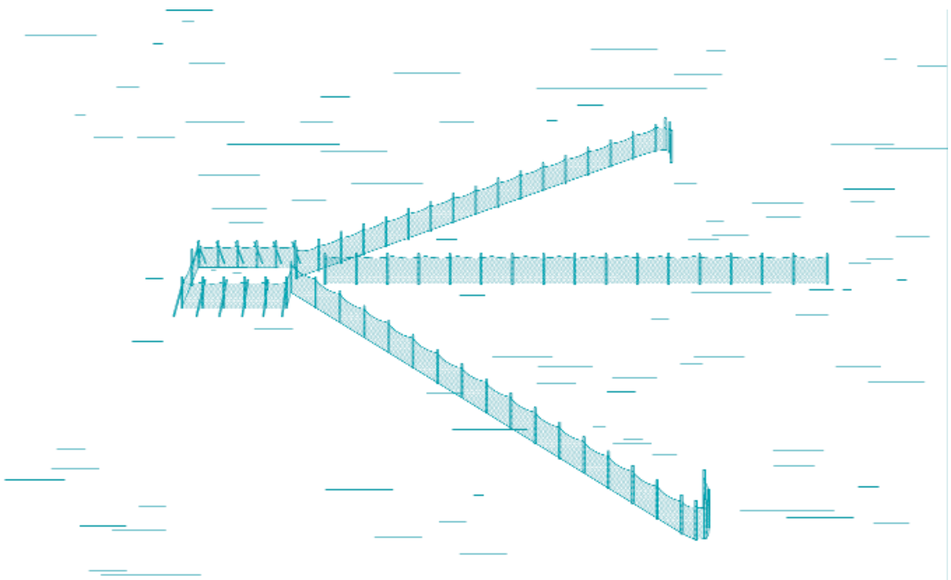
Ter Braak C.F.J. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. 1990. Intercontinental comparison of small lake fish assemblages: The balance between local and regional process. *American Naturalist*, 136: 345-375.

Welcomme R.L. 1985. *River fisheries*. FAO Fisheries Technical Paper 262. Rome, FAO.

Winemiller K.O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia*, 81: 225-241.

Winemiller K.O., Tarim S., Shormann D. & Cotner J.B. 2000. Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. Transactions of the American Fisheries Society, 129: 451-468.



DEPENDENCE OF TROPICAL RIVER FISHERIES ON FLOW

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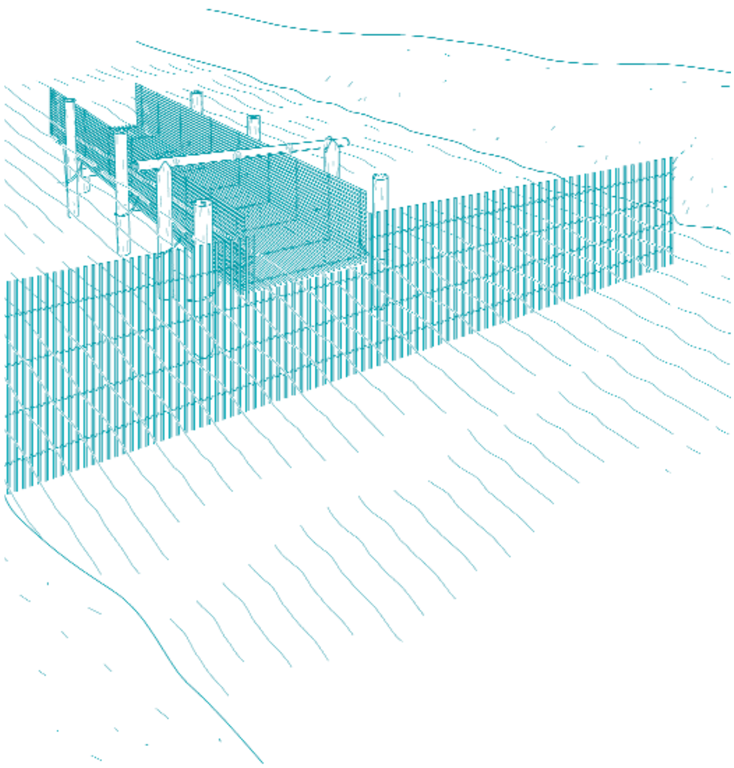


Key Words: fisheries, floods, rivers, floodplains

ABSTRACT

Much work has been done on the flow requirements for maintenance of fish populations and fisheries in temperate rivers but few equivalent studies are available upon which to base criteria for the management of water regimes for fishes and fisheries in large river systems, particularly in the tropics. Fish in such rivers are heavily influenced by flood regimes that fluctuate naturally from year to year. Recently increasing pressure on water for a wide range of uses other than fisheries has led to damming, river training, water abstractions and water transfers that have substantially altered flood regimes of rivers throughout the world. Such alterations usually have resulted in the loss of fish production and biodiversity. The current emphasis on sustainable development and biodiversity conservation is leading to

efforts to mitigate negative impacts of these changes through planning for altered river flows and the release of artificial floods from dams or polder sluices. The typical flood regime contains several characteristics that may influence the recruitment, growth and survival and growth of the individual fish species. Understanding of these characteristics will help determine flow criteria for the maintenance of floodplain fish faunas and design appropriate flood curves that maximize benefits from the water available.

INTRODUCTION

The growing human pressures for water, both as a resource in its own right and for the many other functions that it is called on to provide, impact strongly on the quantity and quality of water available in any river system. Water abstractions and transfers alter the amount of water in the system. Transversal damming of the channel, construction of longitudinal levees and river training structures and the poldering of river floodplains change the form and function of the river (World Commission on Dams 2000; Jackson and Marmulla, in press). Changes to the landscape such as de-forestation, land clearances for agriculture and wetland reclamation may also influence the nature and timing of the hydrograph. The function and structure of floodplain rivers are also conditioned by the pulses of nutrients and alluvial material that vary according to the type of hydrological regime (see for example the PULSO model for the Parana River – www.Neiff.com.ar).

Winemiller (2004) identifies three major types of river according to their hydrology, temperate with aseasonal (seemingly random) flood pulses, temperate with seasonal flood pulses and tropical with seasonal flood pulses. Fish have evolved physiological adaptations, life history strategies and spawning and feeding behaviour to cope with these differing types of fluctuating flow conditions in rivers (see Lowe McConnell 1975; Welcomme 1979 and Bunn and Arthington 2002 for reviews). Through these adaptations, different species are able to respond to changes in flow in different ways. As a result, the relative abundance of species forming riverine fish assemblages changes in response to natural variations in flood regimes between years. For example, rivers, particularly those with highly variable annual hydrographs, appear to have separate components that are adjusted to years of high flow and years of low flow. In years when the floodplains flood normally the high flow elements predominate and in years when the floodplains do not flood the low flow elements are more abundant. This variability may arise from separate species that are adapted to low flow and high flow, as in the Niger (Dansoko 1975; Dansoko, Breeman and Daget 1976; Welcomme 1979; Quensiere, Benech and Dansoko 1994). They may also possibly arise from variation within the genotype of one species, that has both migratory and static elements, as appears to be the case in several European cyprinid species such as roach (*Rutilus rutilus* L. or Bream *Abramis brama* (L.) that have become adapted to the static conditions of canals and regulated rivers but are migratory under more natural conditions (Stott 1967; Linfield 1985; Lucas and Baras 2001). Species, or genotypic variation within species, persist under natural variation in the short term but may be threatened by long-term alterations to flow regimes to which they are less well adapted.

The impacts of changing hydrological regimes on fish populations were early classified by Tennant (1976) using the Montana method and are regularly assessed in north temperate rivers using instream flow incremental methodologies and the related Physical Habitat Simulation System (PHABSIM) [see Bovee (1982) for methodology and Gibbins *et al*. (2001) for an example of the application of the methodology to a reservoir and water transfer system]. Instream flow methodologies have been used in many temperate zone countries to determine legal discharge requirements for the protection of fish and invertebrate faunas of rivers. These methods however are limited to relatively small systems and deal with instream or main channel processes and have little capacity to predict the impacts of changes in flow on floodplains. They have also been elaborated primarily for a relatively limited group of fishes, the salmonids and have not been developed to deal with the far more diverse and complex fish communities of large rivers. Some recent attempts have been made to link the productivity of larger, floodplain rivers to their flow characteristics, for example the DRIFT methodology used in South Africa (King, Brown and Sabet In Press 2003); Arthington *et al.* 2003) and the Benchmarking Methodology (Brizga 2000) and other holistic methodologies developed in Australia (Arthington, 1998; Arthington *et al.* 2003). None of the methods developed so far directly address the problems of the impacts of changing flow regimes on fish catch in the types of multi-species, multi-gear fisheries so common in large rivers, especially those of the tropics.

The biology and ecology of fish in large rivers are strongly linked to the annual hydrological regime in the main channel and the regular flooding of the associated floodplains (Welcomme 1985; Junk, Bayley and Sparks 1989). Current pressures on water from other users, notably agriculture, means that there is an increasing trend to control hydrological regimes. Such interventions almost inevitably act to the detriment of living aquatic resources and fisheries. Losses of fish catch below dams and other river regulating structures are now known to be significant and represent a considerable loss of food and income to the societies exploiting them (World Commission on Dams 2000). Water abstraction and transfer schemes can also induce changes in hydrological regimes that are potentially damaging to fish (Davies, Thoms and Meador 1992; Bunn and Arthington 2002). Impacts on fish and fisheries of schemes that change the form and function of the river and the hydrograph can be anticipated in project planning. For example, ensuring that adequate water is maintained in the system at all times to protect the species of major interest to the fishery or for conservation (environmental flows) can keep losses to a minimum. In some circumstances, releases of water from upstream dams or through the sluice gates of enclosing polders can simulate a flood and this approach is being increasingly advocated to compensate for the highly regulated state of some systems. For example the Phongolo River floodplain has been managed by artificial releases of water from the Phongolopoort dam (Heeg, Breen and Rogers 1980; Weldrick 1996), artificial releases have been tried in Thailand’s Pak Mun dam to encourage migration and breeding in the river downstream (Jutagate pers comm.), systematic releases are planned on the Colorado river to aid in the conservation of the native squaw fishes and releases are planned for the rehabilitation of the Dyje floodplain in the Czech republic (Lusk, Halaèka and Lusková 2003). However, detailed knowledge of the form and function of the river system and of the responses of the fish species are needed for such planning to be effective. Such detailed knowledge of individual systems is generally lacking. As a result, control of the amount of water in the system is often pursued uncritically according to the needs of the major user, usually agriculture, rather than according to the requirements of the fish population and the fishery. This paper is intended to review some of the aspects of hydrological regimes that influence fisheries and that need to be taken into consideration when recommending ecological flows or artificial flow releases. It addresses particularly temperate and tropical rivers with seasonal flood pulses although many of its conclusions apply to other types of flood pattern. It builds on the ideas expressed by Poff *et al.* 1997 and Welcomme and Halls (2001) by synthesising information on the impacts of various characteristics of flooding on the different aspects of fish ecology and fisheries. Of necessity some of the suppositions are based more on theoretical speculation than on hard facts as floodplain research is still at a very early stage and detailed information of the behaviour of most species is not available. However, enough knowledge exists to derive preliminary guidelines for the best way to conserve fish faunas through environmental flow scenarios or water releases to simulate floods.

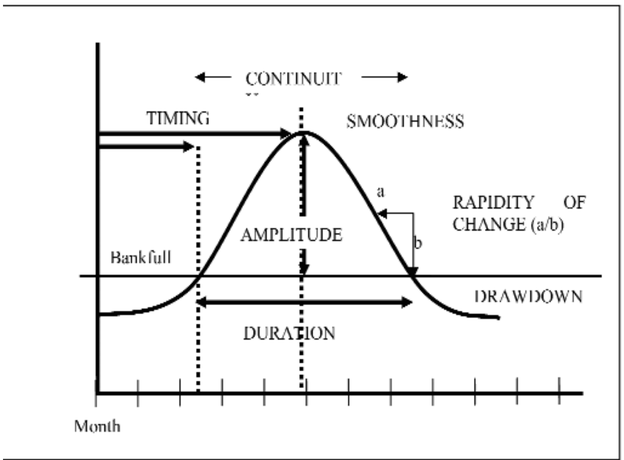
INFLUENCE OF HYDROLOGICAL REGIMES ON FISHERIES

The flood is important for most species of fish because the flooding of the lateral plains increases the area of food rich habitat and shelter from predators and provides ideal sites for young fish to develop and grow (see Welcomme 1979 for review). Older fish too profit from the improved feeding opportunities to lay down sufficient fat to permit them to survive the stresses of the dry season and to complete reproduction. Some species, usually predators, complete their life histories within the main channel of the river and rarely, if ever, venture onto the floodplain. The abundance and biomass of floodplain dependant species fluctuates from year-to-year depending on the strength of flooding. This is believed to reflect greater reproductive success, survival of fry and growth of fry and adults during years of better flooding. The greater biomass of fish in the system is reflected in fisheries catches. Many authors have found correlations between catches in year *y* and the intensity of flooding (usually represented by HI1) in the same or in preceding years – *y-1 or y-n* (see Stankovic and Jankovic 1971) for the Serbian Danube; Krykhtin (1975) for the Amur R.; Holcik and Kmet (1986) and Holcik (1996) for the Slovakian Danube; Moses (1987) for the Cross R.; Novoa (1989) for the Orinoco R.; Quiros and Cutch (1989) for the la Plata system; Payne and Harvey (1989) for the Pilcomayo R.; Lambert de Brito Ribeiro and M. Petrere (1990) for the Amazon; Welcomme (1979) and Lae (1992) for the Niger; Christensen (1993) for the Mahakam R.; Baran, Van Zalinge, Bun *et al.* (2001) for the Dai fisheries of the Mekong R.; and de Graaf, 2003 for floodplain fisheries in Bangladesh. Similar responses are found in estuarine or even coastal marine systems. For example Loneragan and Bunn (1999) found close correlations between high river discharges and the production of coastal fisheries in a Queensland river. Initially many of the earlier authors such as Krykhtin (1975), Welcomme, (1979) and Holcik and Kmet (1986) found the strongest correlations between the catch in year *y* and the strength of flooding in years *y-2* to *y-5* reflecting the time taken for the large fish forming the bulk of the catch to recruit to the fishery. However, more recent workers (Lae 1992; Halls 1998) have found correlations to be generally with the floods of the same year. This shortening of response time between the flood event and the fish catch is due to the fishing-down process, whereby fish are recruited into the fishery in their first year in today's heavily exploited fisheries (Welcomme 1999; Albaret and Lae, 2003). Some authors have also found correlations between catches and the amount of water persisting in the system over the low water period, notably University of Michigan 1971 and Quiros and Cutch 1989, however, best correlations were usually with the indices of flooding. All of this argues that in normal, humid rivers the flood component of the hydrological regime is the most important. The situation in arid rivers has been less well described although, even during the drought years of the Niger River, when the system was in an arid phase, good correlations with the strength of flooding were still obtained (Lae 1992).

Welcomme and Hagborg (1977) as a generic model, Moreau (1980) for fluctuating lake/river systems of Madagascar, Morand and Bousquet (1994) for the Central Delta of the Niger, Halls (1998) and Halls (2001) for the *Puntius sophore* fishery of Bangladesh, have modelled the processes regulating within year and year-to-year abundance and biomass of fish populations. The models employ empirical relations between recruitment, growth, mortality and fish density based on basic parameters of river fish dynamics, the main driver being water height. These models simulate biomass in response to hydrological conditions (Figure 5). They are based primarily on the dynamics of black and grey fish species (*sensu* Regier *et al*. 1989) that spawn on the floodplain and whose fry are assumed to have survival and growth closely correlated with the intensity of flooding. White fish species, which migrate upstream to breed in the channel and whose fry drift downstream with the current and are eventually washed onto the floodplains, may well have a different dynamic, especially with regard to survival and growth during the earliest, drifting phases. Little is understood of the dynamics of fish larvae in the drift and how they are affected by differences in main channel discharge although they are assumed to behave as other species do once they have entered the floodplain.

THE HYDROLOGICAL REGIME

Large rivers generally have one or more pronounced flood events during a year's cycle although in most temperate and some tropical rivers various types of flow regulating structure have modified these to a point where the natural regime has been largely suppressed. The hydrological regime can be described as a curve (Figure 1) that has a number of characteristics, each of which, potentially, has an effect on the various fish species that comprise a fishery. The phase of the regime that exceeds bankfull and either totally or partially inundates the floodplain is referred to as the flood.

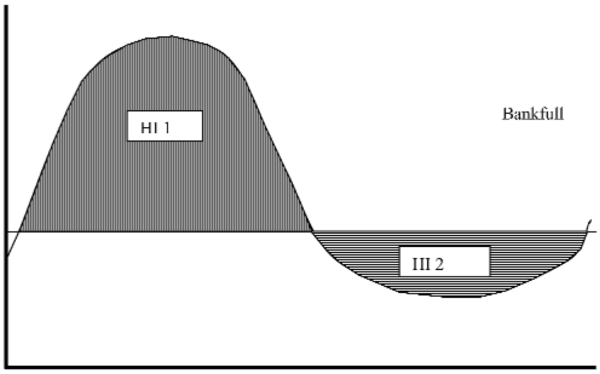


■ **Figure 1.** Various parameters of a flood curve having biological significance

The curve has mostly been defined for fishery purposes by an index (Hydrological Index or HI) that serves to indicate the relative magnitude of the flood or the low water phase during any one event. University of Michigan *et al.* (1971) first proposed this series of indices and since then many fishery workers have used them. Hydrological indices have been formulated from a number of indicators, including rainfall over the basin upstream of the floodplain, water height or discharge at selected gauges or evaporation from the floodplain. See Stankovic and Jankovic 1971; Welcomme (1979); Moses (1987); Holcik and Kmet (1986); Novoa (1989); Payne and Harvey (1989); Lae (1992); Christensen (1993). Typically an index will sum:

the area of the flood curve above the bankfull line, as an indicator of the intensity of flooding (HI 1), or

the area below the bankfull level and the curve defined by the depth of the residual water, as an indicator of the amount of water remaining in the system during the dry period (HI 2) (Figure 2).



