CONTRIBUTED PAPERS

Developing policies for the management of fishery genetic resources

Devin M. Bartley
Fisheries and Aquaculture Department, FAO, Rome

Alvaro Toledo
Commission on Genetic Resources for Food and Agriculture, FAO, Rome

1. SUMMARY

Policy on aquatic genetic resources is primarily guided in FAO by the Code of Conduct for Responsible Fisheries and the Convention on Biological Diversity. These instruments are complementary and both recognize the importance of sustainable use and conservation of aquatic genetic resources. Policies will be influenced by a number of drivers that include the increasing human population, resource limitations, the need to address broad and complex social issues, intensification of farming and fishing systems, increases in technology, and the recognition of sovereign rights of countries in regards to aquatic genetic resources.

2. INTRODUCTION

The Preamble to the 1989 edition of the Constitution of the Food and Agriculture Organization of the United Nations defines the common purpose of the Nations accepting the Constitution as:

- raising levels of nutrition and standards of living of the peoples under their respective jurisdictions;
- securing improvements in the efficiency of the production and distribution of all food and agricultural products;
- bettering the conditions of rural populations; and thus
- contributing toward an expanding world economy and ensuring humanity's freedom from hunger.

The Fisheries and Aquaculture Department of FAO promotes sustainable and responsible fisheries through its work to improve policy, legislative and institutional frameworks, to develop and evaluate technologies in fisheries and aquaculture, to build capacity and to collect and disseminate information on the world's fisheries and aquaculture. In 1995 the FAO Council adopted the FAO Code of Conduct for Responsible Fisheries (CCRF) (FAO, 1995) that has since become the framework and primary mechanism through which Member Governments have addressed the above issues. The vision of the Fisheries and Aquaculture Department is: *A world in which responsible and sustainable use of fisheries and aquaculture resources make an appreciable contribution to human well-being, food security and poverty alleviation.* Working through Governments and appropriate Ministries, the Fisheries and Aquaculture Department acknowledges a focus on fishers and fish farmers.

Collecting information on the status and trends of aquatic genetic diversity is extremely difficult, especially for global repositories of this information such as FAO. The FAO Fisheries and Aquaculture Department receives yearly information on fisheries and aquaculture production from Member Countries. Although this data set represents the *best available scientific information* it is far from complete and includes virtually no information below the species level. Indeed much of the reported information is not identified to species (especially true for inland fishery resources). A disturbing trend is that the quantity of production not reported at the species level is increasing (FAO, 2004). Countries are better at reporting aquaculture production by species, but not by strain, breed, or variety. Thus, we have scant global information on the numerous breeds of carp, catfish, tilapia and other genetically altered species that comprise aquaculture production.

Management of the resources and collection of information from areas beyond national boundaries are further complicated by problems of governance and jurisdiction. Regional fishery bodies have been established in some marine and inland areas. However, there are gaps in coverage and problems with implementation of regional agreements.

3. CODE OF CONDUCT FOR RESPONSIBLE FISHERIES (CCRF) AND OTHER INTERNATIONAL MECHANISMS

The CCRF is a voluntary, non-binding international instrument that the Members of FAO have pledged to help implement as appropriate and to the best of their abilities. Articles of the CCRF relevant to FiGR include:

- **Article 6.2 –** Fisheries management should promote the maintenance of the quality, diversity and availability of fishery resources in sufficient quantities for present and future generations in the context of food security, poverty alleviation and sustainable development. Management measures should not only ensure the conservation target species but also of species belonging to the same ecosystem or associated with or dependent upon the target species.
- **Article 7.2.2 –** …biodiversity of aquatic habitats and ecosystems is conserved and endangered species are protected.
- **Article 9.1.2 –** States should promote responsible development and management of aquaculture, including an advance evaluation of the effects of aquaculture development on genetic diversity and ecosystem integrity, based on best available scientific information.
- **Article 9.3.1 –** States should conserve genetic diversity and maintain integrity of aquatic communities and ecosystems by appropriate management (in particular to minimize adverse impacts from non-native and genetically altered species).
- **Article 9.3.3. –** States should …encourage the adoption of appropriate practices in the genetic improvement of broodstock, ….
- **Article 9.3.5 –** States should, where appropriate, promote research and, when feasible, the development of culture techniques for endangered species to protect, rehabilitate and enhance their stocks, taking into account the critical need to conserve genetic diversity of endangered species.
- **Article 12.8 –** States should conduct research into, and monitor, human food supplies from aquatic sources …and ensure that there is no adverse impact on consumers.

The Fisheries and Aquaculture Department works in close association with a variety of international mechanisms and agencies. The key mechanism relevant to the issue of aquatic genetic resources and biodiversity is the Convention on Biological Diversity (CBD). The FAO CCRF, as well as the CGRFA, have similar principles with, and are complementary to the CBD. Key sections of the CBD that pertain to aquatic genetic resources and biodiversity are:

- **Article 6 –** Each Contracting Party shall, in accordance with its particular conditions and capabilities: (a) Develop national strategies, plans or programmes for the conservation and sustainable use of biological diversity or adapt for this

purpose existing strategies, plans or programmes which shall reflect, inter alia, the measures set out in this Convention relevant to the Contracting Party concerned; and (b) Integrate, as far as possible and as appropriate, the conservation and sustainable use of biological diversity into relevant sectoral or cross-sectoral plans, programmes and policies.

- **Article 7 – Monitoring:** (a) Identify components of biological diversity important for its conservation and sustainable use having regard to the indicative list of categories set down in Annex I; (b) Monitor, through sampling and other techniques, the components of biological diversity identified pursuant to subparagraph (a) above, paying particular attention to those requiring urgent conservation measures and those which offer the greatest potential for sustainable use; (c) Identify processes and categories of activities which have or are likely to have significant adverse impacts on the conservation and sustainable use of biological diversity, and monitor their effects through sampling and other techniques; and (d) Maintain and organize, by any mechanism data, derived from identification and monitoring activities pursuant to subparagraphs (a), (b) and (c) above.
- **Article 8 – *In situ* conservation:** (g) Establish or maintain means to regulate, manage or control the risks associated with the use and release of living modified organisms resulting from biotechnology which are likely to have adverse environmental impacts that could affect the conservation and sustainable use of biological diversity, taking also into account the risks to human health; (h) Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species; (i) Endeavour to provide the conditions needed for compatibility between present uses and the conservation of biological diversity and the sustainable use of its components.
- **Article 9 – *Ex situ* conservation:** (a) Adopt measures for the ex-situ conservation of components of biological diversity, preferably in the country of origin of such components; (b) Establish and maintain facilities for ex-situ conservation of and research on plants, animals and micro- organisms, preferably in the country of origin of genetic resources; (c) Adopt measures for the recovery and rehabilitation of threatened species and for their reintroduction into their natural habitats under appropriate conditions; (d) Regulate and manage collection of biological resources from natural habitats for ex-situ conservation purposes so as not to threaten ecosystems and in-situ populations of species, except where special temporary ex-situ measures are required under subparagraph (c) above …
- **Article 10 – Sustainable use**: b) Adopt measures relating to the use of biological resources to avoid or minimize adverse impacts on biological diversity; (c) Protect and encourage customary use of biological resources in accordance with traditional cultural practices that are compatible with conservation or sustainable use requirements; (d) Support local populations to develop and implement remedial action in degraded areas where biological diversity has been reduced.
- **Article 15 – Access to genetic resources:** Recognizing the sovereign rights of States over their natural resources, the authority to determine access to genetic resources rests with the national governments and is subject to national legislation.

Other key international mechanisms include CITES, the Ramsar Convention on Wetlands, the United Nations Convention on the Law of the Sea, UNESCO and its International Oceanic Convention. Recently, the World Summit on Sustainable Development,[1] the Millennium Development Goals,[2] and the Millennium Ecosystem

[1] http://www.unep.fr/outreach/wssd/postjoburg/wssdoutcomes.htm
[2] http://www.un.org/millenniumgoals/

Assessment[3] have introduced broad goals into the international development arena. Specific goals have been identified in high priority areas such as Africa.[4]

4. DRIVERS IN THE INTERNATIONAL POLICY SECTOR

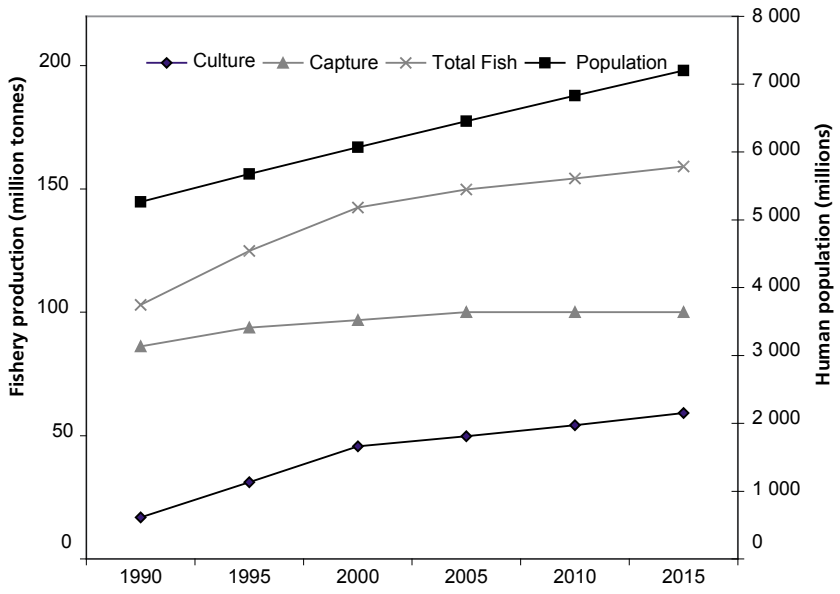
The following trends may act as drivers of change in the use and value of aquatic genetic biodiversity and how international agencies deal with the changes.

Trends in human, economic and biodiversity resources

The production from capture fisheries has levelled and significant increases in production are expected to come primarily from aquaculture (Figure 1). Of the world's major marine fisheries, the percentage of over-exploited, depleted or recovering stocks has increased from about 10% to 28% from 1974 to 2003. During this time under to moderately exploited stocks have decreased from about 40% to 24%, and fully exploited stocks have remained fairly constant at 50% (FAO, 2004).

Aquaculture is the fastest growing food producing sector with an average rate of increase of about 9% over the last two decades (FAO, 2004). Much of this growth has been in developing countries. Today, nearly one of every two fish consumed with be farm-raised (FAO, 2006a). It is further expected that per capita consumption of fish will increase to about 16kg/yr by 2015 (FAO, 2004). With an ever growing human population, fishery production will need to increase to meet these expectations. In response, intensification of farming systems, exploration of new areas and improvement of fishery management are being employed. Intensification has also involved genetic

FIGURE 1
Production from capture fisheries and aquaculture, and human population growth



[3] http://www.eco-index.org/search/pdfs/millenium_ecosystem_assessment.pdf

[4] The New Economic Partnership for African Development Action plan for the Development of African Fisheries and Aquaculture. http://www.iss.co.za/Af/RegOrg/nepad/fishplan.pdf

alteration of species to be consumed. This has led in some cases to a fear of products derived from modern biotechnology.

Trends in technology

At present there is substantial technical ability to identify, characterize and manipulate genetic biodiversity, although it is often not used or is expensive to use. Technology exists that allows genes to be transferred across taxonomic kingdoms, e.g. fish anti-freeze protein genes that have been inserted into strawberries; micro-satellite markers can trace family pedigrees or identify stock structure in wild populations (Liu, 2007), and the products of individual genes can be identified and crafted to meet certain needs. Improvements in technology have increased our ability to perform these manipulations and analyses and have lowered the cost of doing so. Although much of this technology is in developed countries, numerous developing countries have this capacity and many others are seeking it.

Societal trends

In response to the above increase capacity in technology, there has been increased attention given by consumers, non-governmental organizations, and other interests groups to human health safety, environmental safety and ethical concerns associated with genetic manipulation and consumption of fish and fish products. Many of the human health concerns stem from highly publicized aspects of plant genetic engineering where the products of the modification are toxins or resistance to toxins, e.g. herbicide resistant soybeans or Bt-cotton.

From common heritage to sovereign rights

With the signing of the CBD and the CCRF, the international community acknowledged the value of biological diversity and genetic resources in helping improve the human condition. Whereas previously genetic resources were considered to be the "heritage of mankind", these new instruments now recognize the sovereign rights of States to manage their own resources and control access to them (CBD, 1994).

Recognizing stocks and strains

Responsible management of aquatic genetic resources will require information on stocks, strains, and important breeds of aquatic organisms (Grant, 2007; Pullin, 2007; Smith, 2007). Important stocks of marine species have been defined and assessed as to their status, i.e. depleted, recovering, sustainably harvested, over-fished. Some National Governments are granting species status to sub-species and stocks as in the United States of America where the government affords protection to endangered runs of Pacific salmon as species under the USA Endangered Species Act.[5] Breeding centers in Eastern Europe maintain detailed information on strains of common carp (Bakos and Gorda, 2001), and registries of common aquaculture species exist in the United States of America;[6] these are exceptions however, to the general lack of information below the species level.

From simple to complex issues

Although basic information on aquatic genetic resources and biodiversity is extremely important and much work still needs to be done to assess their status and trends,

[5] See listing of specific stocks of coho salmon in Oregon and California, United States of America. http://www.fws.gov/endangered/federalregister/1997/f970506.pdf

[6] See National Fish Strain Registry at http://www.nbii.gov/images/uploaded/151813_1159742065258_FARStrategicPlan.pdf

numerous international and donor agencies and conventions are now stressing the important role that these resources play in poverty reduction, human health, and ecosystem functions (see for example Toledo and Burlingame (2006) and references therein). The complex issues of poverty and livelihoods are becoming superimposed on the technical issues of genetics and biodiversity. The CBD, CG Centers and FAO are working to document not only the aquatic animal diversity found in rice fields, but also the key nutrients such as fatty acids, minerals (Toledo and Burlingame, 2006). While this trend is expected and reasonable, it puts added importance to accurate assessment of aquatic resources for food and aquaculture.

5. REFERENCES

Bakos, J. & Gorda, S. 2001. *Genetic resources of common carp at the Fish Culture Research Institute, Szarvas, Hungary*. FAO Fisheries Technical Paper **417**. FAO, Rome.

CBD. 1994. *Convention on Biological Diversity.* UNEP, Nairobi.

FAO. 1995. *FAO Code of Conduct for Responsible Fisheries*. FAO, Rome.

FAO. 2004. *The state of world fisheries and aquaculture 2004.* FAO, Rome.

FAO. 2006. *FISHSTAT Plus: universal software for fishery statistical time series.* FAO, Rome. http://www.fao.org/fi/statist/fisoft/FISHPLUS.asp

FAO. 2006a. *The state of world fisheries and aquaculture 2006*. FAO Fisheries Technical Paper No. 500. FAO, Rome.

Grant, W.S. 2007**.** Status and trends in genetic resources of capture fisheries. In D.M. Bartley, B.J. Harvey and R.S.V. Pullin (eds and comps). *Workshop on status and trends in aquatic genetic resources: a basis for international policy. Victoria, British Columbia, Canada, 8–10 May 2006.* Rome: FAO. pp. 29–80. FAO Fisheries Proceedings, No. 5.

Liu, Z. 2007. Fish genomics and analytical genetic technologies, with examples of their potential applications in management of fish genetic resources*.* In D.M. Bartley, B.J. Harvey and R.S.V. Pullin (eds and comps). *Workshop on status and trends in aquatic genetic resources: a basis for international policy. Victoria, British Columbia, Canada, 8–10 May 2006.* Rome: FAO. pp. 145–179. FAO Fisheries Proceedings, No. 5.

Pullin, R.S.V. 2007. Genetic resources for aquaculture:status and trends. . In D.M. Bartley, B.J. Harvey and R.S.V. Pullin (eds and comps). *Workshop on status and trends in aquatic genetic resources: a basis for international policy. Victoria, British Columbia, Canada, 8–10 May 2006.* Rome: FAO. pp. 109–143. FAO Fisheries Proceedings, No. 5.