■ **Figure 2.** Flashiness of rivers as a function of basin area exemplified by three rivers from the Chari-Logone River system

Flood indices describe the total amount of water during the period in question but in their existing form say little about the duration and amplitude of the flood. Thus, the same HI could describe a short but deep flood or a long but shallow one. Equally they say nothing about the other parameters of smoothness, rapidity of change or timing. The information needed to derive these parameters is often available from the water height record but is difficult to integrate into a descriptive model that permits comparison between years.

ROLE OF ASPECTS OF THE HYDROLOGICAL REGIME ON RIVER FISH ECOLOGY

This section examines in more detail the significance of the various parameters of the hydrological regime identified in Figure 1.

Timing

The timing of the flood is important to many river fish species because of the synchronisation between physiological readiness to spawn and the flood phase. Most species of river fish have defined breeding seasons centred on a particular flood phase (see Lucas and Baras 2001 for a detailed review of migration). Migratory, whitefish species (*sensu* Regier *et al*. 1989), such as *Prochilodus* (Bonetto and Pignalberi 1964; Bonetto *et al.* 1971) or the cyprinids of the Mekong are especially sensitive to the timeliness of the flood because they begin their migration from their downstream feeding habitat during the dry season and so time their migration as to arrive at the upstream spawning site before, or contemporaneously with, the rising flood (Fuentes and Espinach Ros 1998). Such species may mature during migration or at the upstream site, postponing the last stages of maturation until the waters begin to rise. By contrast (Humphries and Lake 2000) found that the species present in the Murray Darling system were unlikely to rely on discharge as a cue for final maturation and spawning so the generalisation that all river spawning behaviour is linked to the hydrological regime may be incorrect.

Total spawners (*sensu* Lowe-McConnell 1975), such as many characin, cyprinid and siluroid species, tend to have semi-pelagic eggs and larvae that enter the drift. Some hint of the complexity of the drift process is given by the work of Fuentes (1998) who showed that predatory species such as *Salminus* and *Pimelodus* migrate further upstream than the prey species so that, in drifting downstream from upstream, their larvae achieve a size at which they are able to feed upon the prey species as they enter the drift in their turn. Little is known as to the flexibility of such behaviour and its tolerance to substantial temporal displacement of the rising flood phase. Equally important, but little understood, are the population dynamics of the drifting fry with respect to survival, growth and distribution under different flood regimes. However, it is clear that accelerated flows may result in the drifting fry being swept past their destination and that flooding failure in floodplain nurseries will result in the loss of a whole year class of fish Gaygalas and Blatneve 1971; Fuentes 1998). In such species, modified hydrographs and artificial flood regimes must fulfil two requirements. First they must be sufficient and timely enough to induce spawning up-river. Second they must be extensive enough to ensure the flooding of the nursery floodplains downstream.

Timing is also important over shorter periods. In the Mekong and possibly other systems, migration and reproduction are closely linked to the lunar cycle (Sao Leang and Dom Saveun 1955). Inappropriate manipulations or modifications to the hydrological conditions during this cycle may not favour breeding in such species, especially in the flashier regimes of upstream reaches.

Grey fish (*sensu* Regier *et al.* 1989) including many small cyprinid and characin species may also be influenced by the flood as many of these are total spawners with a defined breeding season during the rising flood that so times the release of eggs as to enable the fry to be washed onto the floodplain by the advancing waters. Other grey and blackfish species such as the cichlids and smaller siluroids are partial spawners and small-brood spawners (*sensu* Lowe-McConnell 1975) that may breed on several occasions throughout the flood season or even into the dry season and are thus better adapted to changes in the timing of flow regimes.

Timing of floods is also important for climatic reasons. In many temperate and sub-tropical regions the flood coincides with rising temperatures of spring and summer (thermal coupling). This favours the growth of young fish by increasing the amount of food available and the rate at which it can be metabolised. Delay of flooding until late summer or early autumn in most rivers would result either in failure of the fish to spawn or in poor growth and low survival of the young fish due to the lower floodplain productivity in the cooler season. In some rivers such as the Murray-Darling in Australia and the Okavango in Botswana the downstream flood occurs during winter (thermally decoupled) and floodplain dependent production is relatively low in both these cases. There is little evidence for floodplain use by any life history stage of any fish species in the Murray-Darling system (Humphries, King and Koehn 1999), which may be due to the limited advantage of occupation of the floodplain during the cooler time of year. In some temperate systems occupation of the floodplain or the anabranches and backwaters of the main channel in winter appears more as a refuge from high flow than a feeding and breeding migration (Holcik 1988).

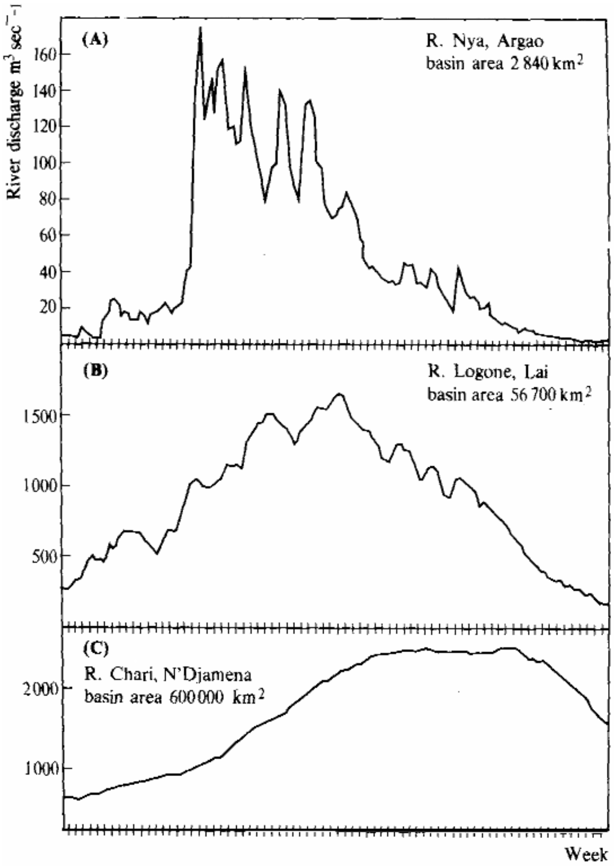
Continuity

In natural systems floods may be interrupted by one or more drought periods. Discontinuities are also induced in regulated systems when the primary user places demands on the water that interrupt the smooth progression of flooding. Such discontinuities may be particularly damaging to white and grey fish total spawners, which may spawn during the first flooding but whose eggs and larvae are then unable to colonise the floodplains because of the temporary recession of the waters. Black and grey fish multiple spawners are less likely to be affected by such discontinuities but may lose one or more broods when the floodplain dries during the recession.

Smoothness

The smoothness of the flood is a measure of the steadiness of the rise and fall of the waters. It is the inverse of flashiness, which is the rapidity with which the river responds to local flood events. As smaller streams respond only to rainfall on their immediate basin they are extremely flashy. As the basin area increases the river tends to average out the rainfall over its surface and thus becomes less and less conditioned by local events (Figure 3).

Fish faunas of smaller rivers and low order streams must have reproductive and shelter seeking behaviours that are adapted to sudden changes in the discharge if they are to survive. However, species living in higher order systems are usually better adapted to smoother flood curves. The smoothness of the flood curve is particularly critical for total spawning white fish, as temporary recessions can interfere with larval drift in the same way as discontinuities in flooding. For example Nikonorov, Maltsev and Morgunov (2001) found that there are no important spawning grounds for sturgeons left downstream of the Volgograd reservoir in the Volga River due to the sharp fluctuations in water level resulting from the operation of the power station. The fluctuations cause mass destruction of sturgeon eggs and oocytes were resorbed in 30 percent of female sturgeons. Severe fluctuations in level also pose potential difficulties for marginal spawners and some classes of nest builders such as *T. zillii*, which can repeatedly move its eggs to new nest sites as water levels rise. Excessive, rapid variation in level can strand attached egg masses of the marginal spawning phytophils resulting in the failure of that batch of spawn. Equally retreating waters could expose nests leaving the eggs and fry to desiccate. Similar arguments apply to many of the invertebrates that serve as one of the major food sources for the growing fish.



■ **Figure 3.** Flashiness of rivers as a function of basin area exemplified by three rivers from the Chari-Logone River system

Rapidity of change

The rate of the rise and fall of the water level is potentially critically important for many organisms. Overly rapid changes in level can affect fish more directly. During the rising waters rapid increases in level can submerge nests of bottom breeding species to too great a depth. Tilapias (*Oreochromis, Sarotherodon* and *Tilapia* species), for example, will tolerate only a narrow range of depths and substrate types for their nests. If the water is too deep, turbidity and low light levels do not permit them to complete their breeding. The rapid currents associated with such transitions in water current can sweep larvae and eggs of phytophilous species that deposit their eggs on the margins of floodplain and species with pelagic and semi-pelagic larvae in the main channel past their appropriate destination. During falling waters an overly rapid retreat of the flood is commonly assumed to increase the risks of stranding of fish in the temporary pools and channels of the floodplain resulting in unduly high mortality at this critical season.

Amplitude

The amplitude of the flood reflects the difference between the water level at low water and the maximum level reached during the flood. The higher the flood the greater the area of floodplain submerged. This means that the area available for nutrient recycling according to the flood pulse concept is greater (Junk *et al.* 1989; Junk and Wantzen 2004). Deeper (higher amplitude) floods produce greater flooded areas that can provide spawning sites, food and shelter for the fish.

The influence of amplitude on fish with drifting larvae is less easy to speculate upon, as the factors affecting survival and growth during the earliest drifting phases is generally unknown.

In some species such a *Prochilodus* and *Semaprochilodus* adult fish may be stranded in floodplain lagoons that are isolated from the river. Those closest to the river are connected yearly during flooding but lagoons at greater distances are connected less frequently and only during floods of greater amplitude. This accounts for the correlation between *Prochilodus* abundance and flood intensity in the Orinoco found by Novoa (1989) and in the La Plata system by Quiros and Cuch (1989). Periodic higher floods would therefore renew the fish and other faunas of lagoons that are more separated from the main channel.

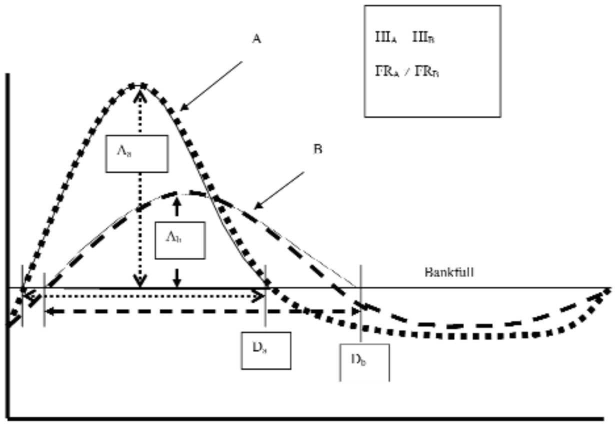
Duration

The duration of flooding (measured from bankfull on the rising flood to bankfull at drawdown) influences the time available for fish to grow and for them to shelter from predators. As such, longer duration of flooding extends the growing season resulting in heavier fish that have a greater potential to survive the following dry season and an improved reproductive potential.

Duration of flooding may also affect the floodplain vegetation. In the Mekong system, flooded vegetation is adapted to a ‘normal’ flood cycle and substantially longer floods lead to die-off and rotting. This in turn contributes to de-oxygenated conditions in the system. Similarly changes in flooding patterns can alter the viability and composition of floodplain forests as with the disappearance of the red gum in parts of Australia (Bren 1988) and *Acacia* species in the Pongolo system in South Africa (Furness 1978).

Relationship of amplitude to duration

Because both amplitude and duration can have positive and negative effects on the dynamics of the various fish species, the optimal flood for any group of species probably lies in a compromise between the two. This can be expressed as a ratio FR = Amplitude/Duration. Any volume of water available for environmental flows or constructed floods can have a number of ratios depending on the way in which the water is released (Figure 4). Models of the dynamics of floodplain fish communities (Welcomme and Hagborg 1977; Halls, Kirkwood and Payne 2001) as well as Weldrick’s 1996 specific model for the Phongolo R., can shed some light on how the two components of the flood interact. Because different species respond differently to different types of flood regime, a correct balance between these various factors for all fish species may be difficult to achieve through a standardised flood repeated annually and a range of flood types over a number of years may be more suitable.



■ **Figure 4.** Configuration of different flood regimes having the same Hydrological Index (HI) but different Flood Ratios (FR) where FR = Ax/dx

Environmental flows and the constructed floods associated with them call for a manipulation of the amounts of water in the river. Very often this will be a determined volume negotiated with other users of the resource as reserved for the needs of the living aquatic organism. It is then essential to make the best use of this water. Given that some degree of flooding of the floodplain is needed to secure the survival of many of the species comprising river fish communities, the relationship between the amplitude and duration of the inundation is critical. In these circumstances a long flood of low amplitude will produce a smaller flooded area for a greater duration, which means that reproductive success and fry survival may be lessened but that growth may be enhanced. However, if the flood is of high amplitude but too short a duration reproductive success may be higher but the young fish may not have sufficient time to grow and store sufficient fat. This would increase later losses through predation, as the smaller fish are more vulnerable and would also lower survival through the prolonged dry season as energy reserves may prove insufficient. Density-dependent mortality might also rise as the larger fish compete for reduced trophic resources.

Baran *et al.* (2001) suggest that amplitude may be more important than duration, at least for the growth of the floodplain spawning *Henicorhynchus spp.* in the Great Lake area of the Mekong, mainly because of the improved influx of nutrient rich silt bought in by the greater volume of water. On the other hand the model of Halls *et al.* (2001) suggests that duration may be more important because of the improved growth of the fish stock (Halls and Welcomme, in press). Unfortunately there are very few analyses of catches by floodplain fisheries that have been carried to the level of detail needed to resolve this question.

Extreme flood events

At intervals flood patterns can deliver extreme events that may challenge the capacity of the physical and living components of the ecosystem. Such extreme floods have tragic consequences for human populations whose occupation of the riparian zone of the river is adapted to more normal events. Living aquatic organisms can be severely affected by both abnormally high and low discharges. High discharges can wash away adult and juvenile fish, especially in rivers that have been hard engineered to contain flow in the main channel. Similarly, drifting eggs and larvae can be washed past suitable floodplain nurseries and lost to the population. Extremely low flows may operate mainly on water quality. They can lead to deoxygenation of the water through natural processes or through the failure of self-purifying mechanisms to correct human induced euthrophication (see articles by Szmes and Leibman and Riechenbach Klinke in Leipolt 1967). In extreme circumstances low flows can lead to desiccation of much of the riverbed and of an increased percentage of floodplain water bodies.

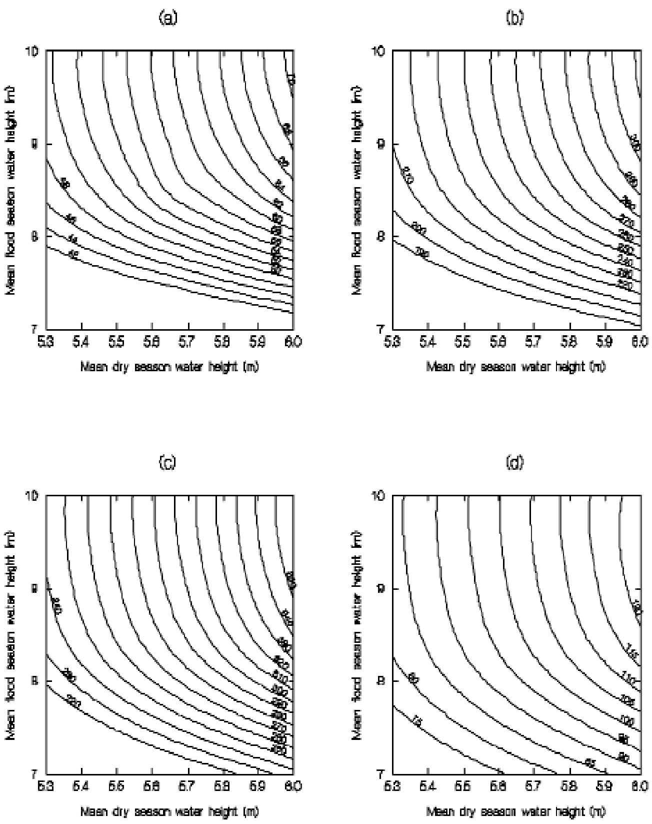
INFLUENCE OF WATER LEVELS IN THE DRY SEASON

The dry season is a period of great stress to the majority of river fish species. At this time most species are confined to the main channels of the river although some specialists can survive in permanent floodplain waterbodies. Variations in water level at this time can have a great impact on the extent and nature of various habitats for a range of organisms including fish, Puckridge *et al.* (1998) and can influence the amount of and access to spawning substrates and dry-season refugia such as riparian vegetation. Flow may cease in the main channel and deoxygenated conditions may appear both in parts of the river channels and in the floodplain waterbodies. The numerous individuals generated during the flood have to find space in the much-reduced environment (on the floodplain itself the water volume during the dry season may be less than 5 percent of the volume during the flood). Many species seek refuge in tributaries and in deep pools within the main channel, thus conservation efforts have to be directed at maintaining adequate water in such habitats. On the floodplain, insufficient channel flooding can result in the permanent waterbodies becoming desiccated and their fish populations defunct. Many species feed little during the dry season, an effect that Lowe-McConnell (1985) termed the physiological winter.

Conservation measures should seek to ensure that adequate water is provided so that a number of floodplain water bodies and the refuge areas within them are maintained with adequate water in them throughout the dry season. Fish are at their most vulnerable to the fishery and other predators during the low water period, so both main channel and floodplain refuges should be protected by law against illegal and excessive fishing. The models of Welcomme and Hagborg (1977) and Halls *et al.* (2001) indicate that the dry phase is limiting to population densities in most unregulated systems, acting as a sort of filter through which the population has to pass to survive into the following year. However, the fact that the better population densities created by good flood years are still detectable in catches as much as five years later implies that the fish assemblages have some type of ‘memory’ that enable years of good recruitment and growth to persist for a period despite the intervening dry seasons.

Stabilizing river flows to an almost constant discharge throughout the year may appear more efficient than retaining a pronounced flood pulse in that it would avoid much of the drawdown mortality and apparently lead to more stable fish stocks. It would favour fish species that are repeat spawners and are able to survive in the main channel alone (Lae 1995). The alternation between dry and wet phases confers an advantage in terms of overall aquatic productivity in fluctuating systems, such as flood rivers and lakes, as compared to more stable systems (Junk *et al.* 1989; Junk and Wantzen 2004). The advantage of the flood cycle to activities other than fishing, such as drawdown and irrigated agriculture, cattle grazing, wildlife is such that it cannot be ignored in planning for sustainable use of such land-water interface zones.

The question of what comprises the optimal relationship between the duration of the flood and the period when the river is separated from the floodplain during the drawdown remains unresolved. Models provide information on the dynamics of fish populations under different regimes of low and high water (Figure 5)



■ **Figure 5.** Contour plots of equilibrium yield (t) for P. sophore generated by the FPFMODEL of Halls, (1998) for different combinations of mean flood and dry season water height and for a range of fishing mortality but assume the flood as a feature of the model. Generally the longer the flood-phase the shorter the period of low water with its attendant high mortality.

CONCLUSIONS

GENERAL

Rivers are used for a number of human functions other than fisheries and the needs of high economic profile activities, such as power generation, frequently cause conflicts between abstractive industries and the water requirements of the fish and of fisher communities. Many of the current provisions for flow and flood regime control are inappropriate to fisheries in that the flood is managed for the conflicting objectives of fisheries, animal grazing and agriculture (particularly drawdown agriculture and rice culture). In such conflicts the agricultural interest invariably prevails. One reason for this, apart from the greater financial and political power of the agricultural lobbies, is that the flood conditions required for agriculture are relatively well understood, whereas the requirements of fisheries are less clearly defined. It is part of the purpose of this paper to draw attention to the need to better refine fisheries models in order to represent fishery interests more effectively in negotiations for the allocation of water to fish.

Four main tools exist for predicting the responses of fish species to differences in flooding in large rivers produced by human agencies.

- Knowledge of the biology of individual species can be used to predict the reaction of the species to some characteristics of the flood curve such as timing, smoothness and rapidity of change.
- Modelling of fish community responses to differences in flood regime are more appropriate when looking at dynamic issues such as amplitude, duration and the relationship between them.
- Evidence can be derived from practical experiences of artificial flood releases such as those carried out on the Pongolo River in South Africa. See for example Bruwer *et al.* (1996) and Heeg and Breen (1994).
- Application of best professional judgement systems such as DRIFT and the Instream Flow Incremental Methodology (IFIM).

Because of the considerable diversity of river fish species in their migratory and spawning behaviour, it is unlikely that any one set of flood conditions will affect all species equally. A good flood for one species may be detrimental to another. The most obvious example of this is in arid zone rivers such as the Sahelian Niger River. Here a group of species that breed preferentially in the main channel assumed dominance over similar species that spawn on the floodplains during the failed floods of the 1970-1980 drought (Quensiere *et al.* 1994; Lae 1995). Indeed much of the year-to-year variation in relative abundance of species in rivers, as reflected in the catch, may be explained by differences in the quality of the floods between years.

Similarly the ability of many European and North American species to adapt to the regulation of temperate zone rivers probably lies in the inherent behavioural and genetic variability within species that first arose as an adaptation to extreme year- to-year variation in flooding intensity. There are indications, for example, that many of the cyprinids that were originally semi-migrant, grey fish species had lotically and lentically oriented genetic components. Evidently the regulation of most modern rivers and canals has favoured the lentic component although there is evidence that, given the opportunity, migratory elements re-emerge (Linfield 1985).

In general, however, Arrington and Winemillers's (2003) analysis of the literature on fish diversity in floodplain rivers indicates that the loss of the flood pulse not only will impact biological production but impoverish regional species pools. Furthermore, the reduction of landscape heterogeneity associated with lowered flows may impair the resilience typically observed in flood river systems. Strategies for the conservation of floodplain rivers must, therefore, protect the hydrological variability characteristic of the river. Likewise strategies for the restoration of such rivers must seek to restore the hydrological regime as a primary objective.

Four main types of flow can be listed depending on how they interact with the fish fauna:

Population flows influence biomass through density dependent interactions with individual population parameters such as growth and mortality. Major criteria here are the magnitudes of the high and low season flows.

Critical flows trigger events such as migration and reproduction. Here the main criteria are timing and quantity.

Stress flows endanger fish because of excess velocity at high water or through desiccation at low water. These are typically extreme flows occurring as isolated peaks in an irregular hydrograph.

Habitat flows are needed for the maintenance of environmental quality including temperature, dissolved oxygen levels or sediment transport (see Bun and Arthington 2002).

Management of environmental flows for the sustainability of fish stocks and fisheries requires an understanding of all four types of flow. In this regard, it is already possible to derive some principles that can serve as guidelines in planning flow requirements and releases.

TOWARDS GUIDELINES FOR ENVIRONMENTAL FLOWS AND ARTIFICIAL RELEASES OF WATER AIMED AT FLOODING FLOODPLAIN RIVERS

In general, projects and interventions in river basins that are likely to alter the amount of water available to the river and the timing of the delivery of the water should make arrangements to release the flows necessary for the maintenance of healthy fish populations. It is insufficient that these flows be calculated only in terms of the total amount of water available to the system. In general, they should be as close to the natural flows as defined by Poff *et al*. (1997) and Bunn and Arthington (2002) as is possible given the resources available and as such should respect certain norms with regard to timing and to the shape of the flood curve that results from planned discharges and releases.

Flood phase

- A flood must be induced, preferably every year but if not every year then at least with sufficient frequency as to allow all species to reproduce within their life spans.
- Flood releases should be timed to arrive after the wetting of the floodplains by local rainfall. This means that the water volume is used to maximum efficiency in flooding rather than in saturating the desiccated soils of the floodplain.
- Flood releases should correspond to the needs of fish for hydrological stimuli that induce migration and spawning.
- Flood curves should be as smooth as possible to avoid repeated advances and withdrawals of the water that strand and desiccate eggs adhering to marginal vegetation and expose nests.
- Rises and falls in level should be relatively slow. This should avoid over-rapid submergence of nesting sites and excessive stranding of biota during the falling phase.
- High short floods should be alternated with lower but longer ones to favour all groups of species.
- Extreme flow events that result in washout of adults, juveniles and drifting fry should be avoided.

Drawdown phase

Adequate dry season flows should be assured. The amount of water remaining in the river is as critical to the survival of the fish population as the flood. Prolonged periods when no water is released, that desiccate the channel of the river and allow it to dry out into a series of de-oxygenated pools should be avoided.

The supply of water for ecological flows and artificial floods in regulated rivers does not come cheap. For example, recent public debate of plans to secure artificial flows in some US rivers are estimated to cost around $2M each in lost revenue from power generation. The quantities of water involved are impressive. Heeg *et al*. 1980 estimated that the Phongolo floodplain (South Africa) [10 265 ha at peak flood and 2700 ha of river and lakes at mean retention level] required 26 x 10^6 m^3 yr^{-1} to maintain mean retention level of its floodplain lakes and a further 100 x 10^6 m^3 yr^{-1} to flood the whole plain. However, a model developed by Weldrick (1996), showed that part of the floodplain could be submerged and the lakes could be filled by a discharge of 100 m^3 s^{-1} for 5 days (equivalent to a total discharge volume of 2.16 x 10^8 m^3). That such interventions are successful in large rivers is, however, attested to by the benefits of floodplain restoration along the Rhine River in the Netherlands (Grift 2001).

ACKNOWLEDGEMENTS

This paper could not have been written without the early comments of Tad Backiel and M. Zalewski and the later contributions by Angela Arthington and Brad Pusey, who carefully reviewed the manuscript and contributed much to the ideas about environmental flows.

REFERENCES

Albaret J.J. & Lae R. 2003. Impact of fishing on fish assemblages in tropical lagoons: The example of Ebrie Laoon, West Africa. *Aquatic Living Resources*, 16: 1-46.

Arrington D.A. & Winemiller K.O. 2003. Organization and maintenance of fish diversity in shallow waters of tropical floodplain rivers. *In* Welcomme R.L. & Petr T. eds. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries: Volume 2. Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp 25-36.

Arthington A.H. 1998. Comparative evaluation of environmental flow assessment techniques: Review of holistic methodologies. *LWRRDC Occasional Paper 26/98*. Canberra, Land and Water Resources Research and Development Corporation.

Arthington A.H. Tharme R.E., Brizga S.O., Pusey B.J. & Kennard M.J. 2003. Environmental flow assessment with emphasis on holistic methodologies. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 2*. Food and Agriculture Organization & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp. 37-66.

Arthington A.H., Rall J.L., Kennard M.J & Pusey B.J. 2003. Environmental flow requirements of fish in Lesotho rivers using the DRIFT methodology. *River Research and Applications*, 19: 641-666.

Baran E., van Zalinge N., Bun N.P., Baird I. & Coates D. 2001. Fish resources and biological modelling approaches in the Mekong Basin. Penang, Malaysia, ICLARM & Mekong River Commission Secretariat. 60 pp.

Bonetto A.A. & Pignalberi C. 1964. Nuevos aportes al conocimiento de las migraciones de los peces en los rios mesopotamicos de la Republica Argentina. *Comm. Inst Nacional Limnologia Santo Tome,* 1: 1-14

Bonetto AA., Pignalberi C., Cordiviola E. & Oliveros O. 1971. Informaciones complementarias sobre migracion de peces en la cuenca de la Plata. *Physis Buenos Aires*, 30: 505-520

Bovee K.D. 1982. *A guide to stream habitat analysis using Instream Flow Incremental Methodology*. US Fish and Wildlife Service, Instream Flow Information Paper No. 12, FWS/OBS – 82/26. 248 pp.

Bren L.J. 1988. Effects of river regulation on flooding of a riparian red gum forest on the River Murray, Australia. *Regulated Rivers*, 2: 65:77.

Brizga S.O. 2000. *Burnett Basin water allocation and management plan: Proposed environmental flow performance measures, Vol. 1&2*. Brisbane, Australia, Department of Natural Resources.

Bruwer C., Poultney C. & Nyathi Z. 1996. Community based hydrological management on the Phongolo floodplain. *In* M.C. Acreman, G.E. Hollis eds. *Water management and wetlands in subsaharan Africa*. Gland, Switzerland, IUCN. pp. 199-211.

Bunn S.E. & Arthington A.A. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30: 492-507.

Christensen M.S. 1993. Artisanal fishery of the Mahakam River floodplain in East Kalimantan, Indonesia. Actual and estimated yields, their relationship to water levels and management option. *J. Appl. Ichyol.*, 9: 202-209.

Dansoko F.D. 1975. Contirbution a l'etude de la biologie d'*hydrocyon* dans le Delta Centrale du Niger. Mali, Bamako, Ministere de l'Education Nationale. (Masters thesis)

Dansoko D.D., Breeman H. & Daget J. 1976. Influence de la secheresse sur les populations de d'*hydrocynus* dans le Delta Centrale du Niger. *Cahier ORSTOM Hydrobiol.*, 10: 71-76.

Davies B.R., Thoms M. & Meador M. 1992. An assessment of the ecological impacts of inter-basin water transfers and their threat to river basin integrity and management. *Aquatic Conservation: Marine and Freshwater Systems*, 2: 325-349.

De Graaf G. 2003. Dynamics of floodplain fisheries in Bangladesh, results of 8 years fisheries monitoring in the compartmentalization pilot project. *Fisheries Management and Ecology*, 10: 191-199.

Fuentes C.M. 1998. *Deriva de larvas de sabalo Prochilodus lineatus Valeniciennes, 1847 y otras especias de peces de interes comercial en el Rio Parana Inferior.* [Drift of larvae of Sabalo *Prochilodus lineatus* Valenciennes, 1847 and other species of commercial interest in the lower Parana River] Universidad de Buenos Aires. (Masters thesis)

Fuentes F. & Espinach Ros A. 1998. Distribucion espacial y temporal del ichthyoplncton en un punto del bajo delta del rio Parana. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'*, 8: 51-61.

Furness H.D. 1978. *Ecological studies on the Pongolo River floodplain. Working Doc. IV*. Workshop on Man and the Pongolo floodplain 14/106/7c. Pitermaritzberg. SA. CSIR.

Gaygalas K.S. & Blatneve D.P. 1971. Growth characteristics and the structure and abundance of the bream *Abramis brama* L. stock in the water-courses of the summer polders of the Nyumunas River delts. *J. Ichthyology*, 11: 682-692.

Gibbins C.N., Soulsby C., Jeffries M.J. & Acornley R. 2001. Developing ecologically acceptable river flow regimes: A case study of Kielder reservoir and the Kielder water transfer system. *Fisheries Management and Ecology*, 8: 463-485.

Grift R. 2001. How fish benefit from floodplain restoration along the lower River Rhine. Wageningen, The Netherlands, Wageningen University. 205 pp. (Doctoral dissertation)

Halls A.S. 1998. An assessment of the impact of hydraulic engineering on floodplain fisheries and species assemblages in Bangladesh. London, Imperial College of Science, Technology and Medicine. 532 pp. (Masters thesis)

Halls A.S., Kirkwood G.P. & Payne A.I. 2001. A Dynamic pool model for floodplain river fisheries. *Ecohydrology and Hydrobiology*, 1: 323-339.

Heeg J. & Breen C. M. 1994. Resolution of conflicting values of the Pongolo River and floodplain South Africa. *In* Patten *et al.* eds. *Wetlands and shallow continental water bodies*, volume 2. The Hague, SPB Academic Publishing. pp. 303-359.

Heeg J., Breen C.M. & Rogers K.H. 1980. The Phongolo floodplain: A unique system threatened. *In* M.N. Bruton, K.H. Cooper eds. *Studies on the ecology of Maputaland*. Cape Town, SA, Rhodes University and the Ntal Branch of the Wildlife Society of Southern Africa.

Holcik J. 1988. Influence of hydrological regime and water temperature on the activity and population density of fishes in the anabranches of the Danube. *Prace Ust. Rybar. Hydrobiol.*, 6: 3358.

Holcik J., & Kmet T. 1986. Simple models of the population dynamics of some fish species from the lower reaches of the Danube. *Folia Zoologica*, 352: 183191

Humphries P. & Lake P.S. 2000. Fish larvae and the management of regulated rivers. *Regulated Rivers: Research & Management.* 16: 421-432.

Humphries P., King A.J. & Koehn J.D. 1999. Fish, flows and floodplains: Links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes*, 56: 129-151.

Jackson D.C, & Marmulla G. *The influence of dams on river fisheries. Review prepared for the World Dams Commission*. (forthcoming)

Junk W. J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 110-127.

Junk W.J. & Wantzon K.M. 2004. The Food Pulse concept: New aspects, Appaooches, and applications-an update. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 2*. Food and Agriculture Organization & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp. 117-140.

King J., Brown C. & Sabet H. 2003. A scenario based holistic approach to environmental flow assessments in rivers. *River Research and Applications*, 19: 619-639.

Krykhtin K.L. 1975. Causes of periodic fluctuations in the abundance of the non-anadromous fishes of the Amur River. *J. Ichthyology*, 15: 826-829.

Lae R. 1992. Influence de l'hydrobiologie sur l'evolution des pecheries du delta Centrale du Niger, de 1966 a 1989. *Aquat. Lvg. Res.*, 5: 115-126.

Lae R. 1995. Climatic and anthropogenic effects on fish diversity and fish yields in the Central Delta of the Niger River. *Aquatic Living Resources*, 8: 43-58.

Lambert de Brito Ribeiro M.C. & Petrere M. 1990. Fisheries ecology and managment of the jaraqui *Semaprochilodus taeniurus, S. insignis* in Central Amazonia. *Regulated Rivers*, 5: 195-215

Leipolt R. ed.1967. Limnologie der Donau. Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung pp. var.

Linfield R.S.J. 1985. An alternative concept to home range theory with respect to populations of cyprinids in major river systems. *J. Fish. Biol.*, 27 Supp. A: 18796.

Loneragan N.R. & Bunn S.E. 1999. River flows and estuarine ecosystems: Implications for coastal fisheries from a review and case study of the Logan River, Southeast Queensland. *Australian Journal of Ecology*, 24: 431-440.

Lowe-McConnell R.H. 1975. Fish communities in tropical freshwaters. London, Longman. 337 pp.

Lowe-McConnell R.H. 1985. Ecological studies in tropical fish communities. Cambridge, Cambridge University Press. 382 pp.

Lucas M.C. & Baras E. 2001. Migration I Freshwater Fishes. London, Blackwell Science. 419 pp.

Lusk S., Halaeka K. & Lusková V. 2003. Rehabilitating the floodplain of the lower River Dyje for fish. *River Research and Applications*, 19: 281-288.

Morand P. & Bousquet F. 1994. Relations entre l'effort de peche la dynamique du peuplement ichthyologique et le niveau des captures dans un systeme fleuve-plaine. *In* J. Quensiere ed. *La Peche dans le Delta Central du Niger*. pp. 267-281. Paris, ORSTOM.

Moreau J. 1980. Essaie d'application au lac Alaotra Madagascar d'un modele d'etude de pecheries pour les plaines inondanles intertropicales. *Chier ORSTOM (Hydrobiologi)*,13: 83-91.

Moses B.S. 1987. The influence of flood regime on fish catch and fish communities of the Cross River floodplain ecosystem, Nigeria. *Environmental Biology of Fishes*, 18(1): 51-65.

Nikonorov S.I., Maltsev S.A.& Morgunov S.V. 2001. The problems of natural spawning of sturgeons and the ways of their decision. *Fish Economy*, No. 5: 42-44.

Novoa D.F. 1989. The multispecies fisheries of the Orinoco River: Development, present status, and management strategies. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 422-428.