Smith, P.J. 2007. Issues, status and trends in deep-sea fishery genetic resources. . In D.M. Bartley, B.J. Harvey and R.S.V. Pullin (eds and comps). *Workshop on status and trends in aquatic genetic resources: a basis for international policy. Victoria, British Columbia, Canada, 8–10 May 2006.* Rome: FAO. pp. 81–108. FAO Fisheries Proceedings, No. 5.

Toledo, A. & Burlingame, B. 2006. Biodiversity and nutrition: a common path. *Special Issue Journal of Food Composition* **19** (6-7), 2006.

Status and trends in genetic resources of capture fisheries

W. Steward Grant
Department of Biological Sciences
University of Alaska, Anchorage

1. SUMMARY

Genetic diversity encompasses three hierarchical levels: differences between species, differences among conspecific populations and genetic differences among individuals in a population. While the protection of each of these levels of genetic diversity is essential for achieving sustainable harvests, overfishing, habitat degradation and climate change generally overshadow concerns for genetic integrity. Capture fisheries for freshwater and diadromous species are marginally increasing globally, but capture fisheries for marine species have leveled or are declining. The demand for fishery products remains unabated and will increase as the economies of developing countries improve.

The continuing development of new molecular genetic tools provides high-resolution markers for assessing genetic population structure, for estimating demographic parameters and for providing insights into breeding biology. A growing body of population and evolutionary theory, and new statistical and computer procedures greatly assist in the interpretation of genetic data. Presently, genetic variables are generally not incorporated into ecological or economic models. Future models incorporating genetic data will be tailored to particular situations.

Fisheries in rivers and lakes are largely focused on species with naturally fragmented populations. These species are prone to inbreeding depression in small populations and to hybridizations with introduced divergent strains. Hence, genetic concerns are usually addressed under the framework of conservation biology and theory relating to inbreeding and unintentional hybridization.

Diadromous species support large commercial fisheries in the North Pacific and North Atlantic. These species are especially vulnerable to ecological disturbances because of their complex life-history cycle, which spans freshwater and marine habitats. The loss of between-population genetic diversity through population extinctions in some species is especially acute in areas of human development. The failures of numerous transplanting programmes for many species indicate that local populations are adapted to particular habitats and seasonal events and cannot be easily moved to other habitats.

In the marine realm, the greatest genetic threats appear to be the extinction of genetically unique subpopulations and loss of genetic diversity through declines in abundance by overfishing and climate change. For species or stocks supplemented with cultured individuals, genetic swamping with artificially propagated individuals can reduce the fitness of wild populations.

Numerous international conventions and agreements recognize the importance of maintaining biological diversity, but generally treat genetic diversity indirectly as a component of biodiversity. Four steps provide a framework for conserving genetic

diversity: 1) identification of objectives, 2) assessment of genetic risk, 3) identification of reference points and 4) monitoring of progress toward objectives.

2. INTRODUCTION

Biological diversity encompasses three components: 'the variety of living forms, ecological roles they perform and the genetic diversity they contain' (Wilcox, 1984). Capture fisheries are faced with several problems that tend to erode these fundamental components of diversity. The most important problem in many environments is overfishing (Pauly *et al*., 1998, 2003; Allan *et al*., 2005), but habitat changes from human development, pollution and physical degradation from trawling are also substantial. The increasing demand for fish and weak enforcement of fishery regulations in many regions have led to serious depletions of once abundant stocks. These problems are especially acute in coastal and estuarine areas close to human development. In addition to these direct human impacts on wild populations, natural (North Atlantic Oscillation, Pacific Decadal Oscillation) and induced (climate warming from greenhouse gases) shifts in climate greatly influence the abundances of local populations (Attrill and Power, 2002; Benson and Trites, 2002).

The chief focus for achieving sustainable harvests of capture fisheries has been on the preservation of species abundances and ecosystems with little attention given to intraspecific diversity (Ryman *et al*., 1995). The reasons for this are twofold. First, management policies are heavily influenced by economic demand and the sustainable use of particular species. Second, the task of characterizing intraspecific diversity for each species is immense and often beyond the will or research capabilities of management agencies, especially those in developing countries. However, the maintenance of intraspecific genetic diversity may be key to preventing species extinctions (e.g., Ehrlich, 1988). The erosion of intraspecific diversity is not limited to small and geographically isolated populations but can also occur in seemingly abundant marine species.

Genetic resources can be viewed as genetic differences at three hierarchical levels of organization: 1) species, 2) populations and 3) individuals. At the highest level, species consist of populations that are reproductively isolated from populations of other species. Genetic isolation occurs because of geographic (allopatric) or behavioural isolation and, together with local adaptation, leads to the appearance of novel genetic traits (Otte and Endler, 1989). Hence, each species harbours a unique set of genetic material. Biologists agree that the process of speciation usually occurs on timescales of several hundreds of thousands of years. However, once species are lost, the fossil record indicates that several million years are required for species diversity to recover (Briggs, 1995).

At the population level of organization, the identification of discrete stocks has been a major theme in fisheries research. The definition of a stock can vary, as the motivations of fishery managers may be influenced by political, economical or biological mandates (Carvalho and Hauser, 1994). As a result, management boundaries are sometimes set at national borders because of issues of jurisdiction, even though a biological perspective may be of far greater importance in promoting the viability of a stock. The problem of managing "straddling stocks" is of particular importance for many highly mobile marine species (Meltzer, 1994).

Finally, the largest store of genetic variability in most species exists as genetic differences among individuals within a population. This variability arises from the physical assortment of genes among offspring during reproduction. Of great importance for the conservation of this genetic variability is the theoretical concept of effective population size, which is usually much smaller than census size. Both theory and empirical results show that the loss of genetic variability is greater in small populations than in large populations. Hence, the goal of preserving genetic variability

in a population coincides with the goal of maintaining large ecologically sound natural populations.

In agriculture, the problem of conserving genetic diversity has been largely framed as the preservation of domesticated plant cultivars and animal breeds, which have adapted to local environments over thousands of years of selective breeding. Technical advances have led to a greater availability of cheaper grains, and this has produced a shift from pastoral grazing to more capital-intensive methods of farming. Intensive farming methods are more productive and more predictable than traditional methods of farming. Consequently, farmers have abandoned many indigenous breeds, and this shift has led to the loss of genetic diversity. Much less attention has been directed toward the conservation of genetic resources in natural, free ranging capture species. The development of domesticated breeding lines for aquatic organisms is still in its infancy and depends on the availability of wild strains to a much greater degree than does the present-day development of breeds of plants and animals for agriculture.

The chief goal of this study paper is to survey the status of genetic resources in freshwater and marine capture fisheries and to develop an argument for conserving genetic resources in these species. These arguments parallel those developed for the conservation of plant and animal genetic resources. A second goal is to outline trends in the development of these methodologies and the concepts used to manage genetic variability in capture fisheries. The methodologies used to describe genetic variability and to assess its value in inland and marine capture species differ somewhat from those used to assess genetic resources in domesticated plants and animals. A third goal is to summarize institutional mandates focused on preserving genetic diversity and to present a framework of action for conserving genetic diversity.

2.1 Why conserve genetic diversity?

Several arguments have been developed to support the notion that the conservation of genetic resources is important in various settings. Biological and normative justifications for conserving genetic diversity are:

1. to ensure the future adaptability of natural populations;
2. to preserve life-history, behavioural and morphological traits that ensure sustainable fisheries;
3. to promote the use of genetic resources in commerce and medicine; and
4. to conserve genetic diversity for cultural reasons.

Although these arguments have been developed for agricultural resources, they are a starting point for developing analogous arguments for the conservation of diversity among and within species supporting capture fisheries.

In agriculture, indigenous breeds have value for the creation of new breeds, even though individually they may not be of high economic value (Mendelsohn, 2003). Locally adapted breeds, for example, may harbour genes that promote disease resistance, which may have been lost in highly selected production strains. Other arguments focus on societal choices. A society may be willing to maintain economically inferior breeds, because these breeds may be part of a local landscape that is valued by society, or because society finds value in maintaining historical activities and traditional livelihoods. The decline of indigenous breeds is often tied to biological and environmental conservation issues in developing countries.

Much less attention has been given to evaluating the importance of genetic resources in species supporting capture fisheries. The chief reason is that little is known about the genetic components of production in wild populations. These populations lack the recorded breeding histories that are maintained for plant cultivars and domesticated livestock. Although many inland and some diadromous species can be bred in captivity, only a few marine species have been bred in captivity. A compelling reason for conserving genetic diversity in wild populations is to provide a large base for

developing strains for aquaculture. Wild populations of plants and animals are now no longer used to a large extent to develop new agricultural strains. However, the development of strains for aquaculture is ongoing and depends on the availability of genetically diverse wild populations.

2.2 Trends in capture fisheries production

Inland and marine capture species together make up the bulk of fishery products, although production from aquaculture is increasing rapidly. Fisheries provided about 140 million tonnes of food and fish products in 2001. Most of this production comes from marine waters (about 85 million tonnes; 59.8%) and almost half consists of small pelagic fishes. The remaining capture production comes from inland waters (8.7 million tonnes; 6.1%) (FAO, 2003). A growing amount of production comes from marine and freshwater aquaculture (48.4 million tonnes; 34.1%). The size of the marine capture fishery has leveled in the last few years and may be declining (Pauly *et al.*, 2003), while inland fisheries have been relatively stable, or marginally increasing (Figure 1). Inland capture fisheries are largest in Asia (5.8 million tonnes) and Africa (2.1 million tonnes), with important fisheries also in Europe (0.3 million tonnes), South America (0.3 million tonnes), North America (0.2 million tonnes) and Oceania (0.02 million tonnes). About 7 million tonnes (80 % of inland fisheries) are produced in countries with low average incomes and food deficits. Inland capture fishery production is the sole source of fish in many of these countries.

2.3 Trends in demand for fishery products

Trends in the consumption of fish suggest continued increases in the demand for fish. A sample of 132 nations indicates that the consumption of fish is greatest in countries with high standards of living, as measured by per capita gross domestic product (York and Gossard, 2004). However, demand differs among regions and among nations. Several developing countries have high fish consumption, including Bangladesh, Cambodia and China (FAO, 2003). The demands for fish products in the nations of Africa, the Middle East and western countries of North and South America and Europe are similar (Figure 2). The largest rate of increase occurs in Asian countries, because of the traditional emphasis on fish consumption, population increases and economic

FIGURE 1
Marine, inland capture fishery production, and aquaculture production (FAO)

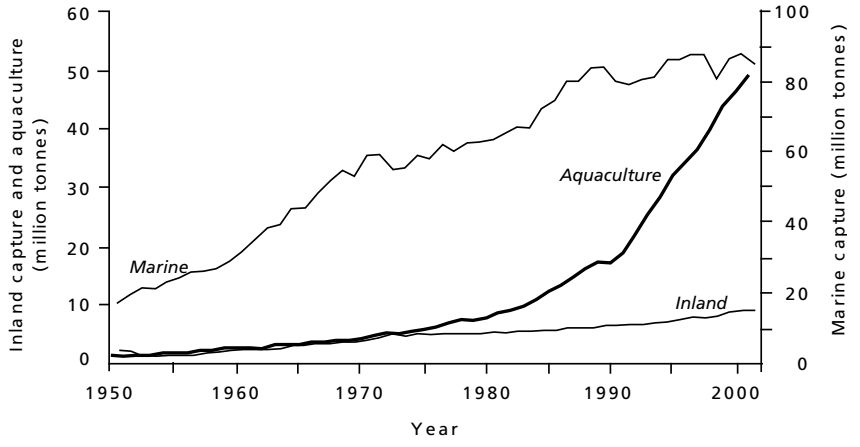
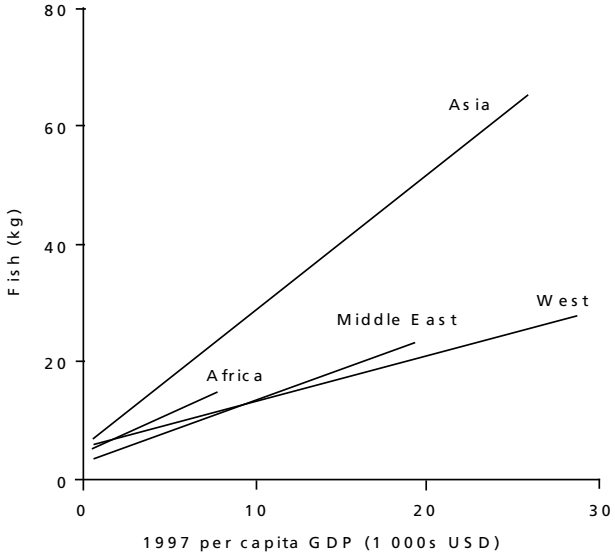


FIGURE 2
Association between per capita annual fish consumption (kilograms) and per capita gross domestic product (GDP) among regionally grouped countries. From York and Gossard (2004)



improvement. The shift of rural populations into cities, which often accompanies economic development, also leads to the increased consumption of fish. These trends indicate that the demand for fish will increase globally, but will increase most in Asian countries as they develop economically.

3. USE OF MOLECULAR MARKETS TO SURVERY GENETIC RESOURCES

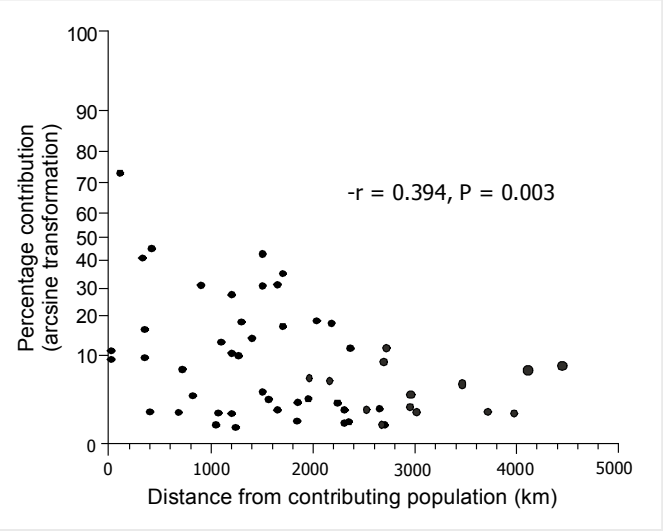
The use of molecular genetic markers to survey genetic variability and to infer population processes has advanced on two fronts in recent years. New technologies have been developed to assay DNA polymorphisms directly, and these methods have produced a range of DNA markers with complementary characteristics to address various questions (Annex 1). These advances provide a means of generating large amounts of data as a basis for statistically testing research and management hypotheses.

3.1 Applications

Assessments of genetic variability in species in capture fisheries are important for several reasons. Molecular genetic markers occur naturally, are inherited in a predictable way, provide a basis for rigorous statistical analysis, and thus are ideally suited to assessing genetic variability in wild populations. Molecular markers have been used to discover morphologically cryptic species (Shaklee and Tamaru, 1981; Knowlton, 1993; Bernardi and Goswami, 1997; Knowlton *et al.*, 1997), define population boundaries (Ruzzante *et al.*, 1998; Waples, 1995), estimate population components in areas of population mixing (Hansen *et al.*, 2001; Nielsen *et al.*, 2001; Hauser *et al.*, 2006) or origins of juveniles during life-history migrations (Teel *et al.*, 2003; Bowen *et al.*, 2006). Box 1 illustrates the use of mitochondrial DNA markers to infer migration patterns of juveniles of endangered hawksbill sea turtles (*Eretmochelys imbricata*).

One promising use of molecular data is to estimate population parameters such as population size (Nunnery and Elam, 1994; Bagley *et al.*, 1999; Turner *et al.*, 2002) (Annex 1) or to reconstruct demographic histories of population growth or

BOX 1
Genetic mixed-stock analysis of Caribbean juvenile hawksbill sea turtles, a CITES listed species. (Bowen *et al.*, 2006)



Genetic stock identification has been especially useful in the management of species that are harvested in areas of stock mixing. In these areas, less abundant stocks may be threatened with overfishing. The method was developed to estimate the proportions of component stocks in harvests of Pacific salmon as they returned to rivers to spawn (Grant *et al.*, 1980), but has proved useful for other species.

Hawksbill turtles (*Eretmochelys imbricate*) are specialized sponge feeders, which migrate between nesting beaches and feeding habitats on tropical reefs. The colourful "tortoiseshell" scutes of this species are especially valued in the production of artisan products. Harvests of this species have brought it close to extinction. A pressing question has been the extent that harvests of juveniles on feeding grounds influence spawning site abundances in other areas, a perennial problem in 'straddling stock' species. The migration biology of juveniles is largely unknown because the physical tagging of nestlings is impossible. A survey of mtDNA variability showed strong haplotype frequency differences among female nesting sites that could be used to identify the origins of juveniles on shallow reefs (Bowen *et al.*, 2006). Bayesian estimates of the origins of 629 juveniles from seven feeding congregations demonstrated that juveniles tend to return to feeding areas close to their birth sites. A significant correlation appeared between the percentage contribution to a feeding area and the distance from the contributing population (Figure). The magnitude of these distances indicates that harvests in one part of the Caribbean will impact nesting sites throughout the region.

of bottlenecks in population size (e.g. Luikhart *et al.*, 1998a). An understanding of responses to past environmental or climate disturbance can give clues to how populations might respond to future challenges. Molecular genetic data have been especially useful for estimating kinship among individuals in natural populations (Bernatchez and Duchesne, 2000; Bentzen *et al.*, 2001; Garant *et al.*, 2001; Banks *et al.*, 2003), for measuring reproductive success (Fiumera *et al.*, 2002) or for forensic identifications (Birstein *et al.*, 2000).

The development of high-resolution population markers provides a means of testing models of population structure. Populations of inland species are largely isolated from one another by terrestrial barriers to movement and the construction of

population models is straightforward. These populations generally act as collections of subpopulations (a metapopulation), in which subpopulations are tied to each other by various levels of gene flow. Local extinctions and colonizations also appear to be a general feature of inland (e.g. Bernatchez and Wilson, 1998; Lafferty *et al.*, 1999).

The structures of marine populations, on the other hand, are less well known. As expected, near shore species with both limited larval and adult dispersal (or homing behaviour to spawning areas) tend to have subdivided population structures (McQuinn, 1997; Robichaud and Rose, 2001). However, many species in capture fisheries have high dispersal abilities and occur in oceanic areas without firm barriers to movement. These species tend to show much less genetic population structure with populations occupying much larger areas than do populations of inland species (see below). How these populations are structured is of considerable importance to their management in capture fisheries. Surveys of molecular population markers continue to be important for testing the various models of population interconnection and structure.

These applications generally assume that molecular markers are not directly influenced natural selection and that the distributions of the markers reflect such parameters as effective population size and gene flow. However, genetic diversity itself is also an important component of ecological and evolutionary health of a species. A rapidly growing field of research focuses on the development of molecular markers linked to quantitative trait loci (genes that affect the ecological fitness of individuals). "Genomic" methods are used to survey portions of the genome directly influenced by selection (Reid *et al.*, 2005; Slate, 2005), to monitor genotoxic pollutants (Newton *et al.*, 2004, Rockett and Dix, 1999) and to study the effects of hybridization (Dowling and Childs, 1992; Rhymer and Simberloff, 1996) and population crashes on gene organization (Luikart *et al.*, 1998a, b; Garza and Williamson, 2001).

Market or production traits, including growth rate, flesh characteristics and disease resistance, are generally influenced by the actions of several genes, which can be evaluated only by breeding experiments (e.g. Law, 2000). In addition to experimental breeding manipulations, information on breeding lines and pedigree analysis form the basis for evaluating genetic resources in domestic livestock and agricultural plants. However, laboratory experiments on most populations targeted in capture fisheries are not possible, so alternative methods are required to assess the genetic status of natural populations.

3.2 Statistical analysis

The development of statistical methodologies and computer programmes has kept pace with laboratory progress in providing a means of analyzing genetic data (Annex 2). A variety of statistics can be used to assess genetic diversity within and among populations. Genetic data for a sample of individuals can provide information about genetic diversity within and among populations (Nei, 1987; Hedrick, 2005) and can be used to infer phylogenetic relationships among species (Felsenstein, 2004). Three measures of diversity are widely used in conservation and population studies (Box 2). The first, average heterozygosity, H, (also called gene diversity) measures the level of genetic variability in a population and is routinely estimated with allozyme and microsatellite DNA data (Nei, 1987). Nucleotide diversity, Θ_{π}, extends the concept of gene diversity by adding a measure of sequence divergence between haplotypes. These statistics can be used to detect the erosion of genetic diversity from historical reductions in population size. A third statistic, F_{ST}, measures diversity among subpopulations in a species.

BOX 2

Statistics used to measure genetic diversity within and among populations

Average heterozygosity or gene diversity: Average heterozygosity can be estimated in two ways. The first way is to count the number of heterozygous individuals in a sample of diploid genes. This is known as observed heterozygosity, H_E. These counts are usually presented as a proportion of all genotypes. A second way of estimating heterozygosity is to assume that the sample of genes from a population does not deviate significantly from Hardy-Weinberg proportions and calculate the proportion of expected heterozygotes from gene frequencies. For a single locus expected heterozygosity, h, can be calculated as:

$$h = 1 - \Sigma p_i^2$$

where p_i is the frequency of the ith allele in a sample. This formula is used to also estimate gene diversities for haplotypic loci such as mitochondrial DNA in animals or plastid DNA in plants. When data for a sample of several loci are available, such as for allozyme and microsatellite DNA data, heterozygosities are averaged,

$$H = \Sigma h/R,$$

Where R is the number of loci sampled. Average heterozygosities estimated from allozyme data usually also include monomorphic loci and are taken as an estimate of genome wide variation when samples sizes of loci are large ($R > 20$). Average heterozygosities based on microsatellite DNA usually only include polymorphic loci and are, therefore, not comparable with allozyme heterozygosities.

Nucleotide diversity: Sequences of DNA provide a basis for estimating divergences between alleles, which is not possible for allozyme or microsatellite data. The amount of sequence divergence between haplotypes in a sample provide information about the age and historical size of a population. Other variable equal, older populations are expected to accumulate more mutations and show larger divergences between haplotypes. One the other hand, larger populations of the same age are also expected to accumulate a greater number of mutations. The loss of low frequency haplotypes in a large population is less than in small populations because the loss of haplotypes through genetic drift is less. These haplotypes, however, are expected to be closely related to each other. These characteristics form the basis for estimating several demographic parameters of populations (Rogers and Harpending, 1992;).

Nucleotide diversity can be estimated from the average number of nucleotide differences between haplotypic sequences, π. The number of nucleotide differences per nucleotide site, $d_{xy,}$ is used to account for differences in the lengths of sequences in different studies. Nucleotide diversity, Θ_π, is the sum of the product of divergences between haplotypes and the frequencies of haplotypes

$$\Theta_\pi = \Sigma\Sigma d_{xy} p_x p_y,$$

Where p_x and p_y are frequencies of haplotypes in a sample.

BOX 2 *(cont.)*

F_{ST}: This statistic is the standardized variance of gene frequencies among populations and is estimated by

$$F_{ST} = \text{var}(p)/p(1 - p)$$

where $p(1 - p)$ is the binomial variance. This statistic ranges from 0.0, indicating identical gene frequencies between populations, to 1.0, indicating fixed gene frequency differences between populations. F_{ST} values are usually averaged over loci when data for several loci (allozymes and microsatellites) are available. The co-distribution of H and F_{ST} can be used to test for the effects of natural selection on gene frequency divergence between populations (Beaumont and Nichols, 1996).

The maximum value of F_{ST} is limited by high heterozygosities, as are commonly found for microsatellite loci. The upper limit of F_{ST} is $(1 - H_S)$, where H_S is the average within subpopulation heterozygosity (Hedrick, 1999). Hedrick (2005), therefore, suggests that F_{ST} be modified

$$F'_{ST} = F_{ST}\,(1 + H_S)/(1 - H_S)$$

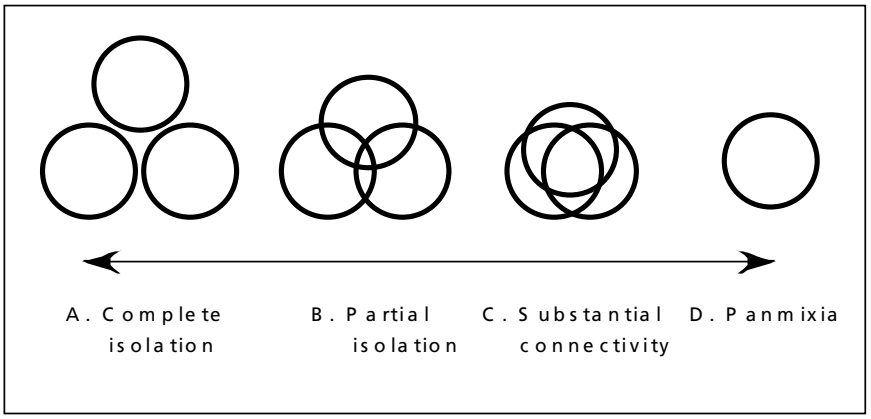
These adjusted values provide a better estimate of differentiation among populations when estimate with microsatellite DNA.

4. PATTERNS OF GENETIC VIABILITY IN NATURAL POPULATIONS

Species generally are divided into a few to numerous populations depending on the dispersal ability of individuals and on the availability of dispersal corridors. At one extreme, some marine fishes with highly mobile adults and with unimpeded movements of planktonic eggs and larvae, consist of only a single global population (Figure 3). At the other extreme, some species are highly subdivided into genetically unique subpopulations because of physical barriers to movement, or because of strong natal and site spawning fidelity. As a consequence, many marine species, such as tunas, tend to be "population poor", while inland and anadromous species tend to be "population rich" with numerous small populations. How populations react to physical and biological variables is a subject of ongoing debate (Sinclair, 1988; MacCall, 1990; Sherman *et al.*, 1993).

Various isolating mechanisms produce different levels of population subdivision among inland, anadromous and marine populations (Table 1). Although the relative amounts of allozyme and microsatellite DNA gene diversity are similar among these groups, how this diversity is partitioned among populations differs among groups. The largest amount of genetic subdivision appears among conspecific populations of freshwater species (mean F_{ST} = 0.222, median F_{ST} = 0.144), because of the physical isolation of lake and riverine habitats. Anadromous species (salmonids) show large amounts of population subdivision (mean F_{ST} = 0.108, median F_{ST} = 0.081). In this group, subdivisions reflect not only geographic isolation between freshwater spawning sites, but also homing to natal spawning sites. Populations of marine fishes show the least amount of genetic subdivision (mean F_{ST} = 0.062, median F_{ST} = 0.020), because of fewer restrictions to the movement of eggs, larvae and adults in marine waters. These statistics have been used to infer the number of migrants between populations each generation. However, the models used to make these estimates are over-simplifications

FIGURE 3
A continuum of population models showing different degrees of differentiation (based on Waples and Gaggiotti, 2006). The circles represent populations with different degrees of geographical overlap or migration between them



A. Independently, self-sustaining population that do not exchange individuals. These populations are expected to show substantial life history, demographic, morphological or genetic differences.
B. Partially isolated populations with some geographic overlap or exchange of individuals, or both. These populations may show small life history, demographic, morphological or genetic differences. Genetic differences are often used to define genetic stocks. Theoretically genetic differences appear between populations over long periods only when migration is limited to 1-5 individuals each generation.
C. Substantial geographical overlap or mixing of individuals. Although life history or demographic differences may still appear between populations, genetic differences are not expected to appear. Genetic methods are incapable of detecting these populations, however, from a fishery management perspective each population may still merit recognition.
D. Panmixia. Only a single population exists with individuals (or gametes) freely moving between areas.

TABLE 1
Components of gene diversity in freshwater, anadromous and marine fishes (summarized from Ward *et al.*, 1994 and Waples, 1998). H_T is the total amount of genetic diversity in a species, and F_{ST} is the variance of allozyme frequencies among subpopulations. H for microsatellite DNA is based on a single or only a few populations (DeWoody and Avise, 2000)

Group	Number of Species	Mean number of populations in sample	H_T	F_{ST}	
				Average	Median
Allozymes					
Freshwater	49	5.9	0.062	0.222	0.144
Anadromous	7	13.1	0.057	0.108	0.081
Marine	57	6.4	0.064	0.062	0.020
Microsatellite DNA					
Freshwater	13		0.54		
Anadromous	7		0.68		
Marine	12		0.66		

of real populations. Hence, these estimates should be used cautiously (Bossart and Prowell, 1998; Whitlock and McCauley, 1999).

4.1 Inland species

Even though inland capture fisheries are much smaller than marine capture fisheries, freshwater fisheries are an important source of protein in many countries. About 7 million tonnes (80 % of inland fisheries) are produced in countries with low average incomes and food deficits (FAO, 2003). Fisheries are the sole source of animal protein in many of these countries. Freshwater habtitats are much more fragmented than marine habitats and experience greater seasonal extremes in temperature and desiccation. Hence, freshwater populations of fishes are expected to be smaller in general, show greater fluctuations in abundance and be genetically more subdivided

than marine fishes. The problems facing populations of freshwater species tend to be addressed largely by principles in conservation biology, rather than in fishery management. Even though the problems facing inland aquatic species are most severe in developing countries, aquatic species in developed countries have best been studied with genetic methods.

4.1.1 Habitat degradation and genetic population structure

The greatest problem facing inland aquatic species is habitat degradation from human activities. Aquatic habitats are often modified by deforestation and watershed erosion, pesticides and agricultural and industrial run-off. Canalization of streams for agriculture, or direct use by humans, destroys riparian zones and impairs natural ecosystem processes that maintain water quality and produce food for aquatic species. Habitat degradation can have important genetic consequences for aquatic populations.

1. Habitat-related reductions in population size inevitably lead to the loss of genetic diversity and often to inbreeding depression. Genetic diversity can decline rapidly in small populations through random genetic drift (Crow and Kimura, 1970). The detrimental effects of inbreeding are well known from agriculture and aquaculture and inbreeding itself can lead to the demise of a population (e.g., Gall, 1987; Leberg and Vrijenhoek, 1994).
2. Habitat degradation often leads to habitat fragmentation and the loss of important connections between populations. The loss of habitats increases genetic isolation and reduces the possibility of genetic rescue of endangered populations and the probability of colonization of empty habitats in a metapopulation (Hanski and Gilpin, 1997).

4.1.2 Genetic risks from introduced species and non-native stocks

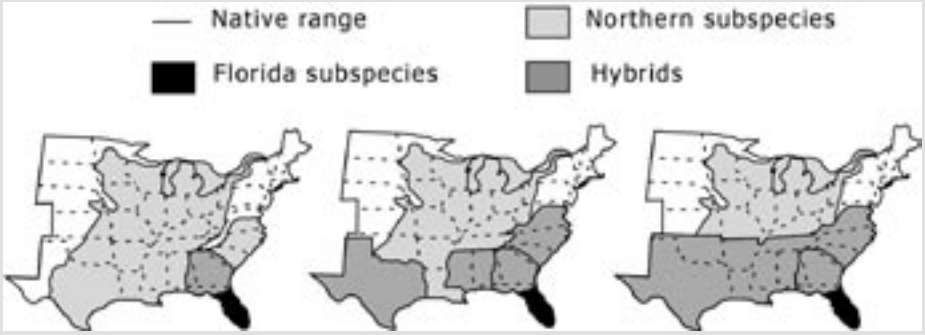
Another important threat to inland species is the introduction of non-native species, or of stocks of the same species adapted to different environments. Introductions can produce a variety of effects.