Payne A.I. & Harvey M.J. 1989. An assessment of the *Prochilodus platensis Holmberg* population in the Pilcomayo River fishery, Bolivia using scalebased and computerassisted methods. *Aquaculture and Fisheries Management*, 203: 23348.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. 1997. The natural flow regime. *BioScience*, 47: 769-784.

Puckridge J.T., Sheldon F., Walker K.F. & Boulton A.J. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, 49: 55-72.

Quensiere J., Benech V. & Dansoko D.F. 1994. Evolution de la composition des peuplements de poissons, pp. 105-121. *In* J. Quensiere ed. *La Peche dans le Delta Central du Niger*. Paris, ORSTOM.

Quiros R. & Cutch S. 1989. The fisheries and limnology of the lower Plata Basin. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 429-443.

Regier H.R., Welcomme R.L., Steedman R.J. & Henderson H.F. 1989. Rehabilitation of degraded river systems. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 86-97.

Sao Leang & Dom Saveun. 1955. Apercu general sur la migration et la reproduction des poisons d'eau douce du Cambodge. *Proc. IPFC,* 5: 138-62.

Sanchez L., Vazquez E. & Blanco L. 1985. Limnological investigations of the rivers Uracoa, Yabo, Morichal Largo and Claro in the Eastern Plains of Venezuela. *Verh. Internat. Verein. Limnol*. 22: 215360.

von Stankovic S. & Jankovic D. 1971. Mechainismus der fischproduktion im gebeit des mittleren Donaulaufes. *Arch. hydrobiol., Suppl. XXXVI,* 4: 299-305.

Stott B. 1967. The movements and population densities of roach *Rutilus rutilus* L. and gudgeon *Cottus gobio* L. in the River Mole. *J. Animal Ecology.,* 36: 407-23.

Tennant D.L. 1976. Instream flow regimens for fish, wildlife, recreation and related environmental resources. *Fisheries*, 1: 6-10.

University of Michigan. 1971. The fisheries of the Kafue River flats, Zambia, in relation to the Kafue Gorge Dam. *Report prepared for the UN/FAO. Ann Arbor, Michigan, University of Michigan Press. FI:SF/ZAM 11: Tech Report*, 1: 161 pp.

Van Zalinge N. Degen P. Pongsri C. Nuor S. Jensen J.G. Nguyen V.H & Choulamany X. 2004. The Mekong River System. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 1*. Food and Agriculture Organization & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/16. pp. 335-358.

Welcomme R.L. 1979. Fisheries ecology of floodplain rivers. London, Longman. 317 pp.

Welcomme R.L. 1985. River fisheries. *Food and Agriculture Organization Fisheries Technical Paper 262*. 330 pp.

Welcomme R.L. 1995. Relationships between fisheries and the integrity of river systems. *Regulated Rivers: Research & Management*, 11: 121-136.

Welcomme R.L. 1999. A review of a model for qualitative evaluation of exploitation levels in multi-species fisheries. *Journal of Fisheries Ecology and Management*, 6: 1-20.

Welcomme R.L. & Hagborg, D. 1977. Towards a model of a floodplain fish population and its fishery. *Env. Biol. Fish.*, 21: 724

Welcomme R.L. & Halls A. 2001. Some considerations of the effects of differences in flood patterns on fish populations. *Ecohydrology and Hydrobiology*, 1: 313-321

Weldrick S.K. 1996. *The development of an ecological model to determine flood release options for the management of the Phongolo floodplain in Kwazulu/Natal South Africa.* Grahamstown, SA, Rhodes University. 81 pp. (Masters thesis)

Winemiller K.O. 2004. Floodplain river food webs: Generalizations and implications for fisheries management. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 2*. Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp. 285-310.

World Commission on Dams 2000. *Dams and Development: A new framework for decision making*. London, Earthscan Publications.

FLOODPLAIN RIVER FOOD WEBS: GENERALIZATIONS AND IMPLICATIONS FOR FISHERIES MANAGEMENT

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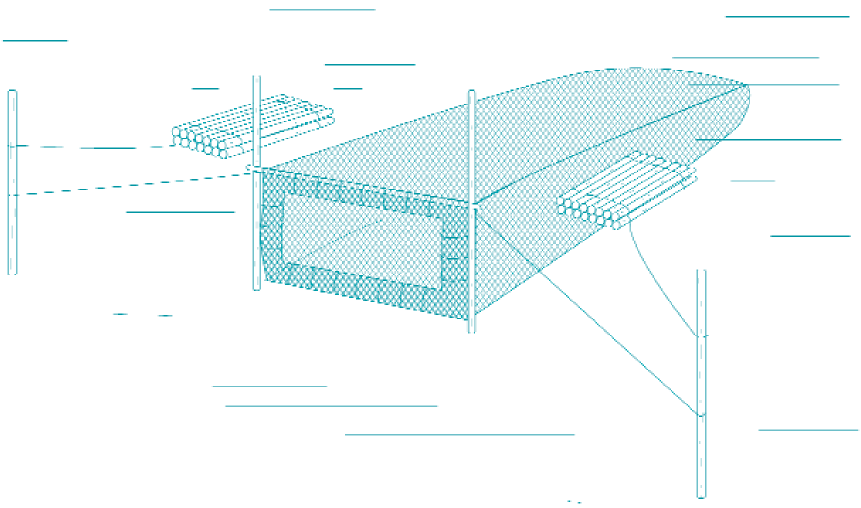


ABSTRACT

Based on the relationship between temperature variation and flood dynamics, three types of floodplain rivers can be identified: temperate stochastic, temperate seasonal and tropical seasonal. The degree to which flooding occurs in phase with warm temperatures and enhanced system productivity influences selection for alternative life history strategies in aquatic organisms. In addition, regional geochemistry and temporal dynamics of disturbance and recovery of local habitats within the landscape mosaic favour different life history strategies, sources of production and feeding pathways. In most habitats, algae seem to provide the most important source of primary production entering

Keywords: connectivity, detritus, migration, primary production, species interaction, trophic position

the grazer web. Large fractions of periphyton and aquatic macrophyte production enter aquatic foodwebs in the form of detritus and detrital consumption is greater during low-water phases. Even in species-rich tropical rivers, most of the material transfer in food webs involves relatively few species and short food chains (3-4 levels, 2-3 links). Longer food chains that involve small or rare species are common and increase ecological complexity, but probably have minor effects on total primary and secondary production. In the tropics, fishes appear to perform many ecological functions performed by aquatic insects in temperate rivers. Oftentimes, a small number of common species disproportionately influences benthic ecosystem structure, productivity and dynamics. Similarly, a relatively small number of predatory species may exert a disproportionately large influence on prey populations, even in species-rich tropical systems. Under seasonal flood-pulse regimes, species have the opportunity to evolve adaptations to exploit predictable resources. Under aseasonal flood-pulse regimes, species are more challenged to respond appropriately to relatively unpredictable patterns of resource variation and access to floodplain habitats, while nonessential for most species, usually enhances recruitment. Seasonal rivers in nutrient-rich landscapes can sustain greater harvest than aseasonal rivers or seasonal rivers in nutrient-poor landscapes. Loss of habitat connectivity and over-harvest of dominant species can have unpredictable effects on food web dynamics and community structure. Maintenance of natural flood regimes is important for biodiversity conservation and sustainable harvest of fishes, especially in strongly seasonal systems.

IMPORTANCE OF RIVER-FLOODPLAIN SYSTEMS

River-floodplain systems, especially in the tropics, support high biological diversity and important fisheries (Welcomme 1985; 1990; Lowe-McConnell 1987). High biological diversity, both taxonomic and functional, is associated with high spatial complexity and the dynamic nature of aquatic, terrestrial and ecotonal habitats (Schiemer 1999; Ward, Tockner and Schiemer 1999; Robinson, Tockner and Ward 2002). River networks are ubiquitous features of landscapes that have provided many opportunities for allopatric speciation of aquatic taxa and also serve as reservoirs that accumulate species over evolutionary time. The high habitat heterogeneity and ecotonal nature of river-floodplain landscapes also fosters high richness of terrestrial taxa.

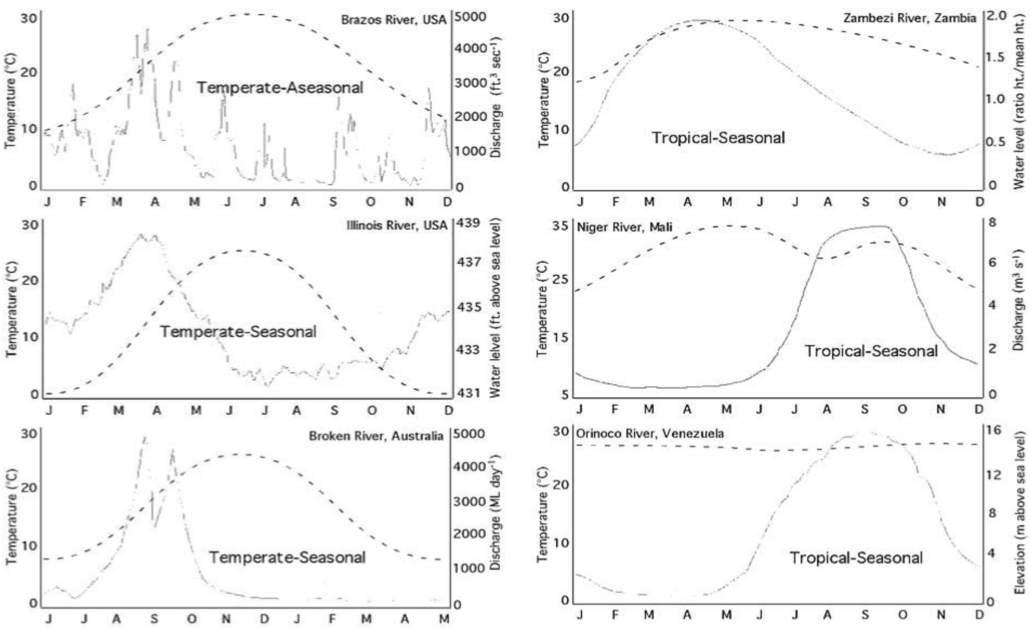
The nutrient-rich alluvial soils often associated with lowland floodplains have always been targets for intensive agriculture. Use of floodplains for agriculture has resulted in construction of levee systems to control flooding. Levees sever aquatic connections between the river channel and aquatic habitats of the floodplain (Sparks 1995; Ward *et al*. 1999). In addition to direct impacts from agriculture and other land uses that destroy natural terrestrial, wetland and aquatic habitats, lowland rivers are impacted by pollution, including nutrient loading, from locations anywhere within their catchments. The natural hydrology of most large rivers in developed nations and increasingly in developing nations has been severely altered by dams, levees, channelization and landscape changes. In spite of their great ecological, economic and cultural importance, large rivers remain one of the most poorly studied among major ecosystems (Thorp and Delong 1994). Recent years have witnessed an increase in research on large rivers, especially in Europe, Australia and the Americas. Even as we begin to understand the ecology of large river ecosystems, with each passing year fewer relatively un-impacted large rivers remain as models for future restoration.

The purpose of this paper is to briefly review food web structure and dynamics in lowland river-floodplain systems and to explore management implications of this body of ecological knowledge. The food web paradigm provides an approach that allows us to model complex communities and ecosystems with the ultimate aim of understanding relationships and predicting dynamics. The historic development of the food web paradigm has been reviewed previously (Hall and Raffaelli 1993; Polis and Winemiller 1996). Woodward and Hildrew (2002) recently reviewed food web structure in rivers, with a strong focus on theories and evidence associated with system stability. Their review emphasized evidence from streams, since comparatively little food web research has been conducted on large rivers. The present review seeks to summarize recent findings and perspectives from large lowland rivers. Additionally, the features of lowland rivers from tropical and temperate regions will be compared and generalizations sought for application to conservation of biodiversity, fisheries and ecosystem integrity and productivity.

TYPOLOGY OF RIVER-FLOODPLAIN ABIOTIC DYNAMICS

The degree to which flooding occurs in phase with warm temperatures and enhanced system productivity influences selection for alternative life history strategies in aquatic organisms. Rivers display at least three general patterns: temperate with aseasonal (seemingly random) flood pulses, temperate with seasonal flood pulses and tropical with seasonal flood pulses. The ramifications of these patterns for ecological dynamics, food web dynamics in particular, are the focus of this paper. Photoperiod and temperature are key environmental drivers of ecological dynamics in fluvial systems. Longer photoperiods during summer support increased primary production. Warmer temperatures increase rates of microbial metabolism, nutrient cycling, primary production and feeding by ectotherms. At high latitudes and elevations, spring warming also is associated with snowmelt and increased water availability. The effect of flooding on feeding, growth and survival of aquatic organisms can be particularly strong in lowland floodplain river systems. Floods stimulate remineralization of nutrients as well as primary and secondary production in floodplain habitats (Welcomme 1985; Junk, Bayley and Sparks 1989).

In temperate regions, temperature varies in a predictable seasonal pattern, with the magnitude of variation greater at higher latitudes and elevations. Regions having fairly unpredictable rainfall and lacking significant runoff from snowmelt display unpredictable, aseasonal flood pulses. Examples of temperate-aseasonal rivers are found along the northwestern Gulf of Mexico coast of North America and in certain regions within Australia's Murray-Darling Basin. In Texas, the Brazos River shows unpredictable hydrology, both within and between-years (Winemiller 1996a, Figure 1). High discharge events vary greatly in



■ **Figure 1.** Examples of lowland floodplain rivers with temperate-aseasonal (Brazos River- from US Geologial Survey database), temperate-seasonal (Illinois River- from Sparks 1995; Broken River- from Humphries *et al.* 2002) and tropical-seasonal (Zambezi River- from Handlos and Williams 1985; Niger River- from Quensiere *et al.* 1994; Orinoco River- from Hamilton and Lewis 1990) abiotic regimes.

magnitude and most are of short duration. Floods that top riverbanks and enter oxbow lakes are infrequent and can occur any time of the year (Winemiller *et al*. 2000). The unpredictable nature of flood pulses and river-floodplain connections pose challenges for species that exploit ephemeral or dynamic ecotonal aquatic habitats.

Many temperate regions have cyclic patterns of precipitation and/or springtime melting of ice and snow that yield seasonal flood pulses. Local flooding may derive from local precipitation and thawing (e.g. Broken River, Australia; Illinois River, United States, Figure 1), precipitation and/or snowmelt in headwater areas (e.g. lower Colorado River, United States), or some combination of local and upstream factors. Seasonal flooding in the temperate rivers also can be strongly influenced by evapotranspiration as a function of seasonal temperature regimes (Benke *al*. 2000). The magnitude of flooding in most temperate rivers is highly variable between years (e.g. Ogeechee River, south eastern United States, Benke *et al*. 2000) and in some systems floods may not occur at all during some years (e.g. Broken River, Australia, Humphries, Luciano and King 2002). Thus, whereas temperate-seasonal rivers provide a relatively predictable temporal regime to which organisms may respond adaptively (Resh *et al*. 1994), stochastic between-year variation may seriously challenge adaptive responses to seasonal environmental periodicity. In most cases, seasonal flooding in the temperate zone coincides with springtime warming, which selects for reproduction during this period. Recruitment is enhanced when early life stages occur in appropriate habitats when warm temperatures stimulate ecosystem productivity, metabolism and growth.

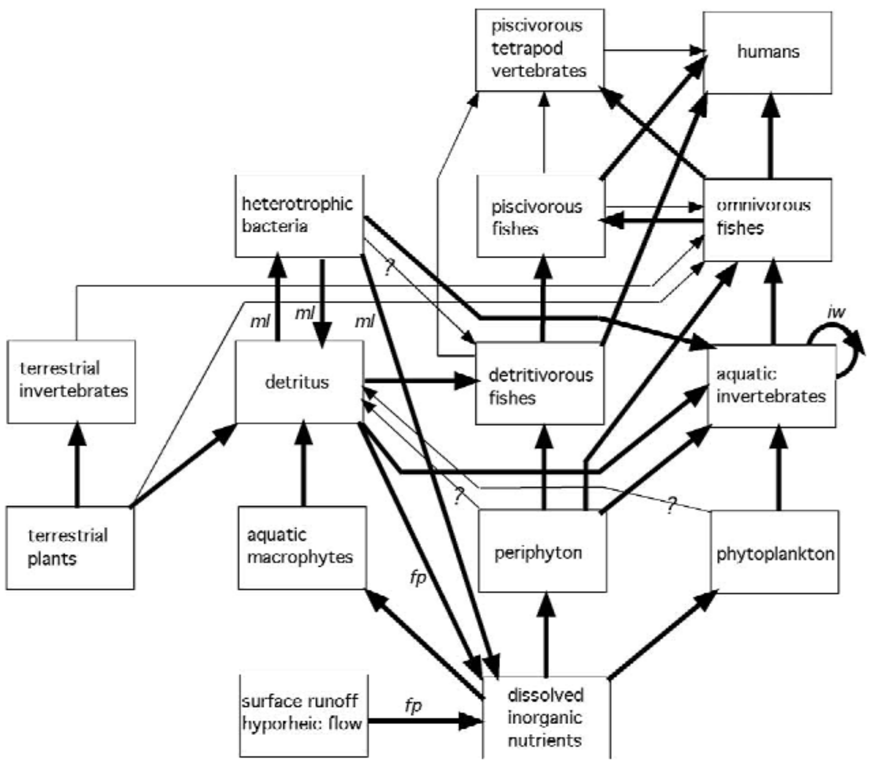
In tropical continental regions, the flood pulse of lowland rivers is almost universally driven by strongly seasonal precipitation. In some cases, local flooding coincides with local precipitation (Upper Orinoco, Upper Paraná, Upper Zambezi and Fly Rivers), whereas in others the seasonal flood pulse is most strongly influenced by rainfall in distant headwaters (e.g. lower Niger, Congo and Solimões-Amazon Rivers). Because temperature varies relatively little in tropical lowland regions, the hydrological regime is the major factor that drives ecological dynamics and natural selection in response to environmental variation. The tropical-seasonal model has dominated thinking about the ecology of river-floodplain systems (e.g. the flood-pulse model, Junk *et al*. 1989), but global generality of this pattern and its consequences has scarcely been discussed (but see below, also Thorp and Delong 1994, 2002; Humphries, King and Koehn 1999: Humphries *et al.* 2002).