First, introductions of non-native species can lead to ecological imbalances. For example, the introduction of the predatory Nile perch (*Lates niloticus*) into the Great Lakes of Africa led to a population explosion that caused the extirpation of about 65% of Lake Victoria's endemic cichlid fish species diversity (Witte *et al.*, 1992; Goldschmidt *et al.*, 1993). The large populations of Nile perch then supported a large fishery in Lake Victoria and the production of choice filets for European and Asian markets (Kitchell *et al.*, 1997). In recent years, the burgeoning fishery has in fact reduced predation pressure on native species to about 10% of its 1970 levels and has allowed the rebound of some of the remaining cichlid species (Kitchell *et al.*, 1997).

Second, fish are sometimes transferred to other areas out of their native range. If the transferred fish are genetically different from local fish, hybridization between the two may lead to outbreeding depression and the loss of fitness (e.g. Morizot *et al.*, 1991; Carmichael *et al.*, 1993). Box 3 gives a case history of stock supplementation and mixing of two subspecies of largemouth bass across North America. Alternatively, if the introduced individuals are competitively superior to local individuals, local native populations may be hybridized to extinction.

Third, introduced individuals of the same species may be genetically compatible with local populations, a condition assumed in most stock supplementation programs and hatchery operations. Great caution, however, is needed to ensure that artificially propagated individuals have not also been genetically modified by adaptation to hatchery conditions. Selection in hatcheries can potentially occur with some feeding methods, the selection of broodstock, or other procedures that modify behaviour. Supplementation of wild populations by hatchery reared individuals can potentially lead to genetic 'swamping' and the loss of genetic diversity in wild populations, even

BOX 3
Introductions of non-native populations of largemouth bass (Philipp, 1991: Philipp *et al*, 1993)



A programme of stock introductions for largemouth bass (*Micropterus salmoides*) illustrates how genetic diversity can be lost through hybridizations with non-native individuals. Largemouth bass originally ranged across central and southeastern United States and consisted of two subspecies. The range of *M. s. floridanus* was formerly restricted to the Florida peninsula, while the range of *M. s. salmoides* extended northward over most of eastern of the United States of America. The two subspecies initially met in a narrow hybrid zone (purple).

A vigorous stocking program of the southern subspecies was initiated in 1949, because the southern subspecies was larger and preferred by fishers. By the 1970s, a study of allozyme population markers indicated that the hybrid zone had expanded northward (Philipp *et al.*, 1983). Continued introductions of *M. s. floridanus* have spread the genes of this subspecies across the entire southern range of largemouth bass. Natural levels of gene flow also helped to spread introduced genes.

As a result of these introductions, populations of the northern subspecies have lost much their distinctiveness because of the loss of between-population diversity that accompanies the homogenization through stock introductions. These two subspecies have different life history patterns and the stock transfers had led to outbreeding depression in hybrid individuals. In northern areas, "common garden" experiments showed that hybrid offspring were less fit than offspring from pure northern parents (Philipp and Whitt, 1991). These results prompted the Minnesota Department of Natural Resources to prohibit further stocking of the southern subspecies.

if hatchery individuals have not be genetically altered in captivity (Ryman and Laikre, 1991).

4.2 Diadromous species

Diadromous fishes include species that spawn in either fresh or marine waters, but spend part of their life cycle in the other habitat. Diadromous species exhibit several life history traits that make them vulnerable to extinction (Jonsson *et al.*, 1999) (Box 4). About 18% of diadromous fishes are considered to be endangered, threatened, rare or vulnerable, whereas only about 5% of fish species in general are considered to be of conservation concern (Barbault and Sastrapradja, 1995; McDowall, 1999).

4.2.1 Catadromous species

These fishes spawn in marine waters, but migrate into fresh or brackish water. The best studied of these species are North American (*Anguilla rostrata*), European (*Anguilla*

anguilla), Asian (*Anguilla japonica*) and shortfinned (*Anguilla australis*) eels, which spawn in the marine waters, but mature in rivers and lakes. In North America, allozyme markers showed significant differences among river populations (e.g. Williams *et al.*, 1973), whereas mtDNA markers indicated a lack of geographic differentiation (Avise *et al.*, 1986; Lintas *et al.*, 1998). Recent studies with high-resolution molecular markers have detected weak, but significant, differences among freshwater populations of European eels (Daemen *et al.*, 2001; Maes and Volckaert, 2002; Wirth and Bernatchez, 2003), but not among North American populations (Wirth and Bernatchez, 2001). Species consisting of a single large breeding population are particularly vulnerable to environmental changes and require international cooperation in their conservation and management.

4.2.2 Anadromous species

Anadromous fishes, on the other hand, spawn in freshwater, but mature in marine waters before returning to freshwater to spawn. The problems facing these species are particularly severe because, in addition to harvest mortality, individuals are tied to aquatic habitats that are often heavily impacted by human activities. One group of special concern includes anadromous and freshwater resident species of sturgeons, which exhibit many of the life history traits predisposing species to extinction (Williot *et al.*, 2002) (Box 4). They occupy different habitats during their life cycle, are large, long-lived, slow growing and late maturing. Habitat degradation, dams and exploitation for caviar have produced alarming population declines (Birstein, 1993). Genetic studies of sturgeons indicate complex population structures (Doukakis *et al.*, 1999; Campton *et al.*, 2000; Wirgin *et al.*, 2000) and confused taxonomies (Phelps and Allendorf, 1983; Birstein *et al.*, 2000; Birstein *et al.*, 2002; Krieger *et al.*, 2000).

Anadromous salmonids, which are distributed across temperate regions of the Northern Hemisphere, are also vulnerable to many of the same threats facing sturgeon (Nehlsen *et al.*, 1991). Considerable effort has been spent on the life history and genetic analyses of these species, because these fishes support substantial commercial, traditional or recreational fisheries. A variety of genetic population structures appear in salmonids that reflect ecological and life history differences, not only among species, but also among some stocks of the same species. For example, Waples *et al.* (2001) found that among seven species of Pacific salmon in the genus *Oncorhynchus* a strong correlation appeared between ecological and life history diversity. Species inhabiting a greater number of ecological provinces tended to exhibit a greater number of life history types as evidenced by degree of anadromy, spawning run timing, time to adult maturity (marine phase duration) and juvenile freshwater residence time (Figure 4). This correlation reflects the direct influence of environmental factors such as temperature and food availability on the expression of life history traits.

An understanding of the nature of adaptive traits is of fundamental importance in the conservation and management of fishery resources. Both rate and mechanism determine the extent to which life history diversity and diversity generating eco-processes should be conserved. Adaptations in many salmonids occur rapidly (Hendry, 2001; Koskinen *et al.*, 2002) and over short distances (Taylor, 1991). Life history characters shifted in only a few decades after introductions of Chinook salmon (*Oncorhynchus tshawytscha*) to New Zealand (Quinn *et al.*, 2000) and into the North American Great Lakes (Kwain and Thomas, 1984). Rapid rates of life history diversification on contemporary time scales have also been documented in sockeye salmon (*Oncorhynchus nerka*) (Hendry 2001) and grayling (*Thymallus thymallus*) (Koskinen *et al.*, 2002). The failures of many stock transfers of salmon between rivers and streams along the west coast of North America indicate

BOX 4

Population or biological traits that predispose stocks or species to depletion and extinction. Declines in effective population sizes can lead to the loss of genetic diversity

1. *Slow growing and long lived*: Species with these traits are vulnerable to the effects of overfishing because standing biomass after harvest is replaced very slowly. These traits are often associated with large body size, late maturity and small numbers of offspring.

2. *Several years to reproductive maturity*: Many species of fish have market value before they reach reproductive maturity. Unless a significant number of individuals are allowed to reproduce the viability of a stock is great reduced. Another component of this problem is that older, larger individuals often have reproductive potentials far larger than younger, mature individuals.

3. *Few offspring per year*: Producing only a few offspring per year is part of a continuum of reproductive strategies. Many fish and invertebrates produce millions of eggs with little or no parental care of larvae. Even though the probability of survival to maturity for individual eggs is very small, at least some of larvae are expected to survive. Other species invest more parental care by producing larger, but energetically more costly eggs, or by guarding offspring. These latter species are most at risk from the effects of overfishing, because fewer offspring are produced.

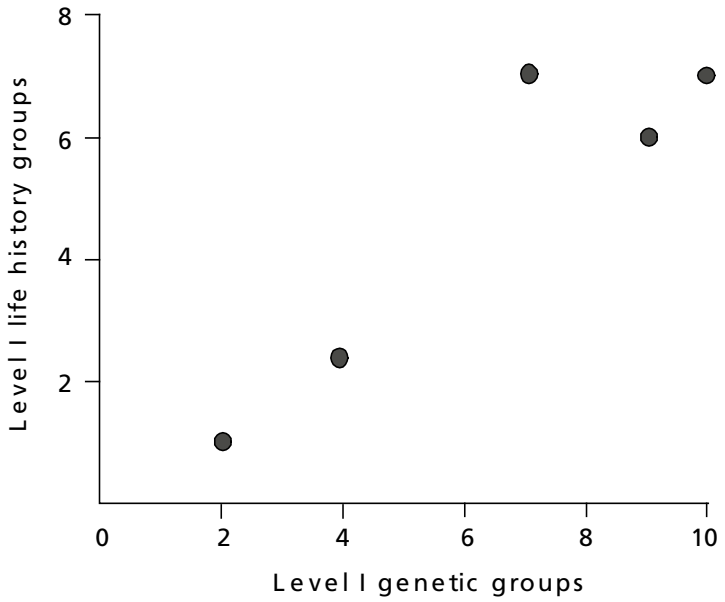
4. *Large body size*: Species with large body sizes are in jeopardy for two reasons. 1) Large, conspicuous animals may be easier to find and harvest than small animals. Visibility is especially detrimental when these species inhabit confined embayments and estuaries. 2) Large animals are inevitably at the top of the food chain and are particularly sensitive to shifts in abundance of species in the food web. Species with large body size are often slow growing, produce few offspring annually and consist of few individuals.

5. *Small natural population numbers*: These species are at particular risk when a large part of their habitat is degraded or destroyed. When core populations become depleted, recovery is hindered by reductions in the number of reproductively active individuals. These species may also be vulnerable to the loss of genetic variability and to such genetic effects as inbreeding depression.

6. *Live in confined habitats*: Species inhabiting confined spaces, such as lakes, estuaries or coastal embayments are much easier to capture than similar species inhabiting the open ocean. Many confined habitats are also associated with human activities, thus increasing the exposure to fishing and habitat changes.

7. *Specialized habitat or life history requirements*: Species with special requirements are at particular risk when only a few suitable habitats are available, or when populations of suitable prey species have been reduced. Species using rivers as migratory pathways may be at risk from the construction of dams and shoreline development. Other species with specialized diets may be at risk when particular items of food are no longer available.

FIGURE 4
Relationship between genetic and life history variability in five species of Pacific salmon (from Waples et al., 2001)



a general lack of ecological inter-changeability between most subpopulations (Utter, 2004).

4.3 Coastal marine species

Most of the World's capture fisheries focus on marine species, some of which support annual harvests of several million tonnes. Species supporting the largest harvests generally occur over the continental shelf in areas with high levels of productivity driven by upwelling. Nutrient rich areas in the eastern boundary currents of North and southern Africa, and North and South America, for example, support large fisheries of pelagic fishes, including hakes, mackerel, anchovies and sardines. Even though many species of marine fishes occur in very large populations, the combination of overfishing and climate change make them susceptible to extinction (Musick *et al.*, 2000; Myers and Ottensmeyer, 2005)

4.3.1 Genetic population structures of marine species

Most marine fishes and invertebrates are broadcast spawners and hence have large potentials for movement between areas by larval drift in currents. Additionally, adults of many species are capable of making long distance migrations. In contrast, adult homing to spawning areas, larval behaviour and hydrographic barriers to movement tend to isolate populations from one another, but not to the same degree as with freshwater fishes. The problem of unraveling demographic and genetic components of stock structure from gene frequency data is especially acute because of ill-defined geographical boundaries and decadal shifts in distributions. For example, early genetic studies of marine fishes indicated that they generally had moderate levels of gene diversity and little population subdivision, often over several hundred kilometers (e.g. Grant 1985; Mork *et al.*, 1985). However, recent studies with high-resolution markers, such as microsatellite DNA and mtDNA, have revealed fine-scale spatial differences (e.g. Ruzzante *et al.*, 1998) and unsuspected deep genetic lineages (e.g. Magoulas *et al.*, 1996).

How populations of marine fishes are structure is a subject of some debate. A persistent problem has been the lack of models that satisfactorily incorporate both ecological and genetic concepts of populations (Annex 3). Ecological models generally assume that populations are highly adapted to local environmental conditions (Sinclair, 1988). The genetic prediction of this model is that species should consist of genetically differentiated, locally adapted populations. This prediction is borne out by genetic data for freshwater and riverine species, but not for many marine species. Other models postulate that contemporary levels of gene flow or historical range expansions and contractions (MacCall, 1990) imprint genetic gradients on populations (e.g. Lecomte *et al.*, 2004). The different implications of these two models are important to formulating management policies and planning locations of marine protected areas.

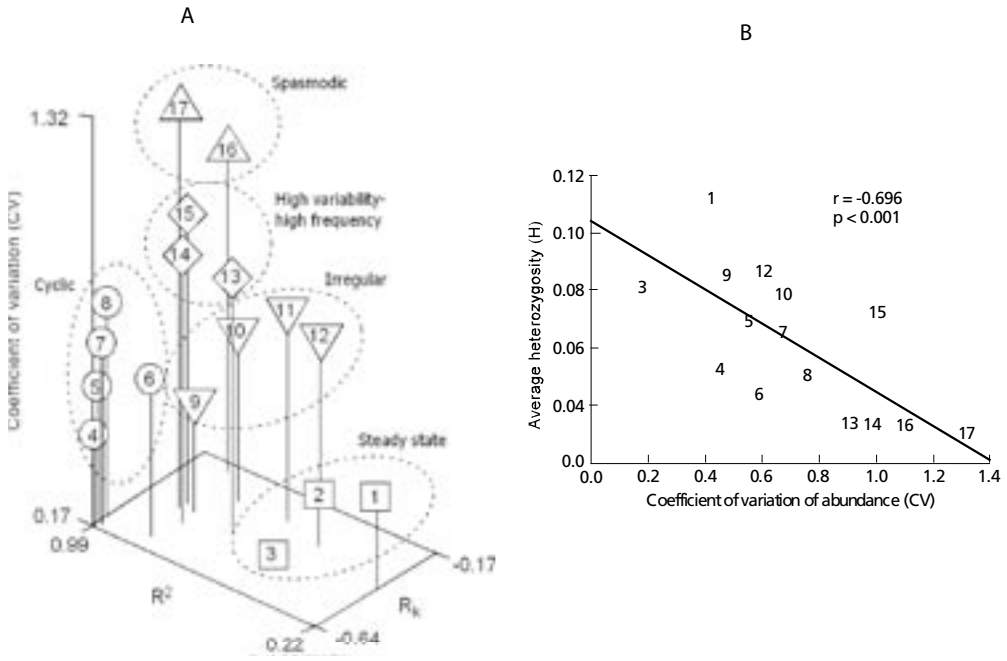
Genetic estimates of gene flow are high in most marine species (Table 1), implying the movements of tens and hundreds of individuals between subpopulations. Mitochondrial DNA data appear to support the basin model for California anchovy (Lecomte *et al.*, 2004), but support a mosaic model for European anchovy (Grant, 2005; Magoulas *et al.*, 2006). However, finer-scale differences have been detected among populations that are not isolated by obvious physical or hydrographic barriers (Hedgecock *et al.*, 1994; Ruzzante *et al.*, 1999). This chaotic variability is likely due to large reproductive variances among families (Hedgecock, 1994), rather than to isolation or to adaptations to particular open-water habitats. The instability of marine waters on annual, decadal and millennial time scales likely prevents adaptations to specific areas. On a decadal scale, anchovy populations, for example, respond rapidly to small climate changes with range contractions and expansions (e.g. Cushing, 1982; Beare *et al.*, 2004).