PRIMARY PRODUCTION SOURCES FOR LOWLAND RIVER FOOD WEBS

A fundamental aspect of any food web is the source of primary production that supports consumer populations. Geology and landscape features influence nutrient and flood dynamics that affect production rates of different primary producers (Rai and Hill 1984). Primary production has high spatiotemporal variation within most river-floodplain systems. In the central Amazon Basin, primary productivity ranges from 50 to 3 500 mg C m^{-2} d^{-1} (Rai and Hill 1984) according to location and flood stage. Macrophytes, both terrestrial and aquatic, appear to be the major producers in floodplains (Bayley 1989; Melack *et al*. 1999; Lewis *et al*. 2001). Analysis of stable isotopes indicates that dominant production sources for higher consumers in river-floodplain food webs appear to be phytoplankton, periphyton and fine particulate organic matter derived from algae (Araujo-Lima *et al*. 1986; Hamilton, Lewis and Sippel 1992; Forsberg *et al*. 1993; Thorp and Delong 1994, 2002; Thorp *et al.* 1998; Benedito-Cecilio *et al*. 2000; Lewis *et al*. 2001; Leite *et al*. 2002). Even in highly turbid floodplain lakes of arid central Australia, benthic filamentous algae in the shallow littoral zone are the major production source supporting higher consumers (Bunn, Davies and Winning 2003).

Both algae and aquatic macrophytes appear to enter aquatic food webs mostly in the form of detritus (fine and coarse particulate organic matter), some being transported in the water column and some settling onto substrates. Direct consumption of aquatic macrophytes is rare, but aquatic macrophytes are consumed by a few fish genera from South America (*Schizodon* [Anosotomidae] and *Pterodoras* [Doradidae]) and Africa (*Tilapia* [Cichlidae]). Detritivory is extremely common in river communities, both among invertebrates and fishes. In seasonal floodplain habitats of the Orinoco and Zambezi rivers, consumption of detritus by fishes was greater during low-water phases (Winemiller 1990, 1996a). As determined from analysis of stomach contents, fishes consumed large fractions of both fine and coarse particulate material. In these systems, coarse detritus is derived almost entirely from aquatic macrophytes. The origin of fine particulate matter in diets could not be determined from microscopic analysis, but isotopic studies suggest mixtures of algae and macrophytes that use the C3 photosynthetic pathway (Jepsen and Winemiller 2002).

Based on isotopic evidence and the fact that coarse particulate matter derived from macrophytes is refractory and of poor nutritional value, Thorp and Delong (1994, 2002) made a case for a dominant role of algae in river food webs. In tropical-seasonal rivers, macrophytes generally produce well over half of the primary production on floodplains, yet only contribute small fractions of the total carbon assimilated by fishes (Forsberg *et al*. 1993; Lewis *et al*. 2001). Macrophyte production is high during the period of floodplain inundation (Rai and Hill 1984; Welcomme 1985; Junk *et al*. 1989). As floodwaters recede, aquatic macrophytes die and produce massive amounts of coarse detritus, only a minor fraction of which is probably consumed in any form by aquatic macrofauna. Most of the labile dissolved organic carbon leaches from this material and is quickly consumed by microbes. Most of the remaining refractory material seems to be consumed by microbes (the microbial loop), without direct entry into the upper food web (Figure 2). The fraction of microbial carbon that makes its way to the upper web is unknown for virtually all rivers, but assumed to be small based on available isotopic evidence (e.g. Bunn *et al*. 2003). In eutrophic floodplains, huge stocks of water hyacinths, grasses, or other macrophytes build up during the flood phase. As water levels drop, microbial metabolism of dead macrophyte tissues can deplete dissolved oxygen within shrinking aquatic habitats (Winemiller 1996b). In many savanna floodplains, such as the Kafue flats of the Zambezi system, submergence of terrestrial grasses during the rising-water phase leads to plant death, decay and aquatic hypoxia over large areas (Junk *et al*. 1989).



■ **Figure 2.** Generalized food web for floodplain-river ecosystems. Boxes are aggregate material pools and vectors represent consumer-resource interactions with thick arrows representing dominant pathways (ml= microbial loop path, fp = nutrient pathways enhanced by flood pulses, iw = invertebrate web having complex trophic structure involving invertebrates and ? = poorly quantified pathways).

In tropical systems, terrestrial sources of primary and secondary production are directly consumed by diverse fish taxa. In the central Amazon, several abundant fish species consume seeds, fruits, arthropods and other forms of allochthonous resources (e.g. Goulding 1980; Goulding, Carvallo and Ferreira 1988). Some characiform fishes (e.g. *Brycon*, *Colossoma*, *Piaractus* and *Myleus* spp.) are morphologically and physiologically specialized to feed on fruits and seeds. Goulding (1980) described large amounts of fruit and seeds in diets of many Amazonian catfishes (Siluriformes). Terrestrial invertebrates and vertebrates also enter the aquatic food webs. The aruana (*Osteoglossum bicirrhosum* Spix and Agassiz) is able to leap several meters above the water surface to feed on arthropods, reptiles, birds and bats. Accounts of direct consumption of allochthonous resources in the flooded forests of the Amazon had a large influence on the development of the flood pulse concept for large rivers. Yet when the aquatic food web is viewed as a whole (i.e. major biomass components) allochthonous carbon sources appear to be less important for macrofaunal populations than autochthonous sources of primary production. The greatest fraction of terrestrial vegetation that enters river-floodplain food webs appears to do so as detritus (leaf litter and woody debris), most of which is highly refractory and processed via the microbial loop.

FOOD WEB STRUCTURE

River food webs are extremely complex and dynamic (Winemiller 1990). Yet one of the most striking features of river communities is the domination of standing biomass by a relatively small number of species. This pattern appears to be true both in low-diversity temperate systems, but more surprisingly the pattern holds also for taxonomically diverse biotic assemblages in tropical rivers. Fishery yields from almost every major floodplain-river system in the world are strongly skewed in favour of a handful of dominant species (e.g. see summaries in Welcomme 1985). In terms of standing biomass, the Orinoco and Amazon river mainstems are dominated by a few species of *Prochilodus*, *Semaprochilodus*, *Mylossoma*, *Hydrolycus*, *Brycon*, *Pseudoplatystoma*, *Pinirampus*, and *Brachyplatystoma*. Obviously, much biomass may be represented by small fishes of little or no commercial value, however, even these small fish assemblages are strongly skewed with few abundant and many uncommon species (e.g. Winemiller 1996b, Arrington and Winemiller 2003). Thus, it is reasonable to assume that matter and energy moving through a local food web are doing so via a comparatively small subset of the total pathways represented in the trophic network. This was indeed the pattern demonstrated for the aquatic food webs in four tropical freshwater systems, including a creek-floodplain system in the Venezuelan llanos and Atlantic coastal plain of Costa Rica (Winemiller 1990). When the magnitude of trophic links was estimated as the volumetric proportion of resource categories in consumer diets, the distribution of link magnitudes was strongly skewed in every instance. In terms of biomass, relatively few dominant producer and consumer taxa and a limited number of major trophic pathways dominate river food webs.

Aquatic and terrestrial macrophytes usually are dominant sources of primary production in floodplains (Rai and Hill 1984) and most of this material is consumed by microbes that ultimately return nutrients to the inorganic pool (Figure 2). However, not all detritus is recycled within the microbial loop, with variable fractions consumed directly by a variety of invertebrate and fish taxa, some of which are dominant food web elements. Important components of aquatic meio- and macro-invertebrate faunas are detritivores (Schmid-Araya and Schmid 2000; Benke *et al.* 1984; Benke *et al.* 2001). Although the standing biomass of these taxa is generally low, they have high rates of population growth and turnover and represent important pathways in river food webs. Much more research is needed to elucidate the functional significance of aquatic invertebrates, particularly meiofauna, in large river food webs.

Detritivorous fishes are always abundant in river-floodplain systems and routinely dominate fishery catches (Welcomme 1985). Although some detritivorous fishes consume coarse vegetative detritus, most of the material classified as detritus in gut contents is fine amorphous material of undetermined origin. Detritivorous fishes are important prey for large piscivores. In the Cinaruco River of Venezuela, *Semaprochilodus kneri* (Pellegrin) were estimated to contribute about 45 percent of the diet of large *Cichla temensis* Humboldt during the falling-water period (Jepsen, Wimemiller and Taphorn 1997; Winemiller and Jepsen 2002). Detritivorous fishes form major portions of the diets of piscivorous catfishes in large South American rivers (Barthem and Goulding 1997; Barbarino and Winemiller unpublished). Tigerfish (*Hydrocynus vittatus* Castelnau) and African pike (*Hepsetus odoe* (Bloch) of the Upper Zambezi River consume large numbers of detritivorous tilapines and cyprinids, respectively. Yet isotopic evidence indicates that comparatively little carbon from macrophytes, especially grasses using the C4 photosynthetic pathway, makes its way to higher consumers (Hamilton *et al.* 1992; Lewis *et al.* 2001; Jepsen and Winemiller 2002). Information currently available from research in large rivers in North and South America indicates that much of the fine particulate organic matter assimilated by detritivorous fishes is derived from algae, even in systems in which aquatic macrophytes dominate aquatic primary production (Araujo-Lima *et al*. 1986, Hamilton *et al*. 1992; Forsberg *et al.* 1993; Winemiller and Akin unpublished).

Table 1: Estimated trophic positions of dominant piscivores in floodplain river ecosystems and estuaries (References are 1- Winemiller 1990, 2- Peterson 1997, 3- Jepsen & Winemiller 2002, 4-Winemiller 1996a, 5- Akin 2001, 6- Winemiller & Akin unpublished data).

Piscivore	Trophic position	Site	Analysis method	Reference
Pygocentrus cariba Valenciennes	3.4	Cañ o Maraca, Venezuela	diet	1
Hoplias malabaricus (Bloch)	3.4	Cañ o Maraca, Venezuela	diet	1
Caquetaia kraussii (Steindachner)	3.5	Cañ o Maraca, Venezuela	diet	1
Cichla orinocensis Humboldt	4.0	Morichal Charcote,Venezuela	diet	2
Hoplias malabaricus	4.0	Morichal Charcote,Venezuela	diet	2
Cichla orinocensis	3.5	Cinaruco River,Venezuela	isotopes	3
Cichla temensis	3.6	Cinaruco River,Venezuela	isotopes	3
Cichla temensis	4.8	Pasimoni River, Veneuela	isotopes	3
Serrasalmus manueli Fernandez-Yepez & Ramñ rez	3.8	Cinaruco River, Venezuela	isotopes	3
Pygocentrus cariba	3.8	Apure River, Venezuela	isotopes	3
Hoplias malabaricus	3.6	Apure River, Venezuela	isotopes	3
Hoplias malabaricus	4.0	Aguaro River, Venezuela	isotopes	3
Hydrolycus armatus (Schomburgk)	3.6	Apure River, Venezuela	isotopes	3
Hydrolycus armatus	4.2	Aguaro River, Venezuela	isotopes	3
Hydrolycus armatus	3.7	Cinaruco River, Venezuela	isotopes	3
Pseudoplatystoma fasciatum (L.)	3.5	Apure River, Venezuela	isotopes	3
Pseudoplatystoma fasciatum	4.4	Pasimoni River, Venezuela	isotopes	3
Nandopsis dovii (Gñ nther)	3.3	Tortuguero River, Costa Rica	diet	1
Gobiomorus dormitor (Lacepede)	3.3	Tortuguero River, Costa Rica	diet	1
Hepsetus odoe	4.3	Zambezi River, Zambia	diet	4
Hydrocynus vittatus	4.6	Zambezi River, Zambia	diet	4
Serranochromis robustus (Gñ nther)	3.7	Zambezi River, Zambia	diet	4
Lepisosteus osseus (L.)	3.6	Brazos River, Texas	diet	4
Lepisosteus oculatus (Winchell)	3.3	Brazos River, Texas	diet	4
Lepisosteus oculatus	3.3	Mad Island Marsh, Texas	diet	5
Lepisosteus oculatus	3.1	Mad Island Marsh, Texas	isotopes	6
Sciaenops ocellatus (L.)	3.4	Mad Island Marsh, Texas	diet	5
Sciaenops ocellatus	3.3	Mad Island Marsh, Texas	isotopes	6
Mean	3.7			

Descriptions of food web structure in river-floodplain ecosystems based on analysis of both diets and stable isotopes reveal short food chains. In terms of biomass, the most important pathways connect detritus to detritivorous fishes (and to a lesser extent invertebrates) and to piscivorous fishes. Consumer trophic positions can be estimated as a continuum using algorithms applied to dietary or isotopic data. In river-floodplain systems, large abundant piscivores almost invariably occupy positions between the third and fourth trophic levels (Table 1). This pattern arises because piscivore diets are dominated by detritivores and other fishes feeding near the second trophic level. In Caño Maraca, a creek-floodplain ecosystem in the Venezuelan llanos, the most abundant species in the fish assemblage, *Steindachnerina argentea* (Gill), also was the dominant prey of abundant red-belly piranhas (*Pygocentrus cariba*) and guavinas (*Hoplias malabaricus*) (Winemiller 1990). In the Cinaruco River, detritivorous and algivorous hemiodid and prochilodontid fishes dominate the diet of abundant *Cichla temensis* (Jepsen *et al*. 1997). In the Apure River, detritivorous *Prochilodus mariae* Eigenmann dominate the diet of the two most abundant large catfishes, *Pseudoplatystoma fasciatum* and *P. tigrinum* (Valenciennes) (Barbarino and Winemiller unpublished). Clearly, most matter and energy passes from the base to the top of the aquatic food web via food chains that are short (2-3 links and 3-4 levels). Isotopic analysis of fishes in a Pantanal lake indicated 3-4 trophic levels, with consumers arranged along a trophic continuum rather than discrete levels (Wantzen, Machado, Voss *et al*. 2002). Lewis et al. (2001) noted that short food chains facilitate efficient transfer of energy from algae to fishes and may explain why large fish stocks in tropical floodplains can be supported by the minor algal component of system primary production.

Given the dominant role of a relatively small number of short food chains, the high complexity of river-floodplain food webs is derived from numerous weak links among diverse species of both common and rare taxa. The most numerically abundant species (e.g. algae, invertebrates, fishes) are small-bodied with low to moderate standing stocks of biomass. Given high rates of population turnover, many of these taxa probably have greater functional significance in food webs than their low abundance implies. Although average food chain length leading to top piscivores is short, this does not imply that all food chains are short. Longer chains involving small or rare species can be identified. Small fishes that consume scales, fins, mucus, or blood of other fishes occur in most large rivers of South America. These fishes represent insignificant components of system biomass, but they contribute to high species diversity and high food web complexity. Thus, longer food chains that involve small or rare species are common and increase ecological complexity, but probably have very minor effects on primary and secondary production. In terms of biomass, tropical river food webs appear to consist of dominant (foundation, or core) species connected by short food chains, plus a much richer assemblage of small (subordinate, or interstitial) species, many of them uncommon, that greatly increase food web complexity while having relatively little influence on material and energy flow with the ecosystem. Of course these species could have important ecological functions that have not yet been identified (e.g. seed dispersal for riparian plants, Goulding 1980).

SPECIES FUNCTIONAL DIVERSITY IN LARGE RIVER FOOD WEBS

The tropics are widely recognized to harbour higher taxonomic and ecological diversity than temperate regions and large river systems provide no exception to this rule. Globally, fish species richness is strongly related to basin size (Welcomme 1985; Oberdorff, Guegan and Hugueny 1995). However, fishes show greater taxonomic and ecological diversity in lowland continental rivers of tropics relative to comparable rivers of temperate regions (Winemiller 1991a). Whereas the core feeding groups are represented in both temperate and tropical regions (i.e. algivores, detritivores, omnivores, invertivores and piscivores), the relative proportions differ. Fish assemblages of large tropical rivers contain greater fractions of detritivorous, herbivorous and omnivorous fishes relative to temperate fish assemblages (Winemiller

1991a). In this regard, tropical river fishes appear to occupy niche space occupied by invertebrates in temperate rivers.

Although no formal comparisons appear to have been made, macroinvertebrate species richness in large rivers does not seem to reveal a latitudinal gradient as steep as that of fishes. Bivalve mollusks actually have greater species richness in temperate rivers of the Western Hemisphere and the abundance and functional diversity of aquatic insects in lowland rivers does not appear to be much greater in tropical than temperate rivers. In tropical blackwater rivers (high concentrations of dissolved organic compounds, low PH and conductivity, low concentrations of nutrients and suspended solids), aquatic insect abundance is low with most species and biomass concentrated in leaf litter and woody debris. Shrimp are abundant in most lowland tropical rivers, with various taxa feeding on detritus, algae and microfauna. Even oligotrophic tropical blackwater rivers can support large populations of atyid and palaemonid shrimp. Leaf litter and woody debris seem to provide particularly important habitats in blackwater rivers (Benke *et al*. 1984). In tropical whitewater rivers (high concentrations of nutrients and suspended sediments in flowing channels, high conductivity, neutral pH), the root zone of floating aquatic macrophytes, such as *Paspalum repens* and *Eichhornia* spp., support high biomass of aquatic macroinvertebrates. Macroinvertebrates in channel habitats are concentrated in patchy, structurally complex habitats, such as woody debris (Benke *et al.* 2001). Clay nodules at the bottom of deep channel areas of Neotropical whitewater rivers support mayfly populations that consume detritus and provide a major food resource for weakly-electric gymnotiform fishes (Marrero 1987). Gymnotiforms also feed heavily on planktonic microcrustacea that feed on phytoplankton (Lundberg *et al*. 1987).