4.3.2 Effects of fishing on genetic variability

Populations of marine fishes, especially species supporting harvests of millions of tonnes, are generally thought to consist of large effective population sizes, and hence to be immune to the same genetic problems facing small populations of inland and anadromous species. Effective sizes of marine populations, however, may be much smaller than previously thought, because large fecundities can lead to large variances in family success. Only offspring spawned during a narrow window of oceanic conditions conducive to larval survival eventually recruit into the adult population (Hedgecock, 1994). As a result, the genetic effective size of a population may be orders of magnitude smaller than its census size (Nunnery and Elam, 1994; Bagley *et al.*, 1999; Turner *et al.*, 2002). Empirical evidence for this hypothesis, however, is mixed (Ruzzante *et al.*, 1996; Herbinger *et al.*, 1997; Li and Hedgecock, 1998). Nevertheless, available evidence indicates that fishing pressures can alter the genetic and demographic structures of seemingly very large marine populations.

The use of molecular genetic markers to estimate contemporary gene diversities is problematic since diversity is influenced by long-term rather than short-term effective population sizes. Long-term effective population size is the harmonic mean of populations each generation, and this mean is most influenced by small populations sizes. Abundances of most populations of marine species fluctuate on decadal and millennial time scales. For example, the analysis of fish scales in anaerobic sediments in the Santa Barbara Basin indicates large shifts in the abundances of anchovies and sardines over the last 2000 years before the onset of fisheries (Baumgartner *et al.*, 1992). Spencer and Collier (1997) classified population fluctuation patterns of several marine fishes based on historical catch statistics. Three variables, coefficient of variation (CV) in abundance, variable around the long-term mean and temporal autocorrelation in abundance revealed five categories of population behaviour: 1) spasmodic, 2) high variability, 3) cyclic, 4) irregular and 5) steady state (Figure 5a). Allozyme data for many of the species in the Spencer and Collier (1997) study show a negative

FIGURE 5
Effect of population instability on genetic diversity (allozyme heterozygosity) (from Grant and Waples, 2000)



A. Populations ordered by the coefficient of historical abundance (CV), variability around a long-term mean (R^2) and temporal autocorrelation of abundance (R^k) (Spencer and Collie, 1997). Species include: 1. Southern African anchovy; 2. Pacific cod; 3. NE Pacific hake; 4. Pacific halibut; 5. Pacific Ocean perch (Aleutian Island Arc); 6. Japanese anchovy; 7. NW Atlantic herring; 8. Bering Sea yellowfin sole; 9. North Sea herring; 10. California anchovy; 11. N Atlantic haddock; 12. Norwegian herring; 13. South African sardine; 14. Namibian sardine; 15. NW Pacific herring; 16. California sardine; 17. Japanese sardine.
B. Linear correlation of average allozyme heterozygosity and the coefficient of variation of historical abundances.

relationship between heterozygosity and the CV of historical abundance (Figure 5b; Grant and Waples, 2000). These results indicate that even temporary reductions in population size can have a strong influence on long-term population size and, hence, on genetic diversity.

Genetic variability in a stock can also be lost through selection by capture methods, in addition to genetic drift and metapopulation dynamics. Effects of fishing on species are evidenced by shifts in the average sizes of individuals (e.g. Ricker, 1969, 1981; Bigler *et al.*, 1996), changes in inherited life history parameters (e.g. Beacham, 1983a, b), reductions in average heterozygosity (e.g. Smith, 1994; Hauser *et al.*, 2002) and by temporal shifts in gene frequencies (e.g. Lacson and Morizot, 1991). Directional selection can occur more rapidly in large populations than in small populations, because random drift, which tends to counter selection, is much less in large populations (Ryman *et al.*, 1994).

5. GENETIC THREATS TO CAPTURE FISHERIES

Population size is a key variable for maintaining the genetic integrity of species in capture fisheries. Several ecological and genetic factors can converge to reduce population abundances. Most important for the marine environment has been overfishing by large industrial fleets. While external factors may play a role in some stock extinctions, intrinsic genetic factors can also be operating. One risk is the loss of genetic diversity, which declines at a rate that is inversely proportional to effective population size because of random genetic drift. The loss of genetic diversity can limit the ability of a population to adapt to changing environmental conditions and

detract from its economic value. Small populations face the risk of inbreeding (mating between close relatives), which increases homozygosity and, hence, the expression of deleterious, recessive genes.

5.1 Overfishing and habitat degradation

Overfishing has been implicated in the collapse of some fishery populations (Jackson *et al.*, 2001; Allan *et al.*, 2005). For example, Dulvy *et al.*, 2003 documented the extinctions of 133 local, regional or global marine populations. Most of these extinctions could be attributed to overfishing (55%) or habitat loss (37%), while the remaining population declines appeared to be due to the effects of invasive species, climate change, pollution or disease. Global fisheries landings are continuing to decline at the rate of about 500 000 tonnes per year from a peak of 80-85 million tonnes in the late 1980s (Watson and Pauly, 2001). The effects of overfishing are not limited to large industrial fisheries. Small subsistence fisheries can also greatly influence species' abundances (Jennings and Polunin, 1996; Friedlander and De Martini, 2002).

These trends are likely to continue because of the increasing demand for fishery products and because of habitat degradation. As fisheries decline in productive waters over continental shelves, fishing is extended into deeper waters aided by the development of new technologies, such as satellite positioning and seafloor imaging. Marine species most vulnerable to stock depletions and extinction have large body sizes, long life spans, late maturities, low reproductive rates, limited geographical ranges, sporadic recruitment and adaptations to unique environments (islands and sea mounts) (Sadovy, 2001; Morato *et al.*, 2006) (Box 4).

Once depressed, stocks may not recover for ecological and genetic reasons (Hutchings, 2005). For example, at very low abundances reproductive output falls off in some species (e.g. Shelton *et al.*, 1999), and the removal of top predators may lead to dramatic shifts in ecosystem structure and food-web dynamics (Hansen *et al.*, 1998; Scheffer *et al.*, 2005). Ecosystem shifts resulting from ocean-climate changes may also retard the recovery of a depleted stock (e.g. Shelton *et al.*, 2006). The reduction of population sizes by intense fishing also appears to have led to the loss of genetic diversity in some marine species (Smith, 1994; Hauser *et al.*, 2002).

Declines in the abundances of natural stocks have stimulated aquaculture production. Although many countries have no alternatives, the aquaculture does not efficiently convert primary production into fishery products. Like the production of meat, which consumes about 40% of the world's grain production to feed livestock (Harrison and Pearce, 2000), aquaculture requires large amounts of fish meal. Wastes from aquaculture often threaten nearby habitats and can severely degrade riverine and sensitive coastal ecosystems. Some aquacultural products are sometimes perceived to be inferior to products from capture fisheries (e.g. Hites *et al.*, 2004; Senkowsky, 2004). Society, therefore, has a strong motivation to maintain wild stocks.

5.2 Genetic signatures of declining populations

The development of molecular methods provides an opportunity for identifying genetically distressed and declining populations. When populations become small, they are expected to lose genetic diversity. This loss is a central concern for declining populations threatened with extinction, as genetic factors can hasten extinction. For example, inbreeding depression is thought to be especially detrimental to the well being of small populations (Frankham, 1995; Hedrick and Kalinowski, 2000). Inbreeding between close relatives tends to increase the homozygosity of deleterious, recessive genes that are relatively harmless in the heterozygous condition. Low levels of gene diversity in themselves may not be universal distress signals, as many species with low gene diversities appear to be thriving after historical bottlenecks in

population size (Hoelzel, 1999). Conversely, moderate or high levels of gene diversity may mask genetic problems in a population. Hybridization, for example, may produce an artificially elevated level of gene diversity (Ferguson 1986; Leary *et al.*, 1993).

Several biological and genetic indicators can be used to identify declining populations (Box 5). Molecular markers, for example, can be used to monitor levels of genetic

BOX 5
Genetic indicators of declining populations

1. *Reduced gene diversity*. Genetic diversity can be lost in several ways. For a gene not under the influence of natural selection, the loss of gene diversity is inversely proportional to population size. Small populations lose diversity faster than large populations. Theory predicts that the loss of heterozygosity each generation from random genetic drift (reproductive sampling error) is 1/2N, where 2N is the number of gene copies in a population for a diploid gene. A recursion formula predicting the loss of gene diversity, h_t, after t generations is

$$h_t = h_o (1 - 1/2N)^t$$

where h_o is the beginning level of gene diversity. Demonstrations of the loss of gene diversity in a population have to be made by comparison to un-fished populations of the same species and not to gene diversities in other species. Variability in gene diversity among species may be due to events on long evolutionary time scales and not to recent population events. Gene diversities can be measured with several molecular genetic markers, including allozymes, nuclear DNA (sequences or SNP polymorphisms) and mitochondrial DNA (RFLP or sequence polymorphisms).

2. *Changes in allelic or haplotypic frequency distribution*. The Ewens' (Ewens, 1972) sampling equation can be used to estimate an allele- or haplotype-frequency distribution from sample size and sample heterozygosity. This distribution is sensitive to the effects of population growth and decline and forms the basis of detecting recent bottlenecks in population size (Luikart *et al.*, 1998a, b; Garza and Williamson, 2001).

3. *Genetic discontinuities among populations*. Geographical fragmentation resulting from population extinctions can lead to discontinuities in allelic or haplotypic frequencies. A demonstration of genetic population fragmentation, however, must be based on a comparison with populations inhabiting undisturbed environments.

4. *Altered phenotypic traits*. Low gene diversities, as measured by molecular markers, may not always detect populations in genetic distress. Selection on phenotypic traits, such as size at age, can be effective in large populations where random drift is unimportant. Shifts in average size for some capture species have been attributed to size-selectivity of fishing gear.

5. *Altered life-history traits*. The timing of fishing effort can alter the genetic profile of a population by eliminating some temporal components of diversity. For example, early spawning migrations in some species of Pacific salmon were eliminated because of fishing pressure on early returning adults.

diversity. In Atlantic salmon (*Salmo salar*), microsatellite DNA markers showed a decline in gene diversity in a contemporary population in Denmark, relative to gene diversity in archived scales from the same area (Nielsen *et al.*, 1997). Other genetic profiles can also be used to identify distressed populations, including the distributions of microsatellite DNA alleles (Garza and Williamson, 2001), the distributions of mtDNA frequency haplotypes (Tajima, 1989) and haplotype mismatch patterns (Rogers and Harpending, 1992). One problem in the application of some of these approaches is that the appearance of some genetic profiles often lags behind population declines, especially rapid declines. For example, Lavery *et al.*,1996 found a mtDNA signature typical of an expanding population in a species that has declined in the past several decades.

5.3 Stock enhancement and supplementation

When capture populations decline, population enhancement and supplementation (the release of cultured individuals to boost wild population abundances) are sometimes used to attempt to rehabilitate wild stocks. Hatchery supplementations of salmonid populations have been practiced for several decades and provide lessons for other species (Utter, 2004). Although supplementation programmes for marine species have only recently been established, numerous projects are underway for fishes and invertebrates in several countries. Stock supplementations will likely increase as stocks continue to decline.

As aquaculture, mariculture and stock supplementation activities become more common, escapees and releases of cultured individuals will increase and potentially influence the genetic integrity of wild populations. The logic of supportive stock supplementation is to increase the survival of individuals in a hatchery without changing their genetic make up before release into the wild. However, the history of hatchery supplementation is filled with examples of genetic changes in cultured individuals, especially of salmonids (Reisenbichler and McIntyre, 1977; Allendorf and Phelps, 1980; Ryman and Ståhl, 1980; Verspoor, 1988; Busack and Currens, 1995; Campton, 1995; Norris *et al.*, 1999; Ford, 2002), but also marine species (Iguchi *et al.*, 1999; Sekino *et al.*, 2002).

Life history variables with an additive genetic variance (e.g. Reisenbichler and McIntyre, 1977; Cross and King, 1983; Taniguchi *et al.*, 1983; Hard, 1995), or developmental and morphological traits (Leary *et al.*, 1985) are also subject to change. Captive breeding and hatchery programmes also can lead to elevated frequencies of deleterious alleles that are otherwise kept at low frequencies in wild populations by selection (Lynch and O'Hely, 2001). Hybridization of genetically altered individuals with wild individuals can lower the fitness of offspring (outbreeding depression). Even if cultured individuals have not been genetically altered, supplementation may still pose a genetic threat to wild populations (Box 6).

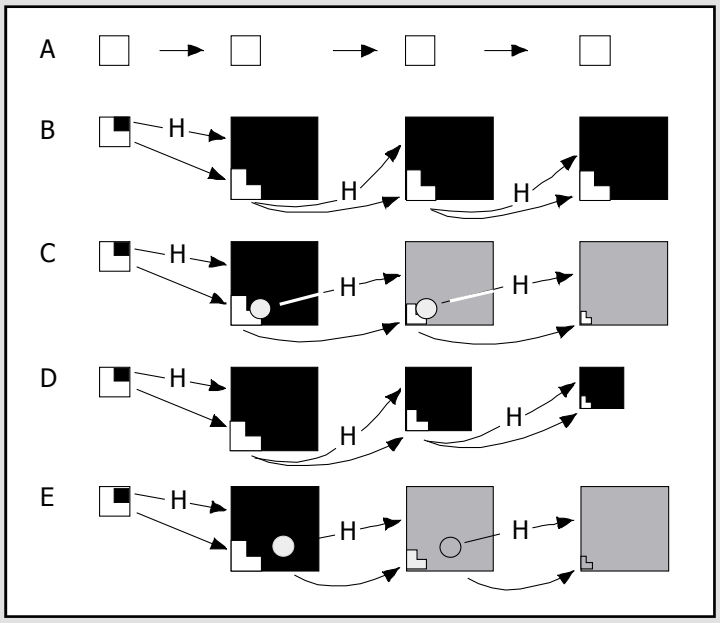
5.4 Hybridization and outbreeding depression

Hybridizations between genetically divergent wild populations can occur for several reasons (Epifanio and Nielsen, 2001). One is the inadvertent or intentional introduction of genetically divergent conspecific individuals into a native population. Non-native individuals can be inadvertently introduced by ship ballast water, or as escapes from mariculture or aquaculture. Less common are natural or intentional habitat modifications that bring previously isolated populations in contact with one another. Ecological or competitive interactions between introduced and native individuals may drive wild populations to extinction. Genetic effects, although less obvious, can be equally detrimental to the survival of a species or stock. Genetic changes are greatest in captive populations closed to wild individuals. These results indicated that releases of

BOX 6
Genetic effects of supplementation

Ryman and Laikre (1991) outlined how stock supplementations can reduce genetic diversity through "genetic swamping", even though the census size of the population in the wild increases. Captive individuals are generally produced from only a small number of parents relative to the number of potential parents in the wild. Releases of cultured individuals increase the parent-offspring variance and reduce the effective population size of the wild population, even though census numbers may be larger. Ryman and Laikre (1991) found that the effective population size equaled the sum of wild (Nw) and captive (Nc) parents only when the fraction of captive progeny was Nc/(Nc + Nw). Effective population sizes at other values of Nc and Nw are smaller. Importantly, supportive breeding in most instances reduces the total effective population size below what it would have been without supplementation. These smaller effective population sizes can lead to a loss of genetic diversity. Genetic swamping is a concern in species with high fecundities and high larval or juvenile mortality rates, a characteristic of most marine species.

Waples and Do (1994) explored this effect in more detail for Pacific salmon. They found that the extent of genetic swamping depended on the number of parents used in culture and not on the fraction of the wild population used for spawning. Genetic swamping can be hastened when individuals of hatchery origin are included a broodstock (Figures C and E). The most important determinant of levels of inbreeding in wild populations is the size of a wild population after supplementation. Even if the supplementation is successful and the wild population remains large, continued supplementation will eventually lead to the complete replacement of wild individuals with hatchery descendents. One of the few attempts to monitor the effects of supplementation showed reductions in genetic diversity in some populations of brown trout *(Salmo trutta)* that are likely due to stocking (Hansen *et al.*, 2000).



BOX 6 *(cont.)*

Genetic effect of supplementing natural stocks with hatchery (H) raised individuals (based on Ryman and Laike, 1991 and Waples and Do, 1994)

Scenario	Result
A. No supplementation to a self-sustaining natural population.	No genetic contamination of natural gene pool.
B. Offspring from captive broodstock are used to supplement a wild population. In this scenario, a portion of the wild population is used as broodstock to produce offspring for release. Hatchery releases are marked so they are not used as broodstock. Also no hybridization occurs between native individuals and releases, and native individuals mate only with other native individuals.	No genetic contamination. However, this scenario is highly unrealistic.
C. Scenario as in B, except hatchery offspring are not marked and both hatchery and native individuals are used as broodstock.	Eventual genetic swamping of native gene pool with genes of hatchery origins.
D. Scenario as in B, except that population abundance declines because of overfishing, or because supplementation exceeds environmental carry capacity.	Natural gene pools are still intact, but native individuals now represent only a small fraction of the population.
E. Scenario as in B initially, but native and hatchery individuals mate in the wild, so broodstock consist of a mix of native and hatchery genes.	Genetic swamping of native gene pool.

captive individuals can pose a genetic risk to wild populations through hybridization (Box 7).

In a survey of the literature on hybridizations in fish, Utter (2001) found several generalizations (modified here).

1. Freshwater species are more susceptible than anadromous species to introgression from distinct lineages. Anadromous species are adapted to a greater number of life history variables (freshwater migration timing, marine migration, natal homing, run timing) than are freshwater species. Hence, introgression may be prevented by outbreeding penalties against hybrids in anadromous species.
2. Genetic distances between lineages of freshwater fishes are poor predictors of introgressive hybridization. Hybrids have occurred between highly diverged lineages and even between species.
3. Anadromous populations may be more prone to displacement than to introgression between major lineages. However, introgression commonly occurs between subgroups within major lineages.
4. Persistent disruption of subgroup adaptation through hybridization with non-native individuals retards the full potential for productivity of natural populations.

When selective pressures on captive populations are not managed, or when introgressive hybridizations are recurrent from long-term supplementation releases, genetic transformations of wild populations can potentially lead to the inability of a wild population to sustain itself without supplementation (Lynch and O'Hely, 2001).

BOX 7
Genetic effects of hybridization

The major genetic risk of hybridization is the disruption of adapted gene complexes and loss of fitness (outbreeding depression) (Rhymer and Simberloff, 1996). In one form of outbreeding depression, native individuals are better adapted to particular habitat conditions than are either the introduced or hybrid individuals. For example, experimental hybrids between even- and odd-year run pink salmon *(Oncorhynchus gorbuscha)* showed much lower survival rates than either of the two control groups (Gharrett and Smoker, 1991). Outbreeding depression can also occur in hybrids between geographically separated groups of the same year type (Gilk *et al.*, 2004). A second form of outbreeding depression occurs when non-native genes are introduced into the genomes of wild individuals after the first generation of hybridization (introgression). Introgression disrupts the genes influencing a particular adaptation. Depending on the mode of expression of the genes, first generation hybrids may not be affected, but genetic recombination during reproduction separates co-adapted genes on parental chromosomes and reduces fitness in the introgressed individuals.

Reduced hybrid fitness has been documented experimentally in 'common garden' experiments for numerous freshwater (e.g. Dowling and Moore, 1985; Philipp *et al.*, 2002; Neff, 2004) and anadromous fishes (e.g. Ferguson, 1986; Hawkins and Foote, 1998; Leary *et al.*, 1985; McGinnity *et al.*, 2003). A much longer list of species shows evidence of introgression from molecular markers (see Utter, 2001). However, virtually no examples exist of outbreeding depression in marine fishes, even though hybridizations are well documented with molecular methods. One reason for the apparent lack of outbreeding depression in marine fishes may be that it is difficult to demonstrate outbreeding experimentally. Another reason may be that local adaptations are not as prevalent in marine species because high levels of gene flow may prevent local adaptations. Generally, the lower levels of genetic divergence between populations of marine fishes and many invertebrates as detected by molecular genetic methods indicate high levels of gene flow. In marine species, substantial supplementation efforts have not always resulted in the expected increases in population abundance (Larkin, 1991; Masuda and Tsukamoto, 1998). These failures could in part be due to undocumented introgressive hybridization with long-term releases of cultured individuals.

6. MAPPING THE POLICY ENVIRONMENT

Numerous national and international initiatives have been proposed to explore ways of reversing declining abundances of the world's biological resources (Table 2). Chief among these is the 1992 Convention on Biological Diversity (CBD, 1993), which calls for the conservation of biological diversity at three levels: genetics, species and ecosystems. Kenchington *et al.* (2003) noted that most initiatives focus on the conservation of species and ecosystems with little attention to genetics. Although ecosystem-based fishery management promotes the preservation of ecosystems and represents a major step toward achieving sustainable uses of natural resources, ecosystem management may not always protect genetic diversity within a species.

In addition to international initiatives, many countries or national organizations have outlined specific national problems and have attempted to implement policies intended to protect biodiversity at several levels. Parts of these policies have been formulated to address genetic issues directly. For example, the Fisheries Society of the British Isles recently published a briefing paper (FSBI, 2004) outlining the effects

TABLE 2
International initiatives on the conservation of aquatic biodiversity and the extent of focus on genetic issues. Modified from Cochrane and Doulman (2005)

Programme or Declaration	General intent	Statements or implications for genetics
Agreement, Convention or Declaration		
1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)	Prohibit international trade of endangered and threatened species.	Indirect: Reduce risk to endangered species.
1982 UN Convention on the Law of the Sea (UNCLOS)	Provides legal framework to strengthen fisheries management.	Indirect: 1. Reduce risk to endangered species; 2. Promote ecosystem-based management; 3. Implement precautionary approach.
1992 UN Conference on Environment andDevelopment (UNCED)	Promote eco-efficiency as a guiding principle 'Earth Summit' for businesses and governments; Agenda 21, comprehensive programme of action for global action to promote sustainable development; Rio Declaration on Environment and Development, principles defining rights and responsibilities of States. Resulted in Convention on Biological Diversity	Indirect: 1. Development of sustainable resources. 2. Conservation and sustainable use of biodiversity 3. Benefit sharing of genetic resources
1993 FAO Compliance Agreement	Promote compliance with international conservation and management measures by fishing vessels on the high seas.	Indirect: Reduce fishing pressure on harvested species.
1995 FAO Code of Conduct for Responsible Fisheries (CCRF). Several subsequent conferences.	Provide holistic framework for developing regulations of inland and marine fisheries and aquaculture.	Indirect: 1. Long-term preservation of fishery resources; 2. Habitat protection; 3. Call for research to support scientific decision making. Direct: 1. Call for management of genetic resources in aquaculture; 2. Management of alien species
1995 Kyoto Declaration	Underscore importance fisheries to food security in developing countries.	Indirect: Sustainable fisheries.
1995 UN Fish Stocks Agreement	Implement provisions of the UNCLOS relating to straddling fish stocks and highly migratory fishes. Developed in response to failure of 1982 UNCLOS to achieve goals.	Indirect: 1. Management of straddling stocks and stocks of highly migratory species. 2. Reduce impacts of fishing on marine environment. 3. Preserve marine diversity. 4. Maintain integrity of ecosystem.

TABLE 2 *(Cont.)*

Programme or Declaration	General intent	Statements or implications for genetics
1995 Jakarta Mandate on Marine and Coastal Biological Diversity (CBD-JM)	Global consensus on conservation of marine and coastal biological diversity;	Indirect: 1. Marine and coastal protected areas; 2. Sustainable use of marine and coastal living resources; 3. Mariculture and introductions of alien species; 4. Ecosystem processes approach to development.
2001 Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem	Recognizes fisheries impact on ecosystem, and hence, on fishery productivity.	Indirect: Preservation of ecosystem services and integrity of fishery populations.
2002 Plan of Implementation adopted by World Summit of Sustainable Development	Reinforce and consolidate existing plans and concepts to achieve sustainable development. Set a deadline (2010) to implement ecosystem approach and the maintenance or restoration of stocks to maximum sustainable levels (2015).	Indirect: Preservation of ecosystems and sustainable use of populations.
Organizations		
1923 International Pacific Halibut Commission	Conduct research and management of the stocks of Pacific halibut in the waters of Canada and the USA.	Indirect: Population management incorporating genetic information.
1945 FAO established as specialized agency within United Nations	Provide forum to address issues relating to development and sustainable use of living marine resources. Provide fishery databases to support formulation of fishery management policies.	Direct: Numerous publications on importance of genetic processes in management and sustainable use of marine resources.
1948 World Conservation Union (IUCN). World's largest conservation network, bringing together 82 States, 111 government agencies, more than 800 non-governmental organizations (NGOs).	Influence, encourage and assist societies throughout the world to conserve the integrity and diversity of nature and to ensure that any use of natural resources is equitable and ecologically sustainable.	Direct: Genetic diversity is one of the three forms of biodiversity recognized by the World Conservation Union (IUCN) as deserving conservation.
1950 Inter-American Tropical Tuna Commission (IATTC)	Conservation and management of fisheries for tunas and other species taken by tuna-fishing Vessels in the eastern Pacific Ocean.	Indirect: Population management and reduction of by-catch.
1969 International Commission for the Conservation of Atlantic Tunas (ICCAT)	Conservation of tunas and tuna-like species in the Atlantic Ocean and adjacent seas.	Indirect: Population management and reduction of by-catch.
1982 Commission for the Conservation of Antarctic Marine Living Resources (CCAMLAR). Part of Antarctic Treaty System	Balance the conservation of Antarctic marine living resources and their rational use.	Indirect: Early focus on harvests of krill. Population management.
1983 FAO Commission on Genetic Resources for Food and Agriculture	Permanent forum where governments discuss and negotiate matters relevant to genetic resources for food and agriculture.	Direct: Discussion of policies and practices influencing genetic diversity in plant and animal resources.

TABLE 2 *(Cont.)*

Programme or Declaration	General intent	Statement or implication for genetics
World Resources Institute (WRI)	Promote sustainable use of living resources through dissemination of information.	Indirect: 1. Reverse ecosystem degradation. 2. Protect global climate system.
1994 Convention for the Conservation of Southern Bluefin Tuna (CCSBT)	Conservation and management of fisheries for southern bluefin tuna	Indirect: Harvest management and reduction of by-catch.
1995 UNEP Global Programme of Action (GPA)	Protection of marine habitats from land-based activities	Indirect: Ecosystem protection
1994 International Coral Reef Initiative (ICRI)	Protection and restoration of reef ecosystems.	Indirect: Recognition that reefs are important fish nursery areas.
Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection (GESAMP)	Provides advice on impact of human activities on marine ecosystems.	Indirect: Population health through sustainable use.
Global Oceans Observing System (GOOS) Created by Intergovernmental Oceanic Commission (IOC) in 1991. Living Marine Resources (LMR) module created in 1998.	Improve information for management of seas and oceans and climate forecasts.	Indirect: Effects of fisheries on living marine resources.
Marine Protected Areas (MPAs) initiated by World Bank, World Conservation Unions (IUCN), Great Barrier Reef Marine Park Authority (GBRMPA) and Global Environmental Facility (GEF).	Establishment of marine protected areas to aid in habitat and species restorations.	Indirect: Restoration of populations through protected marine areas.

of fishing on biodiversity in the North Sea and highlight specific threats to genetic diversity. Elsewhere, endangered species legislation in the United States (Endangered Species Act) has been interpreted by government conservation agencies to protect genetic diversity within and among intraspecific population groups (Waples, 1991). Box 8 gives an example of the use of this legislation to extend protection to threatened population groups of Chinook salmon (*Oncorhynchus tshawytscha*) in western North America.

7. DEVELOPING A FRAMEWORK FOR CONSERVING GENETIC DIVERSITY

It is clear from the arguments presented here that preserving genetic diversity in natural populations subject to capture fisheries is important for maximizing harvests and achieving the sustainable use of fishery resources. Four steps can be taken to develop a framework for conserving genetic diversity in capture fisheries (modified from Kenchington *et al.*, 2003):

Step 1: Identify management objectives

The rationale for developing the objectives of a conservation or management programme differs among disciplines and determines the directions of management efforts. Goals can be evaluated by arguments from several broad disciplines representing perspectives from the past, present and future (Bowen and Roman, 2004). A systematist may argue that a major goal should be the conservation of species representing the heritage of past evolutionary diversifications (Forey *et al.*, 1994; Wheeler and Cracraft, 1996; Vecchione *et al.*, 2000; Bowen, 1999).

From a contemporary perspective, an ecologist might argue that preserving functional ecosystems is the best way to conserve the components of genetic diversity among species and among conspecific populations. Changes in one component of an ecosystem by overfishing, for example, can ripple through an entire system and threaten the stability of species not targeted by a fishery. The loss of an ecological component in an ecosystem can have often unpredicted effects on other parts of an ecosystem (Brodziak and Link, 2002). A sociologist might argue more narrowly for the preservation of genetically influenced traits in a species or population that is valued by society. An economist might argue for the preservation of specific genes with potential pharmaceutical or commercial value.

With an eye to the future, an evolutionary biologist might argue for preserving the breadth of genetic diversity in a species to ensure its capacity to adapt to future environmental changes (Crandall *et al.*, 2002; Bowen and Roman, 2004). The rationale many conservation efforts is the preservation of genetic diversity to allow future adaptive shifts (e.g. Waples, 1995). Ecological and evolutionary considerations, however, are views of the same events on different temporal scales (Frank and Leggett, 1994). All these arguments must be weighed openly by society to set conservation priorities and to provide a foundation for setting management objectives.

In practice, conservation and management goals are often forged by the contradictory demands of industry, politicians, economists, ecologists and conservationists. Unlike conservation efforts, which are often directed at preserving components of genetic diversity, the goals of managing large fisheries are not usually directed at preserving genetic diversity itself, but at the population processes influencing this diversity. An underlying objective might be to maintain populations in a natural setting that allows 'normal' ecological and evolutionary processes to occur and to maintain the full geographical range of a species (Thorpe *et al.*, 1995; Taylor and Dizon, 1999). Other management objectives might include an increase in recruitment or a reversal of the effects of selective fishing on average size, maturation age or spawning timing.

Run timing: closed circles, spring; open square, summer; open circle, fall; asterisk, winter. Twelve geographic provinces (A–L) were delineated with allozyme frequencies and life-history information, such as spawning migration timing and the length of juvenile freshwater residence (Waples *et al*., 2004).

The "Endangered Species Act" (ESA) of 1973 in the United States of America mandated that endangered or threatened species be identified for special conservation efforts. Waples (1991) developed a framework to identify "distinct population segments", which could be considered to be "species" under the ESA and receive the same protections as an endangered species. This framework invoked two criteria based on genetic and evolutionary considerations. A population represented a distinct population segment if it was reproductively isolation from other populations in the same species and if it represented an important component of the evolutionary legacy of a species. Genetic, ecological, geographical and life-history information was used to evaluate the statuses of populations in seven species of anadromous salmonids inhabiting western of the United States of America. While coastal fisheries can potentially limit the abundances of salmon populations, spawning biology and early life-history stages appear also to be important limiting factors.

Step 2: Assess genetic risk

This step is related to the first step. A clear understanding of the risks associated with the loss of genetic variability through inbreeding and stock extirpations, or the disruption of genetic structure through hybridizations, will help to guide the development of management goals. One important research agenda addresses the extent and rapidity of adaptation in local populations and the extent that human activities disrupt local adaptation (e.g., Taylor, 1991; Miller and Kapuscinski, 1994; Currens and Busack, 1995;

Sheridan, 1995; Conover, 1998; Law, 2000). Answers to these questions bear on the extent that evolutionary processes should be factored into management objectives. A growing body of evidence indicates that fish are often finely adapted to local habitats (Gilk *et al.*, 2004; Utter, 2004), and that genetic changes can occur rapidly after transplantation (e.g. Kinnison *et al.*, 1998), in culture (e.g. Hindar *et al.*, 1991) or in response to fishing selectivity (e.g. Heino, 1998; Stokes and Law, 2000). Other genetic risks may come from intraspecific hybridizations between wild and fish that have been genetically modified in captivity (e.g. Leary *et al.*, 1985; Philipp *et al.*, 2002).