As noted above, a relatively small fraction of the total species in a community appear to have large roles in the flow of matter and energy in floodplain river food webs. Yet species affect ecosystem properties via mechanisms besides consumer-resource interactions. Some of the most dominant species of large lowland rivers have been shown to have strong effects on ecosystem structure and processes. A few benthivorous fish species have been shown to disproportionately influence sediments of channel or floodplain habitats. Using field experiments, Flecker (1996) showed how benthivorous *Prochilodus mariae* remove organic-rich sediments and change the structure of benthic algae and insect assemblages in a whitewater river of the Andean piedmont in Venezuela. *Semaprochilodus kneri* have similar effects in clearwater and blackwater rivers in Venezuela (Winemiller unpublished). North American gizzard shad (*Dorossoma cepedianum* (Lesueur) feed on detritus and move nutrients from sediments to the water column in reservoirs (Vanni 1996). The gizzard shad is a common detritivore and periphyton grazer of lowland rivers in North America and could significantly affect ecosystem dynamics. Benthic feeding by large omnivorous cypriniform fishes (e.g. *Ictiobus* spp., *Cyprinus carpio* L.) can increase sediment suspension in the water column (Drenner, Smith and Threlkeld 1996). Other grazing taxa have been shown to affect standing stocks of algae and organic sediments in tropical and temperate rivers. Field manipulations have shown grazer effects on standing stocks of algae and organic sediments in upland tropical and temperate rivers, including studies involving shrimp (Crowl *et al*. 2001), tadpoles (Flecker, Feifarek and Taylor 1999) and aquatic insect larvae (Power 1990, 1992).

In tropical lowland rivers, a few predatory species may disproportionately influence the distribution or abundance of prey populations. Jackson (1961) proposed that tigerfish (*Hydrocynus* spp.) restrict use of main channels of African rivers to a subset of the fish fauna that possess morphological features that inhibit predation (e.g. deep body, dorsal and pectoral spines). In South American rivers, piranhas appear to restrict the use of open-water off-shore areas by many fishes (Winemiller 1989a). Experimental exclusion of *Cichla* species and other large piscivores significantly affected the abundance and size distribution of fishes in the Cinaruco River, Venezuela (Layman and Winemiller unpublished).

FOOD WEB DYNAMICS IN RESPONSE TO FLOOD PULSES

EFFECT OF THE FLOOD PULSE ON PRODUCTION DYNAMICS

The temporal dynamics of disturbance and recovery of local habitats in the river-floodplain habitat mosaic drive spatiotemporal variation in primary production sources and favour alternative life history strategies. According to the flood-pulse model, flood conditions should be associated with greater nutrient availability, aquatic primary production (dominated by macrophytes), allochthonous inputs and secondary production, especially among juvenile fishes, in floodplain habitats. Low-water conditions result in contraction of marginal aquatic habitats, death and decay of aquatic macrophytes and higher densities of aquatic organisms, including phytoplankton and zooplankton in floodplain lagoons (Rai and Hill 1984; Putz and Junk 1997). Because overall productivity is lower during low-water conditions and densities of consumer taxa are high, there is a strong advantage for spawning during flood pulses, but only if these pulses endure long enough to yield sufficient survival and growth of early life stages prior to flood subsidence.

In a strongly seasonal environmental regime, species have the opportunity to evolve adaptations to exploit relatively predictable habitats and resources (Southwood 1977, Winemiller and Rose 1992, Resh *et al*. 1994). Under this regime, a periodic life history strategy is favoured (i.e. seasonal spawning, high fecundity, small eggs and larvae, little parental care). In tropical-seasonal systems, temperature is relatively constant and periodic flooding is the primary factor driving ecological dynamics. Access to floodplain habitats is important for successful recruitment by many fish species in tropical-seasonal rivers. Interannual variation in fish recruitment generally is more strongly associated with flood duration than flood magnitude. In the Upper Paraná floodplain-river system, years with higher and longer duration floods were associated with increases in condition, growth and recruitment of *Prochilodus scrofa* Steindachner (Gomes and Agostinho 1997). In tropical northern Australia, fish abundance in billabongs (oxbows) was positively correlated with duration of the annual flood (Madsen and Shine 2000). Even so, a range of successful life-history strategies is observed among fish species of tropical lowland rivers (Winemiller 1989b, 1996a, 1996b). Small opportunistic species with high reproductive effort protracted spawning periods and short-life spans are common in shallow marginal habitats that are constantly shifting across the river-floodplain landscape as water level rises and falls. The most extreme examples of the opportunistic strategy are observed among annual killifishes (Aplocheilidae) that inhabit shallow ephemeral pools. Many equilibrium strategists (relatively low fecundity with well-developed parental care) spawn just prior to the annual flood pulse and then move into newly flooded areas to brood. Based on growth variation, this seasonal spawning pattern seems to apply to *Cichla* species in Venezuela (Jepsen *et al.* 1999) and *Serranochromis* species in the Upper Zambezi River (Winemiller 1991b). Fishes with the equilibrium strategy may have higher reproductive success when water fluctuation is low. Some of the brood-guarding species of the upper Paraná River have greater abundance during years with low floods (Agostinho *et al*. 2000).

In temperate-seasonal rivers, access to flooded habitats may be non-essential, beneficial but non-essential, or detrimental to recruitment. Flooding enhances nutrient concentrations; particle loads and phytoplankton biomass in connected floodplain habitats (Hein *et al*. 1999), but can reduce densities of crustacean zooplankton (Baranyi *et al*. 2002). In temperate regions, temperature may have an influence on reproductive strategies that is equal to or greater than flooding. When warming temperatures coincide with a reliable annual flood pulse, selection should favour a periodic strategy just as in the tropics. Indeed, contracted spawning of large batches of small eggs is the dominant pattern observed in temperate-seasonal river fish faunas. Greater availability of floodplain habitats enhances fish recruitment and species diversity in lowland rivers in Europe (Copp 1989; Schiemer *et al.* 2001a) and North America (Sparks 1995). As in tropical systems, other life history strategies succeed in temperate-seasonal systems (e.g. sunfishes with relative equilibrium strategies and small cyprinids and poeciliids with opportunistic strategies). Humphries, King, and Koehn (1999); Humphries *et al.* 2002) identified three fish life-history strategies (gradient similar to model of Winemiller and Rose 1992) among fishes of Australia's Murray-Darling system. Flood regimes of many rivers of this region are regulated. Unregulated rivers display a temperate-seasonal pattern (Figure 1) but with large inter-annual variation in the magnitude of the seasonal flood-pulse. Humphries and co-workers discovered that virtually all fish species spawn each year with variable recruitment success depending on flow and temperature conditions. Because large floods do not occur each year, many species are able to recruit successfully by spawning and completing their life cycle entirely within main-channel habitats (the "low flow recruitment hypothesis"). Their studies demonstrate the potential importance of marginal channel habitats with low current velocity and abundant benthic micro-invertebrates that support fish early life stages.

In aseasonal flood-pulse regimes, aquatic organisms are more challenged to respond appropriately to relatively unpredictable patterns of resource variation. As in the Murray-Darling system, spatiotemporal connectivity of habitats and access to floodplain habitats is nonessential for most species, but greatly enhances recruitment for many, if not most, species in temperate-aseasonal rivers. Winemiller *et al.* (2000) discovered that certain fish species dominated oxbow lakes and others were more common in the active channel of the Brazos River, Texas. Opportunistic species numerically dominated the river channel and shallow oxbow lakes with high rates of disturbance and periodic strategists dominated deeper oxbow lakes with irregular but periodic flood connections to the river (Winemiller 1996a). When flooding occurs during springtime, recruitment by periodic strategists, such as gizzard shad, buffalo (*Ictiobus bubalus* (Rafinesque)) and crappie (*Pomoxis annularis* Rafinesque) is high. Yet springtime floods only occur during some years, so that spawning during most years is associated with low recruitment success (Winemiller unpublished data). Interspecific differences in responses to hydrologic regimes in habitats across the lateral floodplain gradient have been shown for other taxonomic groups in other regions, including trees (Junk 1989), phytoplankton (van den Brink *et al.* 1993) and benthic macroinvertebrates (Marchese and Ezcurra de Drago 1992).

Effect of the flood pulse on consumption dynamics

The expansion and contraction of aquatic habitats in response to flooding has a major influence on consumer-resource interactions. Newly expanded floodplain habitats provide an immediate influx of allochthonous detritus and invertebrates and, with time, greater nutrient availability and aquatic primary production. Densities of aquatic organisms are low initially and increase over time as new individuals recruit under productive flood conditions. Fish growth rate and condition are high in flooded habitats (Welcomme 1985). In the central Amazon, juveniles of omnivorous species, but not detritivorous species, grew faster during the rising-water period (Bayley 1988). Growth of omnivores was positively associated with flood magnitude and in all cases growth appeared to be density-independent.

Highest fish abundance and per-unit-area densities typically occur as floodwaters recede. As dictated by the functional response, the falling-water period is when predator-prey interactions are most intense. This is also the period when resource limitation may occur for species that exploit algae and aquatic and terrestrial invertebrates. Bayley (1988) found that juveniles of only 2 of 8 omnivorous species in the central Amazon showed significant evidence of density-dependent growth during the falling water period. For piscivores, the falling-water period represents a time of resource abundance, as fishes become increasingly concentrated in aquatic habitats of reduced volume. Piscivore feeding rates increase during the falling water period and piscivore growth and body condition increase (Jepsen *et al.* 1999). If piscivores deplete prey populations during the falling-water period, they may eventually become resource limited for several months during the lowest water stages. For size-selective (gape-limited) piscivores, optimal prey sizes become depleted first and piscivores shift to increasingly smaller prey as water levels continue to fall. Jepsen *et al*. (1997) described a decline in mean prey size consumed by *Cichla* species in the Cinaruco River during the 6-month falling water period. This shift in the average size of consumed prey size almost exactly matches the shift in the mode for the size distribution of fishes in the littoral zone (Layman and Winemiller unpublished data).

The scope of seasonal changes in population densities and predator-prey interactions obviously depends on the timing, magnitude and duration of flooding. The scope of these changes will be smaller in temperate-aseasonal rivers and greater in seasonal rivers with floras and faunas well adapted to take advantage of periodic changes in habitat and resource quality and availability. As a result, seasonal rivers can sustain greater fish harvest than aseasonal rivers in landscapes with comparable geomorphology and nutrient availability. Power *et al*. (1995) created a simple simulation model that linked floodplain river hydrology to food web dynamics based on the Lotka-Volterra algorithms. They examined four scenarios: a river with connection to its floodplain and seasonal (sinusoidal) discharge, a river confined by levees with sinusoidal discharge and regulated rivers with low and average discharge that never lead to flooding. Only the connected river with seasonal discharge produced stable populations of predators and grazers. The leveed river yielded unstable predator-prey dynamics as a result of channel confinement and regulated rivers resulted in low or oscillating grazer populations that ultimately were unable to sustain viable predator populations. Whereas this model represents a gross oversimplification of natural food webs, the findings highlight the influence of discharge dynamics and channel-floodplain connections on community dynamics.

Effects of the flood pulse on migration

In addition to its effects on population dynamics and consumer-resource interactions, flooding also influences movement of materials and organisms. Movement in response to flooding may be essentially longitudinal or lateral and passive or active. Seasonal succession and food web dynamics are influenced by all of these forms of movement. The initial stages of a flood pulse submerge terrain which results in inputs of dissolved inorganic nutrients from terrestrial vegetation, both living and dead (Junk *et al*. 1989). Surface runoff and floodwater recession carries these nutrients into channel areas where aquatic production may be stimulated (Rai and Hill 1984; Putz and Junk 1997; Lewis *et al*. 2000). Likewise, phytoplankton, zooplankton, floating macrophytes and terrestrial allochthonous resources are washed into flowing channels as well as deeper permanent floodplain lagoons. Based on a mass-balance approach, Lewis *et al*. (2000) concluded that the floodplain of the lower Orinoco River exports no organic carbon to the river channel. They concluded that this hydrologically open system behaves like a closed system with respect to organic carbon balance. They observed that the natural levee of the floodplain restricts water movement to a direction parallel to the longitudinal axis of the river channel. Thus, passive export of organic carbon is low because only a minor fraction of water actually passes from the floodplain to the channel. Presumably then, floodplains internally recycle organic carbon captured from surrounding uplands.

The Lewis *et al*. (2000) carbon-balance model does not consider active movement by aquatic organisms. Fishes, in particular, migrate between channel and floodplain locations in response to seasonal changes in the relative benefits and costs associated with conditions in each area (Welcomme 1985). Flooding provides fishes with almost unlimited access to a range of habitats. In tropical-seasonal rivers, fish movements from river channels into floodplain habitats are particularly regular (Goulding 1980; Welcomme 1985; Fernandes 1997; Hocutt and Johnson 2001). In temperate-seasonal and temperate-aseasonal rivers, these fish movements are common, but apparently less predictable. Depending on the taxon and region, tropical river fishes may migrate locally (1-100 km) or regionally (>100 km). In the llanos region of the Orinoco Basin, many and probably most, fishes perform local migrations into seasonally inundated savannas for reproduction. These seasonal habitats are highly productive and serve as classic nursery areas that enhance juvenile growth and survival (Winemiller 1989b, 1996b). When water levels drop, these areas become hypoxic and fishes that fail to migrate downstream to deeper channels risk death from hypoxia or stranding in drying pools (Lowe-McConnell 1964). Even though many floodplain fishes possess special adaptations for dealing with aquatic hypoxia (Kramer *et al*. 1978), a great deal of aquatic biomass moves out of floodplain habitats into deeper creeks and rivers. During the annual falling-water period, piscivores in mainstem rivers feed heavily on fishes that migrate out of tributaries draining the floodplains (Winemiller 1996a; Winemiller and Jepsen 1998). Thus, if we add these higher food web components to Lewis *et al.* (2000) calculation of organic carbon mass-balance, floodplains export large amounts of organic carbon to river channels.

Some river fishes undergo regular seasonal migrations on regional scales. Welcomme (1985) summarized evidence of longitudinal and lateral migrations by South American and African fishes. Highly migratory fishes can be extremely abundant with strong effects on local food webs. In rivers of the North Pacific region, the decaying carcasses of anadromous salmon import significant amounts of limiting nutrients that can enhance ecosystem productivity during summer (Kline *et al*. 1990; Willson, Gende and Marston 1998; Cederholm *et al*. 1999). In South American rivers, prochilodontid and other characiform fishes perform seasonal migrations of hundreds of kilometres (Bayley 1973; Vazzoler, Amadio and Daraciolo-Malta 1989; Ribeiro and Petrere 1990). Immigration of these abundant fishes during the falling-water period produces large effects on local food webs. First, prochilodontids have large effects on sediments and ecological dynamics in benthic communities (discussed above). Thus, prochilodontids are both ecosystem engineers as well as strong interactors with benthic elements of the food web (Flecker 1996). Second, immigrating prochilodontids provide an abundant food resource for resident piscivores (discussed above), which can be particularly significant for oligotrophic systems that receive young migrants from more productive systems. In this capacity, prochilodontids provide a spatial food web subsidy (Polis, Anderson and Holt 1997), in which material from a more productive ecosystem (floodplain wetlands) enters the food web in a less productive ecosystem (flowing channel). Food web subsidies can have major effects on food web dynamics, including induction of trophic cascades (Polis *et al*. 1997; Winemiller and Jepsen 2002) and stabilization of complex systems (Huxel and McCann 1998).

Some large predatory fishes of floodplain rivers also undergo long-distance regional migrations. Barthem and Goulding (1997) described migrations by large pimelodid catfishes that span almost the entire Amazon Basin. African tigerfish (*Hydrocynus* spp.), *Alestes* and *Labeo* species migrate longitudinally according to seasonal hydrological regime (Jackson 1961; Welcome 1985). Predatory ariid, centropomid and eleotrid fishes of Australia, Southeast Asia, the East and West Indies and tropical Americas habitually migrate between rivers and coastal marine waters. The food web implications of these “reverse subsidies” have scarcely been explored. If the effects of exotic piscivores on lake communities (Zaret and Paine 1973; Kaufman 1992) provide any indication, the effects of immigrant piscivores on fish populations in local fluvial habitats are potentially great. Likewise, removal of resident piscivores can affect local populations. Negative impacts of commercial fishing on large piscivores in floodplain lagoons of the Cinaruco River had a significant effect on local assemblage structure of small prey fishes (Layman and Winemiller unpublished).

MANAGEMENT IMPLICATIONS OF FOOD WEB ECOLOGY

Floodplains of lowland rivers provide important ecosystem services (i.e. nutrient cycling, flood mitigation) and renewable natural resources (e.g. fishery and forest products). Human impacts on river-floodplain systems have been described repeatedly (Welcomme 1985; Ward and Stanford 1989; Bayley 1995; Sparks 1995; Dudgeon 2000; Pringle, Freeman and Freeman 2000), but the focus of discussion here will be the interaction between food web ecology, human impacts and sustainable fisheries.

HABITAT CONNECTIVITY

Dams obviously fragment rivers in the longitudinal dimension. Many important river fishes undergo seasonal longitudinal migrations that make them highly vulnerable to impacts from not only dams, but also other channel obstructions such as weirs and gillnets. As discussed above, some of these fishes have large ecosystem effects (e.g. salmon affecting nutrients). In addition to affecting sediments and benthic biota, migratory prochilodontids also provide nutritional subsidies to piscivores that likely affect food web dynamics in the receiving communities.

A major human impact on large rivers is levee construction for the purpose of preventing floodplain inundation or draining of wetlands for agriculture and other land uses. Levees obviously disrupt important connections between river channels and floodplains, which cuts off exchanges of material and organisms among dynamic habitats critical for completion of species life cycles (Ward *et al*. 1999; Amoros and Bornette 2002) and ecosystem dynamics (Junk *et al*. 1989; Aspetsberger *et al*. 2002). Disconnecting the river channel from its floodplain has obvious negative impacts on nutrient cycling (Tockner *et al*. 1999), system productivity (Bayley 1989; Junk *et al*. 1989; Agostinho and Zalewski 1994) and biodiversity (Schiemer *et al*. 2001a; Robinson *et al*. 2002). Magnitudes of these impacts should be greater for tropical- and temperate-seasonal rivers than for temperate-aseasonal rivers. For example, recruitment by fishes in temperate-aseasonal rivers usually is more dependent on temperature regime than flood regime. Reproductive timing and recruitment by fishes in tropical floodplain rivers are strongly correlated with dynamics of the annual flood pulse. Large cichlids in South America (*Cichla*, *Hoplarchus*, *Heros* spp.) and Africa (*Serranochromis*, *Oreochromis* spp.) exhibit protracted spawning periods in reservoirs, but seasonal, contracted spawning periods in rivers (Winemiller personal observation). Evidence from temperate rivers indicates that many fish species complete their entire life cycle within the main channel (Galat and Zweimüller 2001; Dettmers *et al*. 2001) although even these species are strongly dependent on natural flood regimes (Schiemer *et al*. 2001b). Early life stages of these lotic-adapted species frequently depend on nearshore channel habitats with relatively lentic conditions. The inshore retention of fish larvae and their food resources is a critical feature influenced by river geomorphology and hydrology (Schiemer *et al*. 2001b).

Human impacts that reduce habitat connections in river-floodplain landscapes also can affect biodiversity and food webs by inhibiting patch colonization and community succession (Sedell *et al*. 1990). Recent research on the Cinaruco River in Venezuela indicates that fishes and macroinvertebrate communities of the littoral zone are significantly structured in relation to substrate type (Arrington and Winemiller unpublished). Habitat patches are colonized and abandoned in sequence as they are submerged and exposed by the moving littoral zone. Field experiments demonstrated that artificial habitat patches undergo community succession that is accompanied by increasing degrees of non-random assemblage structure (Winemiller *et al*. unpublished). The littoral food web appears to conform to Holt's (1996) spatial model of food web dynamics. In this model, taxa at lower trophic levels are restricted to the smallest habitat patches, with larger, more mobile consumers at higher trophic levels feeding across multiple patches. This pattern continues in a trophic hierarchy that ultimately yields a sink web defined by food chains terminating with a single large, mobile top predator. River channelization, levee construction and wetland drainage disrupt not only community dynamics in the littoral zone, but also restrict access by predators to habitat patches containing prey (Toth *et al*. 1998). Disruption of both factors (community assembly and predation by large mobile fishes) is certain to affect biodiversity.

Fishes are not the only vertebrates that depend on dynamic connections between channel and floodplain aquatic habitats. Dynamic habitats of river-floodplain systems enhance species diversity of aquatic insects (Smock 1994), mussels (Tucker, Theiling and Camerer 1996), turtles (Bodie and Semlitsch 2000), birds (Remsen and Parker 1983) and mammals (Sheppe and Osborne 1971).

FLOW REGIMES

Regulation of river hydrology changes natural flood regimes that determine elemental cycles, system productivity, reproduction and population dynamics of aquatic organisms and consumer-resource interactions. Clearly, significant alteration of the natural flood-regime in temperate- and tropical-seasonal rivers will have detrimental effects for native fish species that time reproduction to maximize recruitment success under predictable patterns of spatio-temporal environmental variation. High primary production and inputs of allochthonous resources that accompany flood-pulses tend to enhance fish recruitment success, but some species are less responsive than others. Many species achieve low to moderate recruitment even under no-flow conditions (Humphries *et al*. 2002). Consequently, community dynamics are partially a function of the timing and magnitude of flooding and this is bound to have large effects on food web dynamics that in turn influence dynamics of exploitable fish stocks. For example, years in which the Upper Paraná River, Brazil experiences higher, longer duration floods produce greater abundance of age-0 *Prochilodus scrofa*, the most important commercial fish of the region (Gomes and Agostinho 1997). *Prochilodus* is a principal prey for *Salminus maxillosus* Valenciennes, *Plagioscion squamosissimus* (Heckel) and other large piscivores that are important in the local fishery (Hahn *et al*. 1997). Thus, flood pulses affect these large predators both directly, in terms of their own recruitment success, as well as indirectly via food chain interactions. Management of multispecies fisheries in large rivers requires a food web perspective. Stock dynamics are influenced both by bottom-up factors related to ecosystem productivity and by top-down factors influenced by relative densities of predator and prey populations.

Flood dynamics affect both bottom-up and top-down effects in food webs. In large tropical rivers, flooding occurs predictably over large areas, which results in a pulse of primary production (Junk *et al*. 1989). This, in turn, is efficiently transferred to higher trophic levels due to species life history strategies that maximize fitness (i.e. population rate of increase) under predictable regimes of environmental variation. Harvest rates increase as fish populations become vulnerable to fishing when flood subsidence increases their per-unit-area densities (i.e. a functional response). The world’s most productive river fisheries are associated with seasonal flood-pulse dynamics in tropical areas. Holding all other factors equal, nutrient-rich landscapes in the tropics (e.g. Mekong, Niger, Zambezi, middle Orinoco and lower Amazon rivers) produce greater fish yields than nutrient-poor regions (Rio Negro and other rivers draining South America’s Guyana Shield region). In temperate regions, lower temperatures result in lower annual productivity. On geologic-evolutionary time scales, temperate regions have experienced more recent and frequent climatic disturbances that have inhibited biological diversification and ecological specialization within regional fish faunas. Currently, there is much interest in the potential positive relationship between biodiversity and community productivity (e.g. Tilman 1999) and this relationship could contribute to the greater productivity of seasonal tropical-seasonal river fish assemblages relative to those of temperate-seasonal rivers.

Fish production should be lowest in temperate-aseasonal rivers for three reasons. The timing of floods often will not coincide with periods with highest temperatures. Additionally, the timing of floods often will not synchronize with the spawning periods innately cued to photoperiodicity and seasonal temperature variation. Finally, temperate faunas are less likely to have evolved life history strategies and ecological adaptations designed to capitalize on flood pulse conditions, because these conditions are unpredictable on both intra- and inter-annual time scales. All other factors being equal, temperate-aseasonal rivers are less resistant to intense sustained harvest, of the kind practiced for generations in many tropical regions.

Direct consumption of allochthonous resources by fishes is particularly important in forested lowland regions of the Amazon Basin, with some species notably adapted for consuming fruits and seeds (Goulding 1980; Loubens and Panfili 2001). Reduced flood frequency, in addition to deforestation, will negatively impact direct entry of allochthonous resources into aquatic food webs, to the detriment of yields of several commercially important stocks (Goulding 1980; Reinert and Winter 2001).

On geological time scales, flood regimes maintain physical habitat heterogeneity by alternately eroding and depositing sediments on the landscape (Kellerhals and Church 1989). On shorter time scales, erosion and deposition of sediments are disturbances to vegetation communities. Natural hydrological processes create new substrates for community succession. The result is a rich mosaic of habitat patches with different degrees of structural complexity, exposure to natural disturbances and community composition (Shiel, Green and Neilsen 1998). Thus, chronic absence of flooding results in altered disturbance regimes and ultimately lowers habitat heterogeneity and species diversity (Schiemer *at al.* 2001a).

Flow regimes, in concert with soils and landscape geomorphology, also influence suspended sediment loads. Turbidity influences predatory-prey interactions and community composition and dynamics. Highly turbid systems often are dominated by siluriform fishes and, in Africa and South America respectively, weakly electric fishes (mormyriforms and gymnotiforms). Predators that rely on vision, such as cichlids and many characiform and cypriniform fishes, tend to be scarce in turbid whitewater rivers. In turbid river-floodplain systems, visually orienting fishes are most abundant in clear tributaries creeks and lacustrine habitats of floodplains where sediments settle out. Turbidity varies among floodplain lagoons as a function of local soils and other landscape features. During the dry season, water transparency is associated with a fairly consistent pattern of fish assemblage composition in Orinoco River floodplain lagoons, with turbid lagoons having more siluriforms and gymnotiforms and clear lagoons having more characids (Rodríguez and Lewis 1997). Wet-season flooding mixes water and allows organisms to move freely across the landscape, which presumably homogenizes these lagoon fish assemblages. The effect of turbidity on river food web structure and dynamics has not been investigated.

Fisheries harvest

Fisheries obviously impact river food webs in many different ways. Overfishing changes consumer-resource dynamics and the distribution of interaction strengths in the food web. If affected populations are species with large functional importance to the community or ecosystem, the effect of their depletion may be large and immediate. For example, overharvest of benthivorous prochilodontids would fundamentally alter the sediment dynamics and benthic ecology in Andean piedmont rivers. There is some evidence that this is already occurring in Venezuela where extensive gillnetting removes large numbers of *Prochilodus mariae* during their upstream migrations (Barbarino-Duque, Taphorn and Winemiller 1998). With reduced densities of *Prochilodus* that consume and resuspend fine sediments, river channels accumulate a thick layer of soft sediments that inhibit development of a benthic community dominated by diatoms and grazing insects (Flecker 1996). Because benthic primary production is the principal energy source in this system, the entire food web undoubtedly changes with unknown consequences for biodiversity and secondary production. Similar effects of prochilodontids on benthic processes have been demonstrated experimentally in channel and lagoon habitats of the Cinaruco River (Winemiller et al. unpublished data).

In North America and Europe, commercial fishing in rivers is relatively insignificant. In cold-water regions, salmonids, esocids and percids are heavily targeted by sportfishers, sometimes with negative impacts on stocks. Tropical river fisheries provide a major source of animal protein for people of developing countries. Fishing effort in African and Asian rivers is generally more intense than in South American rivers, the latter having fisheries that continue to be dominated by a relatively small number of large and economically valuable species (Welcomme 1990). Yet some regions of South America have extremely high fishing effort (Welcomme 1990) and effort is generally increasing everywhere, in some cases rapidly. Size overfishing is pervasive in large rivers worldwide (e.g. Mekong River fisheries discussed during LARS 2). In Venezuela, maximum and average sizes of *Cichla temensis* has declined markedly in rivers over the past 20 years and *C. temensis* abundance declined precipitously in the Rio Aguaro with commencement of commercial netting in the 1970s. The migratory characid *Salminus hillari* Valenciennes was a popular sportfish in rivers of the Andean piedmont of Venezuela until the early 1960s. The species is now extremely rare due to dam construction and gillnetting (Winemiller, Marrero and Taphorn 1996). *Salminus* was once the principal predator of *Prochilodus mariae* that migrated *en mass* into piedmont rivers during the dry season. Although *Prochilodus* also have declined in piedmont rivers (Barbarino-Duque *et al*. 1998), this species, unlike *Salminus*, has a broad dry season distribution with large populations maintained in lowland rivers.

Large piscivores often are among the first fishes to be targeted by river fisheries. The phenomenon of "fishing down food webs" was described for marine systems globally (Pauly *et al.* 1998). This pattern may apply equally to river fisheries. In the Amazon, the abundance and size of pirarucu (*Arapaima gigas* (Cuvier) and pimelodid catfishes has declined steadily in most regions. Although less well documented, a similar pattern is observed for pimelodid catfishes and payaras (*Hydrolycus* spp.) of the Orinoco, *Salminus maxillosus* of the Paraná and *Lates niloticus* (L.) and *Hydrocynus* spp. of the Niger, Oeme and other West African rivers. As stocks of these large piscivores become depleted, fish markets become even more strongly dominated by less valuable but more numerous detritivorous and omnivorous species, such as prochilodontids, *Mylossoma* and *Brycon* species in South America and tilapiine cichlids and *Barbus* spcies in Africa. Some of the major predatory fishes inhabiting large warmwater rivers of North America are nocturnal catfishes (siluriforms) and lepisosteid gars, the latter having no commercial value and generating little sportfishing interest. Because commercial river fisheries are insignificant in North America and Europe and sportfisheries essentially target predatory species, the fishing-down-food-webs phenomenon has not been observed in rivers of these regions.

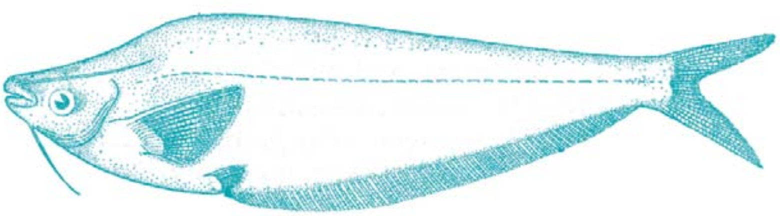
Overharvest of fish stocks changes population abundance and the structure and dynamics of river food webs. The elimination of top predators could yield top-down effects in food chains, but in many cases prey populations are targeted just as intensely. Virtually no information is available from any large river to enable even modest predictions regarding fishing effects on food web dynamics. In tropical rivers, fish communities are species rich and food webs are complex. Even when top predators feed on a similar broad array of prey taxa, fisheries that exploit multiple predator species can yield chaotic dynamics of individual populations (Wilson *et al*. 1991). Fisheries harvest also can change population size structure, which in turn affects population dynamics via effects on life history strategies (e.g. reduction in size at maturity) and size-dependent predator-prey interactions. These effects have been demonstrated in fish populations from streams, lakes and marine systems, but so far little information has been gathered from large rivers. Strong sustained harvest of the largest individuals selects for earlier age and smaller size of maturation (Conover and Munch 2002). The combined effects of overharvest of the largest size classes and the evolution of smaller size at maturation should profoundly influence both predator and prey populations when predation is size-limited. Smaller predators will result in smaller average and maximum size of consumed prey. If large piscivores are targeted more intensely than their prey, as is frequently the case, this could lead to a negative feedback that affects predator populations negatively, with potential positive effects on prey abundance. The study of predator-prey dynamics in large-river food webs remains in its infancy and a great deal of research is needed before we can even begin to construct predictive models.

CONCLUSION

The study of food web ecology in river-floodplain systems remains in its infancy. This review has highlighted only a few of the most basic issues, most of which are largely unresolved. For example, the influence of flood regimes on population dynamics of aquatic organisms with different life history strategies and regional/evolutionary histories is highly variable. Therefore, it may be erroneous to assume that regular flood pulses, of the sort that occur in large tropical rivers, are required for maintenance of high biodiversity in every instance. The flood pulse concept of Junk *et al*. (1989) probably overestimates the role of floodplains for river biota in systems with flood regimes that are naturally unpredictable or out of phase with spring-summer. Certainly at some scale of spatial and temporal resolution, flood pulses are essential for biodiversity in any river ecosystem. The challenge is to identify the biological responses to variation at multiple scales. Food webs are complex and influenced by many abiotic and biotic factors. Although several of the most important and obvious factors were discussed here, many more must be examined. For example, exotic species sometimes dominate river communities (e.g. European carp in rivers of North America and Australia), usually with undetermined effects on food web dynamics and ecosystem processes. Given the important ecosystem services provided by floodplain rivers, the high value of river fisheries, especially in the tropics, as well as the multiple human impacts on river-floodplain systems, vastly greater research investment is warranted.

ACKNOWLEDGEMENTS

Rosemary Lowe-McConnell, Craig Layman and Alexandre Miranda Garcia read earlier drafts of the manuscript and provided helpful comments. New information and ideas developed here were aided by U.S. National Science Foundation Grant 0089834.



REFERENCES

Agostinho A.A. & Zalewski 1994. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Paraná River, Brazil. *Hydrobiologia*, 303: 141-148.

Agostinho A.A., Thomaz S.M., Minte-Vera, C.V. & Winemiller K.O. 2000. Biodiversity in the high Paraná River floodplain. *In* B. Gopal, W.J. Junk & J.A. Davis eds. *Wetlands Biodiversity*. Leiden, The Netherlands, Backhuys Publishers. pp. 89-118.

Akin S. 2001. Ecological dynamics of the aquatic community in a Texas coastal salt marsh. College Station, TX, USA, A&M University. (Doctoral dissertation)

Amoros C. & Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47: 761-776.

Araujo-Lima C.A.R.M., Forsberg B.R., Victoria R. & Martinelli L.A. 1986. Energy sources for detritivorous fishes in the Amazon. *Science*, 234: 1256-1258.

Arrington D.A. &. Winemiller K. O. 1993. Organization and maintenance of fish diversity in shallow waters of tropical floodplain rivers. In R.L. Welcomme & T. Petr, eds. *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Volume 2.* Food and Agriculture Organization of the United Nations & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/17. pp. 25-36.

Aspetsberger F., Huber F., Kargl S., Scharinger B., Peduzzi P. & Hein T. 2002. Particulate organic matter dynamics in a river floodplain system: Impact of hydrological connectivity. *Archives fur Hydrobiologie,* 156/1: 23-42.

Baranyi C., Hein T., Holarek C., Keckeis S. & Schiemer F. 2002. Zooplankton biomass and community structure in a Danube River floodplain system: Effects of hydrology. *Freshwater Biology*, 47: 473-482.

Barbarino-Duque A., Taphorn D.C. & Winemiller K.O. 1998. Ecology of the coporo, *Prochilodus mariae* Characiformes, Prochilodontidae, and status of annual migrations in western Venezuela. *Environmental Biology of Fishes,* 53: 33-46.

Barthem R. & Goulding M. 1997. *The catfish connection: ecology, migration, and conservation of amazon predators*. New York, Columbia University Press.

Bayle P.B. 1973. Studies on the migratory characin *Prochilodus platensis* Holmberg 1889 Pisces, Characoidei in the Rio Pilcomayo, S. America. *Journal of Fish Biology*, 5: 25-40.

Bayley P.B. 1988. Factors affecting growth rates of young tropical fishes: Seasonality and density-dependence. *Environmental Biology of Fishes,* 21: 127-142.

Bayley P.B. 1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.,* 106: 399-408.

Bayley P.B. 1995. Understanding large river-flooplain ecosystems. *BioScience*, 45: 153-158.

Benedito-Cecilio E., Araujo-Lima C.A.R.M., Forsberg B.R., Bittencourt M.M. & Martinelli L.C. 2000. Carbon sources of Amazonian fisheries. *Fisheries Management and Ecology*, 7: 303-315.

Benke A.C., VanArsdall T.C., Jr., Gillespie D.M. & Parrish F.K. 1984. Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. *Ecological Monographs*, 54: 25-63.

Benke A.C., Chaubey I., Ward G.M. & Dunn E.L. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. *Ecology*, 81: 2730-2741.