Step 3: Identify reference points

Setting benchmarks to evaluate progress toward fulfilling management objectives is a critical step in the process. Reference points have been defined by an ICES working group (ICES, 2001) as "specific values of measurable properties of systems (biological, social, or economic) used as benchmarks for management and scientific advice". The purpose of setting benchmarks is to increase the awareness of the consequences of inaction on a particular problem. Two kinds of reference points can be distinguished (ICES, 2001). The first are 'target reference points', which are properties of stocks, species or ecosystems that help to achieve biological, social and economic goals. The second are 'limit reference points', which are threshold values of resource variables that trigger a conservation concern of unacceptable risk or irreversible harm. The setting of reference points for the preservation of genetic diversity depends on defining particular genetic risks to short-term goals such as maintaining stock abundance, economic return and species survival, and to long-term goals of preserving the capacity to adapt to environmental change.

The challenge in setting reference points is to understand what facets of genetic diversity are important for achieving particular goals. Only an integrated research agenda that includes genetics, ecology and economics can provide this understanding. Even a basic understanding of some genetic mechanisms is lacking. For example, little is known about what levels of genetic diversity are needed for a species to thrive and adapt. Generally, the wisdom is that as much gene diversity should be conserved as possible and that the loss of diversity leads to reductions in production. Theoretical considerations indicate that populations should not drop below 1 000-5 000 individuals to minimize the loss of gene diversity through random drift (Lynch and Lande, 1998). Yet, counter examples show that species can thrive after experiencing bottlenecks in population size that eliminated nearly all genetic diversity (Hoelzel, 1999).

Step 4: Monitor progress

Patterns of genetic variability within and among populations of a species can be monitored directly with molecular genetic methods or indirectly with models and population baseline data. Surveys of molecular genetic variability are costly, but have been vital for estimating levels of connectivity among and gene diversity within populations. Temporal sampling is needed to monitor the effects of management actions, after an initial survey establishes a baseline. One constraint on genetic monitoring is the lack of historical data. Major declines in stock abundances from fishing occurred several decades before molecular methods were first used to survey genetic variability on a large scale in the 1970s. Hence, a pre-fishing baseline is difficult to establish for most species. Temporal datasets have been instrumental in showing gene-frequency shifts in some species that appear to be due to fishing intensity (Hauser *et al.*, 2002). Another constraint in using molecular genetic markers to monitor the effectiveness of management on short time scales is that genetic profiles may not respond rapidly to environmental and demographic events. The development of high throughput methods of surveying genetic diversity (e.g., SNPs, Smith *et al.*, 2005; DNA microarrays, Cossins and Crawford, 2005) will make genetic monitoring more feasible in the future.

Avise (2001) outlines how cyto-nuclear signatures of genetic variability can be used to detected hybridizations and introgressions. Dowling *et al.,* 2005 provide an example of monitoring the genetic effects of supplementing over 11 years populations of endangered Catostomid fish.

Genetic parameters can also be monitored indirectly with theoretical models and data for population abundance, population demography and geographical distribution. For example, population models indicate that strong reductions in population size, metapopulations extinction dynamics and population fragmentation can lead to the loss of genetic variability.

8. CONCLUSIONS

The relative importance of genetic processes in species supporting capture fisheries differs among ecosystems and species. Fisheries in rivers and lakes are largely focused on species with naturally fragmented populations. Dams and land transformations further isolate some populations by destroying migration corridors between populations. Inland species are therefore vulnerable to the loss of genetic diversity through the metapopulation processes of extinction and colonization and through random drift in small populations. Hence, genetic concerns are largely addressed under the framework of conservation biology and theory relating to inbreeding and inadvertent hybridization.

Anadromous species support large commercial fisheries in the North Atlantic and North Atlantic. These species are especially vulnerable to ecological disturbances because of their complex life-history cycle, which spans freshwater and marine habitats. The loss of between-population genetic diversity through population extinctions in some species is especially acute in areas of extensive human development and degraded habitats. Native salmonids appear to be particularly at risk from hybridizations with genetically divergent conspecific individuals.

In the marine realm, species supporting capture fisheries also face genetic threats. Marine species in open waters can experience the loss of genetic diversity through the extinction of local subpopulations, genetic swamping through stock enhancements with artificially propagated individuals and intentional or inadvertent introductions of related species. The loss of genetic variability through random genetic drift appears to be less important for marine species than for inland and anadromous species. Even so, shifts in gene frequencies from drift induced by overfishing have been documented in some marine species and imply reductions to small effective population sizes.

Overfishing, habitat degradation and climate shifts appear to be far more important threats to stocks of most species than are genetic risks. This assessment is illustrated by a recent collection of papers from a symposium, entitled "Fisheries, past, present and future" (Philosophical Transactions of the Royal Society B, 2005, vol. 360), which did not include a single article dedicated to genetic issues in the management of capture fisheries. Although genetic processes were briefly discussed in some of the 14 major articles, highlights of genetic issues were absent from the introductory summary of the conference (Beddington and Kirkwood, 2005). Genetic processes appear to be perceived as far less important than ecological and life history processes influencing stock abundances.

9. REFERENCES

Allan, J.D., Abell, R., Hogan, Z., Revenga, C., Taylor, B.W., Welcomme, R.L. & Winemiller, K. 2005. Overfishing of inland waters. *BioScience*, **55**, 1041–1051.

Allendorf, F.W. 2006. Text

Allendorf, F.W. & Phelps, S.R. 1980. Loss of genetic variation in a hatchery stock of cutthroat trout. *Transactions of the American Fisheries Society*, **109**, 537–543.

Attrill, M.J. & Power, M. 2002. Climatic influence on a marine fish assemblage. *Nature*, **417**, 275–278.

Avise, J.C. 1994. *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York.

Avise, J.C. 2001. Cytonuclear genetic signatures of hybridization phenomena: Rationale, utility, and empirical examples from fishes and other aquatic animals. *Reviews in Fish Biology and Fisheries*, **10**, 253–263.

Avise, J.C., Helfman, G.S., Saunders, N.C. & Hales, L.S. 1986. Mitochondrial DNA differentiation in North Atlantic eels: population genetic consequences of an unusual life history pattern. *Proceedings of the National Academy, United States of America*, **83**, 4350–4354.

Bagley, M.J., Lindquist, D.G. & Geller, J.B. 1999. Microsatellite variation, effective population size, and population genetic structure of vermilion snapper, *Rhomboplites aurorubens*, off the southeastern of the United States of America. *Marine Biology*, **134**, 609–620.

Banks, M.A., Eichert, W. & Olsen, J.B. 2003. Which genetic loci have greater population assignment power? *Bioinformatics*, **19**, 1436–1438.

Barbault, R. & Sastrapradja, S. 1995. Generation, maintenance and loss of biodiversity. In: *Global Biodiversity Assessment,* Heywood, V. H. (ed.), pp. 193–274. Cambridge, UK: Cambridge University Press.

Baumgartner, T.R., Soutar, A. & Ferreira-Bartrina, V. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *California Cooperative Oceanic Fisheries Investigations Report*, **33**, 24–40.

Beacham, T.D. 1983a. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian shelf in the Northwest Atlantic Ocean. *Fishery Bulletin*, US, **81**, 303–321.

Beacham, T.D. 1983b. Variability in size and age at sexual maturity of American plaice and yellowtail flounder in the Canadian Maritimes Region of the northwest Atlantic Ocean. *Canadian Technical Report of Fisheries and Aquatic Sciences*, **1196**, 1–75.

Beare, D., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E. & Reid, D. 2004. An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology*, **10**, 1209.

Beddington, J. & Kirkwood, G. 2005. Introduction: fisheries, past, present and future. *Philosophical Transactions of the Royal Society* B, **360**, 3–4.

Bensen, A.J. & Trites, A.W. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries*, **3**, 95–113.

Bentzen, P., Olsen, J.B., McLean, J. E., Seamons, T.R. & Quinn, T.P. 2001. Kinship analysis of Pacific salmon: insights into mating, homing, and timing of reproduction. *Journal of Heredity*, **92**, 127–136.

Bernardi, G. & Goswami, U. 1997. *Molecular evidence for cryptic species among the Antarctic fish Trematomus bernacchii and Trematomus hansoni.* Antarctic Science, *9, 381–385.*

Bernatchez, L. & Duchesne, P. 2000. Individual-based genotype analysis in studies of parentage and population assignment: how many loci, how many alleles? *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1–12.

Bernatchez, L. & Wilson, C.C. 1998. Comparative phylogeography of Nearctic and Palearctic fishes. *Molecular Ecology*, **7**, 431–452.

Bigler, B.S., Welch, D.W. & Helle, J.H. 1996. A review of size trends among North Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 455–465.

Birstein, V.J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. *Conservation Biology*, **7**, 773–787.

Birstein, V.J., Doukakis, P. & DeSalle, R. 2000. Polyphyly of mtDNA lineages in the Russian sturgeon, *Acipenser gueldenstaedtii*: forensic and evolutionary implications. *Conservation Genetics*, **1**, 81–88.

Birstein, V.J., Doukakis, P. & DeSalle, R. 2002. Molecular phylogeny of Acipenseridae: nonmonophyly of Scaphirhyninae. *Copeia*, **2002**, 287–301.

Bossart, J.L. & Prowell, D.P. 1998. Genetic estimates of population structure and gene flow: limitations, lessons and new directions. *Trends in Ecology and Evolution*, **13**, 202–206.

Bowen, B.W. 1999. Perserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Molecular Ecology*, **8**, S5–S10.

Bowen, B.W. & Roman, J. 2004. Gaia's Handmaidens: the orlog model for conservation biology. *Conservation Biology*, **19**, 1037–1043.

Bowen, B.W., Grant, W.S., Hillis-Starr, Z., Shaver, D.J., Bjorndal, K.A., Bolten, A.B. & Bass, A.L. 2006. Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricate*) in the Caribbean Sea. *Molecular Ecology*, **in press**.

Briggs, J.C. 1995. *Global Biogeography*. Elsevier, Amsterdam.

Brodziak, J. & Link, J. 2002. Ecosystem-based fishery management: what is it and how can we do it? *Bulletin of Marine Science*, **70**, 589–611.

Busack, C.A. & Currens, K.P. 1995. Genetic risks and hazards in hatchery operations: fundamental concepts and issues. *American Fisheries Society Symposium*, **15**, 71–80.

Campton, D.E. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: what do we really know? *American Fisheries Society Symposium*, 15, 337–353.

Campton, D.E., Bass, A. L., Chapman, F.A. & Bowen, B.W. 2000. Genetic distinction of pallid, shovelnose, and Alabama sturgeon: emerging species and the US Endangered Species Act. *Conservation Genetics*, **1**, 17–32.

Carmichael, G.J., Hanson, J.N., Schmidt, M.E. & Morizot, D.C. 1993. Introgression among Apache, cutthroat and rainbow trout in Arizona. *Transactions of the American Fisheries Society*, **122**, 121–130.

Carvalho, G.R. & Hauser, L. 1994. Molecular genetics and the stock concept in fisheries. *Reviews in Fish Biology and Fisheries*, **4**, 326–350.

CBD. 1993. Convention on Biological Diversity. United Nations Environment Programme. http://www.biodiv.org/doc/legal/cbd-un-en.pdf

Cochrane, K.L. & Doulman, D.J. 2005. The rising tide of fisheries instruments and the struggle to keep afloat. *Philosophical Transactions of the Royal Society, London* B, **360**, 77–94.

Conover, D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. *Bulletin of Marine Science*, **62**, 305–311.

Cossins, A.R. & Crawford, D. L. 2005. Fish as models for environmental genomics. *Nature Reviews in Genetics*, **6**, 324–333.

Cross, T.F. & King, J. 1983. Genetic effects of hatchery rearing in Atlantic salmon. *Aquaculture*, **33**, 33–40.

Crow, J.F. & Kimura, M. 1970. *An Introduction to Population Genetics Theory*. Harper & Row, New York.

Currens, K.P. & Busack, C.A. 1995. A framework for assessing genetic vulnerability. *Fisheries*, **20**, 24–31.

Cushing, D.H. 1982. *Climate and Fisheries*. Academic Press, London.

Daemen, E., Cross, T., Ollevier, F. & Volckaert, F.A.M. 2001. Analysis of the genetic structure of European eel (*Anguilla anguilla*) using microsatellite DNA and mtDNA markers. *Marine Biology*, **139**, 755–764.

DeWoody, J.A. & Avise, J.C. 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. *Journal of Fish Biology*, **56**, 461–473.

Doukakis, P., Birstein, V.J., Ruban, G.I. & DeSalle, R. 1999. Molecular genetic analysis among subspecies of two Eurasian sturgeon species, *Acipenser baerii* and *A. stellatus*. *Molecular Ecology*, **8**, S117–S127.

Dowling, T.E. & Childs, M.R. 1992. Impact of Hybridization on a Threatened Trout of the Southwestern United States. *Conservation Biology*, **6**, 355–364.

Dowling, T.E. & Moore, W.S. 1985. Evidence for selection against hybrids in the family Cyprinidae (genus *Notropis*). *Evolution*, **43**, 620–634.

Dowling, T.E., Marsh, P.E., Kelsen, A.T. & Tibbets, C.A. 2005. Genetic monitoring of wild and repatriated populations of endangered razorback sucker (*Xyrauchen texanus*, Catostomidae, Teleostei) in Lake Mohave, Arizona-Nevada. *Molecular Ecology*, **14**, 123–135.

Dulvy, N.K., Sadovy, Y. & Reynolds, J.D. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries*, **4**, 25–64.

Ehrlich, P. R. 1988. The loss of diversity: Causes and consequences. In *Biodiversity*. Wilson, E. O. (ed.), pp. 21–27. National Academy Press, Washington, D.C.

Epifanio, J. & Nielsen, J. 2001. The role of hybridization in the distribution, conservation and management of aquatic species. *Reviews in Fish Biology and Fisheries*, **10**, 245–251.

Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. *Theoretical Population Biology*, **3**, 87–112.

FAO. 2003. Review of the state of world fishery resources: Inland fisheries. *FAO Fisheries Circular*, **942**, i-v, 1–60.

Felsenstein, J. 2003. *Inferring phylogenies*. Sunderland, MA: Sinauer Associates.

Ferguson, M.M. 1986. Developmental stability of rainbow trout hybrids: genomic coadaptation or heterozygosity? *Evolution*, **40**, 323–330.

Fiumera, A.C., Porter, B.A., Grossman, G.D. & Avise, J.C. 2002. Intensive genetic assessment of the mating system and reproductive success in a semi-closed population of the mottled sculpin, *Cottus bairdi*. *Molecular Ecology*, **11**, 2367–2377.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology*, **16**, 815–825.

Forey, P.L., Humphries, C.J. & Vane-Wright, R.I. 1994. *Systematics and Conservation Evaluation*. Systematics Association Special Volume, no. 50. Clarendon Press, Oxford.

Frank, K.T. & Leggett, W.C. 1994. Fisheries ecology in the context of ecological and evolutionary theory. *Annual Review of Ecology and Systematics*, **25**, 401–422.

Frankham, R. 1995. Inbreeding and extinction: a threshold effect. *Conservation Biology*, **9**, 792–799.

Friedlander, A.M. & DeMartini, E.E. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, **230**, 253–264.

FSBI. 2004. Effects of fishing on biodiversity in the North Sea. Briefing Paper 3, Fisheries Society of the British Isles, Granta Information Services, Cambridge.

Gall, G.A.E. 1987. Inbreeding. In: *Population Genetics & Fishery Management*. Ryman, N., Utter, F. (eds), pp. 47–87. University of Washington Press, Seattle, WA.

Garant, D., Dodson, J.J. & Bernatchez, L. 2001. A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *Journal of Heredity*, **92**, 137–145.

Garza, J.C. & Williamson, E.G. 2001. Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology*, **10**, 305–318.

Gharrett, A.J. & Smoker, W.W. 1991. Two generations of hybrids between even- and odd-year pink salmon (*Oncorhynchus gorbuscha*): a test for outbreeding depression? *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1744–1749.