Benke A.C., Wallace J.B., Harrison J.W. & Koebel J.W. 2001. Food web quantification using secondary production analysis: Predaceous invertebrates of the snag habitat in a subtropical river. *Freshwater Biology*, 46: 329-346.

Bodie J.R. & Semlitsch R.D. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia*, 122: 138-146.

Bunn S.E., Davies P.M. & Winning M. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology*, 48: 619-635.

Cederholm C.J., Kunze M.D., Murota T. & Sibatani A. 1999. Pacific salmon carcasses: Essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries*, 24: 6-15.

Conover D.O. & Munch S.B. 2002. Sustaining fisheries yields over evolutionary time scales. *Science*, 297: 94-96.

Copp G.H. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes*, 26: 1-27.

Crowl T.A., McDowell W.H., Covish A.P. & Johnson S.L. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology*, 82: 775-783.

Dettmers J.M., Wahl D.H., Soluk D.A. & Gutreuter S. 2001. Life in the fast lane: Fish and foodweb structure in the main channel of large rivers. *Journal of the North American Benthological Society*, 20: 255-265.

Drenner R.W., Smith J.D. & Threlkeld S.T. 1996. Lake trophic state and the limnological effects of omnivorous fish. *Hydrobiologia*, 319: 213-223.

Dudgeon D. 2000. Large-scale hydrological changes in tropical Asia: Prospects for riverine biodiversity. *BioScience*, 50: 793-806.

Fernandes C.C. 1997. Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish*, 6: 36-44.

Flecker A.S. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology*, 77: 1845-1854.

Flecker A.S, Feifarek B.P. & Taylor B.W. 1999. Ecosystem engineering by a tropical tadpole: Density dependent effects on habitat structure and larval growth rates. *Copeia* 1999: 495-500.

Forsberg B.R., Araujo-Lima C.A.R.M., Martinelli L.A., Victoria R.L. & Bonassi J.A. 1993. Autotrophic carbon sources for fish of the Central Amazon. *Ecology*, 74: 643-652.

Galat D.L. & Zweimüller I. 2001. Conserving large-river fishes: Is the highway analogy an appropriate paradigm. *Journal of the North American Benthological Society*, 20: 266-279.

Gomes L.C. & Agostinho A.A. 1997. Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in upper Paraná River, Brazil. *Fisheries Management and Ecology*, 4: 263-274.

Goulding M. 1980. *The Fishes and the Forest*. Berkeley, CL, USA, University of California Press.

Goulding M.M., Carvalho L. & Ferreira E.G. 1988. Río Negro: Rich life in poor water. The Hague: SPB Academic Publishing.

Hahn N.S., de Andrian I.F., Fugi R. & Lescano de Almeida V.L. 1997. Ecologia trófica. *In* Editora da Universidade Estadual de Maringá. *A Planície de indundação do Alto Rio Paraná: Aspectos Físicos, Biológicos e Socieconômicos. Maringá*. pp. 209-248.

Hall S.J. & Rafaelli D.G. 1993. Food webs: Theory and reality. *Advances in Ecological Research*, 24: 187-239.

Hamilton S.K., Lewis W.M. Jr. & Sippel S.J. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: Evidence from stable isotopes. *Oecologia*, 89: 324-330.

Handlos W.L. & Williams G.J. 1985. The Zambian section of the Zambezi catchment– an overview. *In* W.L. Handlos & G.W. Howard eds. *Development Prospects for the Zambezi Valley in Zambia*. Lusaka, Zambia, Kafue Basin Research Committee, University of Zambia. pp. 1-28.

Hein T., Heiler G., Pennetzdorfer D., Riedler P., Schagerl M. & Schiemer F. 1999. The Danube restoration project: Functional aspects and planktonic productivity in the floodplain ecosystem. *Regulated Rivers: Research & Management*, 15: 259-270.

Hocutt C.H. & Johnson P.N. 2001. Fish response to the annual flooding regime in the Kavango River along the Angola/Namibia border. *South African Journal of Marine Science*, 23: 449-464.

Holt R.D. 1996. Food webs in space: An island biogeographic perspective. *In* G.A. Polis & K.O. Winemiller eds. *Food Webs: Integration of Patterns and Dynamics*. New York, Chapman & Hall. pp. 313-323.

Humphries P., King A.J. & Koehn J.D. 1999. Fish, flows and flood plains: Links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes*, 56: 129-151.

Humphries P., Luciano G.S. & King A.J. 2002. River regulation and fish larvae: Variation through space and time. *Freshwater Biology*, 47: 1307-1331.

Huxel G.R. & McCann K. 1998. Food web stability: The influence of trophic flows across habitats. *American Naturalist*, 152: 460-469.

Jackson P.B.N. 1961. The impact of predation, especially by the tiger-fish *Hydrocynus vittatus* Cast. on African freshwater fishes. *Proceedings of the Zoological Society of London*, 136: 603-622.

Jepsen D.B. & Winemiller K.O. 2002. Structure of tropical river food webs revealed by stable isotope ratios. *Oikos*, 96: 46-55.

Jepsen D.B., Winemiller K.O. & Taphorn D.C. 1997. Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. *Journal of Fish Biology*, 51: 1085-1108.

Jepsen D.B., Winemiller K.O., Taphorn D.C. & Rodriguéz-Olarte D. 1999. Variation in age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela. *Journal of Fish Biology*, 55: 433-450.

Junk W.J. 1989. Flood tolerance and tree distribution in central Amazonian floodplains. *In* L.B. Holm-Nielsen, I.C. Nielsen & H. Balslev eds. *Tropical Forests: Botanical Dynamics, Speciation and Diversity*. London, Academic Press. pp. 47-64.

Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 110-127.

Kaufman L. 1992. Catastrophic change in species-rich freshwater ecosystems. *Bioscience*, 42: 846-858.

Kellerhals R. & Church M. 1989. The morphology of large rivers: Characterization and management. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 31-48.

Kline T.C. Jr., Goering J.J., Mathisen O.L., Poe P.H. & Parker P.L. 1990. Recycling of elements transported upstream by runs of Pacific Salmon: I. $_^{15}$N and $_^{13}$C evidence in Sashin Creek, southeastern Alaska. *Canandian Journal of Fisheries and Aquatic Sciences*, 47, 136-144.

Kramer D.L., Lindsey C.C., Moodie G.E.E. & Stevens eds. 1978. The fishes and the aquatic environment of the central Amazon Basin, with particular reference to respiratory patterns. *Canadian Journal of Zoology*, 56: 717-729.

Leite R.G., Araujo-Lima C.A.R.M., Victoria R.L. & Martinelli L.A. 2002. Stable isotope analysis of energy sources for larvae of eight fish species from the Amazon floodplain. *Ecology of Freshwater Fish*, 11: 56-63.

Lewis W.M., Jr., Hamilton S.K., Lasi M.A., Rodríguez M. & Saunders J.F. III. 2000. Ecological determinism on the Orinoco floodplain. *BioScience*, 50: 681-692.

Lewis W.M., Jr., Hamilton S.K., Rodríguez M., Saunders, J.F. III & Lasi M.A. 2001. Foodweb analysis of the Orinoco floodplain based on production estimates and stable isotope data. *Journal of the North American Benthologial Society*, 20: 241-254.

Loubens G. & Panfili J. 2001. Biologie de *Piaractus brachypomus* Teleostei:Serrasalmidae dans basin du Mamoré Amazonie bolivienne. *Ichthyological Explorations of Freshwaters*, 12: 51-64.

Lowe-McConnell R.H. 1964. The fishes of the Rupununi Savanna District of British Guiana, South America. Pt I Ecological groupings of fish species and effects of the seasonal cycle on the fish. *Journal of the Linnean Society Zoology*, 45: 103-144.

Lowe-McConnell R.H. 1987. *Ecological Studies of Tropical Fish Communities*. Cambridge, UK, Cambridge University Press.

Lundberg J.G., Lewis W.M. Jr., Saunders J.F. III & Mago-Leccia F. 1987. A major food web component in the Orinoco River channel: Evidence from planktivorous electric fishes. *Science*, 237: 81-83.

Madsen T. & Shine R. 2000. Rain, fish and snakes: Climatically driven population dynamics of Arafura filesnakes in tropical Australia. *Oecologia*, 124, 208-215.

Marrero C. 1987. Notas preliminares acerca de la historia natural de los peces del Bajo Llano. *Revista Hydrobiología Tropical*, 20: 57-63.

Melack J.M., Forsberg B.R.,Victoria R.L. & Richey J.E. 1999. Biogeochemistry of Amazon floodplain lakes and associated wetlands. *In* M. McClain, R. Victoria & J. Richey eds. *The Biogeochemistry of the Amazon Basin and Its Role in a Changing World*. Oxford, UK, Oxford University Press. pp. 1-50.

Marchese M. & Ezcurra de Drago I.E. 1992. Benthos of the lotic environments in the middle Parana River system: Transverse zonation. *Hydrobiologia*, 237: 1-13.

Oberdorff T., Guégan J.F. & Hugueny B. 1995. Global scale patterns of fish species richness in rivers. *Ecography*, 18: 345-352.

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres F. Jr. 1998. Fishing down marine food webs. *Science*, 279: 860-863.

Peterson C.C. 1997. Food webs of two Venezuelan clearwater streams with seasonal fluctuations in hydrology. College Station, TX, USA, A&M University. (Master thesis)

Polis G.A. & Winemiller K.O. 1996. *Food Webs: Integration of Patterns and Dynamics*. New York, Chapman and Hall.

Polis G.A., Anderson W.B. & Holt R.D. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28: 289-316.

Power M.E. 1990. Effects of fish in river food webs. *Science*, 250: 811-814.

Power M.E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology*, 73, 1675-1688.

Power M.E., Sun A., Parker G., Dietrich W.E. & Wootton T.J. 1995. Hydraulic food-chain models. *BioScience*, 45: 159-267.

Pringle C.M., Freeman M.C. & Freeman B.J. 2000. Regional effects of hydrological alterations on riverine macrobiota in the New World: Tropical-temperate comparisons. *BioScience*, 50: 807-823.

Putz R. & Junk W. 1997. Phytoplankton and primary production. *In The Central Amazon Floodplain*. Heidelberg, Springer-Verlag. pp. 207-222.

Quensiere J., Olivry J.-C., Poncet Y. & Wuillot J. 1994. Environnment deltaïque. *In* J. Quensiere ed. *La Pêche dans le Delta Central du Niger*. Paris: ORSTOM Editions. pp. 29-80.

Rai H. & Hill G. 1984. Primary production in the Amazonian aquatic ecosystem. *In* H. Sioli ed. *The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin*. Dordrecht, Dr. W. Junk Publishers. pp. 311-335.

Reinert T.R. & Winter K.A. 2001. Sustainability of harvested pacú *Colossoma macropomum* populations in the northeastern Bolivian Amazon. *Conservation Biology*, 16: 1344-1351.

Remsen J.V. & Parker T.A. 1983. Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica*, 15: 223-231.

Resh V.H., Hildrew A.G., Statzner B. & Townsend C.R. 1994. Theoretical habitat templets, species traits, and species richness: A synthesis of long-term ecological research on the Upper Rhone River in the context of concurrently developed ecological theory. *Freshwater Biology*, 31: 539-554.

Ribeiro M.C.L. de B. & Petrere M. Jr. 1990. Fisheries ecology and management of the jaraqui *Semaprochilodus taeniurus*, *S. insignis* in central Amazonia. *Regulated Rivers: Research & Management*, 5: 195-215.

Robinson C.T. Tockner K. & Ward J.V. 2002. The fauna of dynamic riverine landscapes. *Freshwater Biology*, 47: 661-677.

Rodríguez M.A. & Lewis, W.M. Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, 67: 109-128.

Schiemer F. 1999. Conservation of biodiversity in floodplain rivers. *Archives fur Hydrobiologie Supplement 115/3*. pp. 423-438.

Schiemer F., Keckeis H., Winkler G. & Flore L. 2001a. Large rivers: The relevance of ecotonal structure and hydrological properties for the fish fauna. *Archives fur Hydrobiologie Supplement 135/2-4*. pp. 487-508.

Schiemer F., Keckeis H., Reckendorfer W. & Winkler G. 2001b. The inshore retention concept and its significance for large rivers. *Archives fur Hydrobiologie*, 135/2: 509-516.

Schmid-Araya J.M. & Schmid P.E. 2000. Trophic relationships: Integrating meiofauna into a realistic benthic food web. *Freshwater Biology*, 44: 149-163.

Sedell J.R., Reeves G.H., Hauer F.R., Stanford J.A. & Hawkins C.P. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management*, 14: 711-724.

Sheppe W. & Osborne T. 1971. Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs*, 41: 179-207.

Shiel R.J., Green J.D. & Nielsen D.L. 1998. Floodplain biodiversity: Why are there so many species? *Hydrobiologia*, 387/388: 39-46.

Smock L.A. 1994. Movements of invertebrates between stream channels and forested floodplains. *Journal of the North American Benthological Society*, 13: 524-531.

Southwood T.R.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, 46: 337-365.

Sparks R.E. 1995. Need for ecosystem management of large rivers and their floodplains. *BioScience*, 45: 168-182.

Thorp J.H. & Delong M.D. 1994. The riverine productivity model: An heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, 70: 302-308.

Thorp J.H. & Delong M.D. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*, 96: 543-550.

Thorp J.H., Delong M.D., Greenwood K.S. & Casper A.F. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia*, 117: 551-563.

Tilman D. 1999. The ecological consequences of changes in biodiversity: The search for general principles. *Ecology*, 80: 1455-1474.

Tockner K., Pennetzdorfer D., Reiner N. Schiemer F. & Ward J.V. 1999. Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river-floodplain system. *Freshwater Biology*, 41: 521-535.

Toth L.A., Melvin S.L., Arrington D.A. & Chaimberlain J. 1998. Hydrologic manipulation of the channelized Kissimmee River. *Bioscience*, 48: 757-764.

Tucker J.K., Theiling C.H. & Camerer J.B. 1996. Utilization of backwater habitats by unionid mussels Bivalvia: Unionidae on the lower Illinois River and in pool 26 of the upper Mississippi River. *Transactions of the Illinois Academy of Science,* 89: 113-122.

Van den Brink F.W.B., de Leeuw J.P.H.M, van der Velde G. & Verheggen G.M. 1993. Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the lower Rhine and Meuse. *Biogeochemistry Dordrecht,* 19: 103-128.

Vanni M.J. 1996. Nutrient transport and recycling by consumers in lake food webs: Implications for plankton. *In* G.A. Polis & K.O. Winemiller eds. *Food Webs: Integration of Patterns and Dynamics*. New York, Chapman and Hall. pp. 81-95.

de Vazzoler A.E.M., Amadio S.A. & Daraciolo-Malta M.C. 1989. Aspectos biológicos de peixes Amazônicos. XI. Reprodução das espécies do gênero *Semaprochilodus* Characiformes, Prochilodontidae no baixo Rio Negro, Amazonas, Brasil. *Revista Brasiliera de Biologia*, 49: 165-173.

Wantzen K.M., Machado F.D.A., Voss M., Boriss H. & Junk W.J. 2002. Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. *Aquatic Science*, 64: 239-251.

Ward J.V. & J.A. Stanford. 1989. Riverine ecosystems: The influence of man on catchment dynamics and fish ecology. *In* D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 56-64.

Ward J.V., Tockner K. & Schiemer F. 1999. Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers: Research & Management* 15: 125-139.

Welcomme R.L. 1985. River Fisheries. *Food and Agriculture Organization Fisheries Technical Paper 262*. Rome, FAO. pp. 1-330.

Welcomme R.L. 1990. Status of fisheries in South American Rivers. *Interciencia*, 15: 337-345.

Willson M.F., Gende S.M. & Marston B.H. 1998. Fishes and the forest: Expanding perspectives on fish-wildlife interactions. *Bioscience*, 48: 455-462.

Wilson J.A., French J., Kleban P., McKay S.R. & Townsend R. 1991. Chaotic dynamics in a multispecies fishery: A model of community predation. *Ecological Modeling*, 58: 303-322.

Winemiller K.O. 1989a. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes*, 26: 177-199.

Winemiller K.O. 1989b. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia*, 81: 225-241.

Winemiller K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60: 331-367.

Winemiller K.O. 1991a. Ecomorphological diversification of freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61: 343-365.

Winemiller K.O. 1991b. Comparative ecology of *Serranochromis* species Teleostei: Cichlidae in the Upper Zambezi River. *Journal of Fish Biology*, 39: 617-639.

Winemiller K.O. 1996a. Factors driving spatial and temporal variation in aquatic floodplain food webs. *In* G.A. Polis & K.O. Winemiller eds. *Food Webs: Integration of Patterns and Dynamics*. New York, Chapman and Hall. pp. 298-312.

Winemiller K.O. 1996b. Dynamic diversity: Fish communities of tropical rivers. *In* M.L. Cody & J.A. Smallwood eds. *Long-term Studies of Vertebrate Communities*. Orlando, FL, USA, Academic Press. pp. 99-134.

Winemiller K.O. & Jepsen D.B. 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, 53 Supplement A. pp. 267-296.

Winemiller K.O. & Jepsen D.B. 2002. Migratory neotropical fish subsidize food webs of oligotrophic blackwater rivers. *In* G.A. Polis, M.E. Power & G. Huxel eds. *Food Webs at the Landscape Level*, Chicago, University of Chicago Press. (forthcoming)

Winemiller K.O. & Rose K.A. 1992. Patterns of life-history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2196-2218.

Winemiller K.O., Marrero C. & D.C. Taphorn D.C. 1996. Perturbaciones causadas por el hombre a las poblaciones de peces de los llanos y del piedemonte Andino de Venezuela. *Biollania Venezuela*, 12: 13-48.

Winemiller K.O., Tarim S., Shormann D. & Cotner J.B. 2000. Spatial variation in fish assemblages of Brazos River oxbow lakes. *Transactions of the American Fisheries Society*, 129, 451-468.

Woodward G. & Hildrew A.G. 2002. Food web structure in riverine landscapes. *Freshwater Biology*, 47: 777-798.

Zaret T.M. & Paine R.T. 1973. Species introduction in a tropical lake. *Science*, 182: 449-455.





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