Gilk, S.E., Wang, I.A., Hoover, C.L., Smoker, W.W., Taylor, S.G., Gray, A.K. & Gharrett, A.J. 2004. Outbreeding depression in hybrids between spatially separated pink salmon, *Oncorhynchus gorbuscha*, populations: Marine survival, homing ability, and variability in family size. *Environmental Biology of Fishes*, **69**, 287–297.

Goldschmidt, T., Witte, F. & Wanink, J. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorus species in the sublittoral areas of Lake Victoria. *Conservation Biology*, **7**, 686–700.

Grant, W.S. 1985. Biochemical genetic stock structure of the southern African anchovy, *Engraulis capensis* Gilchrist. *Journal of Fish Biology*, **27**, 23–29.

Grant, W.S. 2005. A second look at mitochondrial DNA variability in European anchovy (*Engraulis encrasicolus*): assessing models of population structure and the Black Sea isolation hypothesis. *Genetica*, **125**, 293–309.

Grant, W.S. & Waples, R.S. 2000. Spatial and temporal scales of genetic variability in marine and anadromous species: Implications for fisheries oceanography. In: *Fisheries Oceanography: An Integrative Approach to Fisheries Ecology and Management*, Harrison, P. J., Parsons, T. R. (eds), pp. 61–93. Blackwell Science, Oxford.

Grant, W.S., Milner, G.B., Krasnowski, P. & Utter, F.M. 1980. Use of biochemical genetic variants for identification of sockeye salmon (*Oncorrhynchus nerka*) stocks in Cook Inlet, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 1236–1247.

Hansen, M.M., Kenchington, E. & Nielsen, E.E. 2001. Assigning individual fish to populations using microsatellite DNA markers. *Fish and Fisheries*, **2**, 93–112.

Hansen, M.M., Nielsen, E.E., Ruzzante, D.E., Bouza, C. & Mensberg, K.-L.D. 2000. Genetic monitoring of supportive breeding in brown trout (*Salmo trutta* L.), using microsatellite DNA markers. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2130–2139.

Hanski, I.A. & Gilpin, M.E. (eds) 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, CA.

Hansson, L.A., Annadotter, H., Bergman, E., Hamrin, S.F., Jeppesen, E., Kairesalo, T., Luokkanen, E., Nilsson, P-Å, Søndergaard, M. & Strand, J. 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems*, **1**, 558–574.

Hard, J. J. 1995. Genetic monitoring of life-history characters in salmon supplementation: problems and opportunities. *American Fisheries Society Symposium*, **15**, 212–225.

Harrison, P. & Pearce, F. 2000. *AAAS Atlas of Population and Environment*. University of California Press, Los Angeles.

Hauser, L., Adcock, G.J., Smith, P.J., Bernal-Ramírez, J.H. & Carvalho, G.R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Science, United States of America*, **99**, 11742–11747.

Hauser, L., Seamons, R., Dauer, M., Naish, K.A. & Quinn, T.P. 2006. An empirical verification of population assignment methods by marking and parentage data: hatchery and wild steelhead (*Oncorhynchus mykiss*) in Forks Creek, Washington, United States of America. *Molecular Ecology*, **15**, 3157–3173.

Hawkins, D.K. & Foote, C.J. 1998. Early survival and development of coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead (*Oncorhynchus mykiss*), and reciprocal hybrids. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2097–2104.

Hedgecock, D 1994. Does variance in reproductive success limit effective population sizes of marine organisms? In: *Genetics and Evolution of Aquatic Organisms*, Beaumont, A. (ed.), pp. 122–134. Chapman and Hall, London.

Hedgecock, D., Hutchinson, E.S., Li, G., Sly, F.L. & Nelson, K. 1994. The central stock of northern anchovy is not a randomly mating population. *California Cooperative Oceanic Fisheries Investigation Reports*, **35**, 121–136.

Hedrick, P.W. 1999. Perspective: highly variable loci and their interpretation in evolution and conservation. *Evolution*, **53**, 313–318.

Hedrick, P.W. 2005. A standardized genetic differentiation measure. *Evolution*, **59**, 1633–1638.

Hedrick, P.W. 2005. *Genetics of Populations, Third Edition*, Boston: Jones & Bartlett.

Hedrick, P.W. & Kalinowski, S.T. 2000. Inbreeding Depression in Conservation Biology. *Annual Review of Ecology and Systematics*, **31**, 139–162.

Heino, M. 1998. Management of evolving fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences*. **55**, 1971–1982.

Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. *Genetica*, **112-113**, 515–534.

Herbinger, C.M., Doyle, R.W., Taggart, C.T., Lochmann, S.E. & Cook, D. 1997. Family relationships and effective population size in a natural cohort of cod larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, **54** (Suppl. 1), 11–18.

Hindar, K., Ryman, N. & Utter, F. 1991. Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 945–957.

Hites, R.A., Foran, J.A., Carpenter, D.O., Hamilton, M.C., Knuth, B.A. & Schwager, S. J. 2004. Global assessment of organic contaminants in farmed salmon. *Science*, **303**, 226–229.

Hoelzel, A.R. 1999. Impact of population bottlenecks on genetic variation and the importance of life-history; a case study of the northern elephant seal. *Biological Journal of the Linnean Society*, **68**, 23–39

Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*. **62**, 824–832.

ICES. 2001. Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES CM/ACME: 09. (cited in Kenchington et al., 2003)

Iguchi, K., Watanabe, K. & Nishida, M. 1999. Reduced mitochondrial DNA variation in hatchery populations of ayu (*Plecoglossus altivelis*) cultured for multiple generations. *Aquaculture*, **178**, 235–243.

Jackson, J.B.C., Dirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R. Erlandson, J.A., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Leniihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–637.

Jennings, S. & Polunin, N.V.C. 1996. Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *Journal of Applied Ecology*, **33**, 400–412.

Jonsson, B., Waples, R. S. & Friedland K.D. 1999. Extinction consideration for diadromous fishes. *ICES Journal of Marine Science*, **56**, 405–409.

Kenchington, W., Heino M. & Nielsen, E.E. 2003. Managing marine genetic diversity: time for action? *ICES Journal of Marine Science*, **60**, 1172–1176.

Kinnison, M.T., Unwin, M., Boustead, N. & Quinn, T. 1998. Population-specific variation in body dimensions of adult Chinook salmon (*Oncorhynchus tschawytscha*) from New Zealand and their source population, 90 years after introduction. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 554–563.

Kitchell, J.F., Schindler, D.E., Ogutu-Ohwayo, R. & Reinthal, P.N. 1997. The Nile perch in Lake Victoria: interaction between predation and fisheries. *Ecological Applications*, **7**, 653–664.

Knowlton, N. 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics*, **24**, 189–216.

Knowlton, N., Mate, J.L., Guzman, H.M., Rowan, R. & Jara, J. 1997. Direct evidence for reproductive isolation among the three species of the *Montastraea annularis* complex in Central America (Panama and Honduras). *Marine Biology*, **127**, 705–711.

Koskinen, M.T., Haugen, T.O. & Primmer, C.R. 2002. Contemporary fisherian life-history evolution in small salmonids populations. *Nature*, **419**, 826–830.

Krieger, J., Fuerst, P.A. & Cavender T.M. 2000. Phylogenetic relationships of the North American sturgeons (order Acipenseriformes) based on mitochrondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **16**, 64–72.

Kwain, W. & Thomas, E. 1984. The first evidence of spring spawning by chinook salmon in Lake Superior. *North American Journal of Fishery Management*, **4**, 227–228.

Lacson, M. & Morizot, D.C. 1991. Temporal genetic variation in subpopulations of bicolor damselfish (*Stegastes partitus*) inhabiting coral reefs in the Florida Keys. *Marine Biology*, **110**, 353-357.

Lafferty, K.D., Swift, C. C. & Ambrose, R.F. 1999. Extirpation and recolonization in a metapopulation of the endangered fish, the tidewater goby. *Conservation Biology*, **13**, 1447–1453.

Larkin, P. 1991. Mariculture and fisheries: future prospects and partnerships. In: *The Ecology and Management Aspects of Extensive Mariculture*, Lockwood, S. J., (ed.), pp. 6–14, vol. 192. International Council for the Exploration of the Sea.

Lavery, S., Moritz, C. & Fielder, D.R. 1996. Genetic pattersns suggest exponential population growth in a declining species. *Molecular Biology and Evolution*, **13**, 1106–1113.

Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, **57**, 659–668.

Leary, R.F., Allendorf, F.W. & Knudsen, K.L. 1985. Developmental stability as an indicator of the loss of genetic variation in hatchery trout. *Transactions of the American Fisheries Society*, **114**, 230–235.

Leary, R.F., Allendorf, F.W. & Knudsen, K.L. 1993. Null alleles at two lactate dehydrogenase loci in rainbow trout are associated with decreased developmental stability. *Genetica*, **89**, 3–13.

Leberg, P.& Vrijenhoek, R.C. 1994. Genetic variation and the susceptibility of native populations to attach by parasites associated with exotic species. *Conservation Biology*, **8**, 419–424.

Lecomte, F., Grant, W.S., Dodson, J.J., Rodriguiez-Sanchez, R. & Bowen, B.W. 2004. Living with uncertainty: genetic imprints of climate shifts in east Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). *Molecular Ecology*, **13**, 2169–2182.

Li, G. & Hedgecock, D. 1998. Genetic heterogeneity, detected by PCR-SSCP, among samples of larval Pacific oyster (*Crassostrea gigas*) supports the hypothesis of large variance in reproductive success. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1025–1033.

Lintas, C., Hirano, J. & Archer, S. 1998. Genetic variation of the European eel (*Anguilla anguilla*). *Molecular Marine Biology and Biotechnology*, **7**, 263–269.

Luikart, G. Sherwin, W. B., Steele, B. M. & Allendor, F. W. 1998a. Usefulness of molecular markers for detecting population bottlenecks via monitoring genetic change. *Molecular Ecology*, 7, 963-974.

Luikart, G., Allendorf, F.W., Cornuet, J.-M. & Sherwin, W.B. 1998b. Distortion of allele frequency distributions provides a test for recent population bottlenecks. *Journal of Heredity*, **89**, 238–247.

Lynch, M. & Lande, R. 1998. The critical effective size for a genetically secure population. *Animal Conservation*, **1**, 70–72.

Lynch, M. & O'Hely, M. 2001. Captive breeding and the genetic fitness of natural populations. *Conservation Genetics*, **2**, 363–378.

MacCall, A.D. 1990. *Dynamic geography of marine fish populations*. Sea Grant, University of Washington Press, Seattle, WA.

Maes, G.E. & Volckaert, F.A.M. 2002. Clinal genetic variation and isolation by distance in the European eel *Anguilla anguilla* (L.). *Biological Journal of the Linnean Society*, **77**, 509–521.

Magoulas, A., Tsimenides, N. & Zouros, E. 1996. Mitochrondrial DNA phylogeny and the reconstruction of the population history of a species: the case of the European anchovy (*Engraulis encrasicolus*). *Molecular Biology and Evolution*, **13**, 178–190.

Magoulas, A., Castilho, R., Caetano, S., Marcato, S. & Patarnello, T. 2006. Mitochondrial DNA reveals a mosaic pattern of phylogeographical structure in Atlantic and Mediterranean populations of anchovy (*Engraulis encrasicolus*). *Molecular Phylogenetics and Evolution*, in press.

Masuda, R. & Tsukamoto, K. 1998. Stock enhancement in Japan: Review and perspective. *Bulletin of Marine Science*, **62**, 337–358.

McDowall, R. M. 1999. Different kinds of diadromy: different kinds of conservation problems. *ICES Journal of Marine Science*, **56**, 410–413.

McGinnity, P., Prodöhl, Ferguson, A., Hynes, R., Maoiléidigh, N.Ó., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J. & Cross, T. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society,* London, B, **270**, 2443–2450.

McQuinn, I. 1997. Metapopulations in Atlantic herring. *Reviews in Fish Biology and Fisheries*, **7**, 297–329.

Meltzer, E. 1994. Global overview of straddling and highly migratory fish stocks: The nonsustainable nature of high seas fisheries. *Ocean Development and International Law*, **25**, 255–344.

Mendelsohn, R. 2003. The challenge of conserving indigenous domesticated animals. *Ecological Economics*, **45**, 501–510.

Miller, L. & Kapuscinski, A. 1994. Estimation of selection differentials from fish scales: a step towards evaluating genetic alteration of fish size in exploited populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 774–783.

Morato, T., Cheung, W.W. L. & Pitcher, T.J. 2006. Vulnerability of seamount fish to fishing: fuzzy analysis of life-history attributes. *Journal of Fish Biology*, **68**, 209–221.

Morizot, D.C., Calhoun, S.W., Clepper, L.L., Schmidt, M.E., Williamson, J.H. & Carmichael, G.J. 1991. Multispecies hybridization among native and introduced centrarchid basses in central Texas. *Transactions of the American Fisheries Society*, **120**, 283–289.

Mork, J., Ryman, N., Ståhl, G., Utter, F. & Sundnes, G. 1985. Genetic variation in Atlantic cod (*Gadus morhua*) throughout it range. *Canadian Journal of Fisheries and Aquatic Sciences*. **42**, 1580–1587.

Musick, J.A., Harbin, M.M., Berkeley, S.A., Burgess, G.H., Eklund, A.M., Findley, L., Gilmore, R.G., Golden, J.T., Ha, D.S., Huntsman, G.R., McGovern, J.C., Parker, S. J., Poss, S.G., Sala, E., Schmidt, T.W., Sedberry, G.R., Weeks, H. & Wright, S.G. 2000. Marine, estuarine and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries*, **25**, 6–29.

Myers, R.A. and Ottensmeyer, C. A. 2005. Extinction risk in marine species. In: (eds), *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*, Norse, E. A., Crowder, L. B. (eds), pp. 126–173. Island Press, Washington, D.C.

Nehlsen, W., Williams, J.E. and Lichatowich, J.A. 1991. Pacific salmon at crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, **16**, 1–21.

Nei, M. 1987. *Molecular Evolutionary Genetics*. New York: Columbia University Press.

Newton, R.K., Aardema, M. and Aubrecht, J. 2004. The Utility of DNA Microarrays for Characterizing Genotoxicity. *Environmental Health Perspectives*, **112**, 420–422.

Nielsen, E.E., Hansen, M.M. & Loeschke, V. 1997. Analysis of microsatellite DNA from old scale samples of Atlantic salmon *Salmo salar*: a comparison of genetic composition over 60 years. *Molecular Ecology*, **6**, 487–492.

Nielsen, E.E., Hansen, M.M., Schmidt, C., Meldrup, D. & Grønkjær, P. 2001. Population origin of Atlantic cod. *Nature*, **413**, 272.

Norris, A.T., Bradley, D.G. & Cunningham, E.P. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. *Aquaculture*, **180**, 247–264.

Nunnery, L. & Elam, D.R. 1994. Estimating the effective population size of conserved populations. *Conservation Biology*, **8**, 175–184.

Otte, D. & Endler, J.A. (eds) 1989. *Speciation and its consequences*. Sinauer, Sunderland MA.

Pauly, D., Christensen, B., Dalsgaard, J., Froese, R. & Torres, F. 1998. Fishing down marine food webs. *Science*, **279**, 860–862.

Pauly, D., Alder J., Bennett, E., Christensen, V., Tyedmers, P. & Watson, R. 2003. The future of fisheries. *Science*, **302**, 1359–1361.

Phelps, S.R. & Allendorf, F.W. 1983. Genetic identity of pallid and shovelnose sturgeon (*Scaphirhynchus ablus* and *S. platorynchus*). *Copeia*, **1983**, 696–700.

Philipp, D.P. 1991. Genetic implications of introducing Florida largemouth bass, *Micropterus salmoides floridanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 58–65.

Philipp, D.P. & Whitt, G.S. 1991. Survival and growth of northern Florida and reciprocal Fl Hybrid Largemouth Bass in Central Illinois. *Transactions of the American Fisheries Society*, **120**, 58–61.

Philipp, D.P., Childers, W.F. & Whitt, G.S. 1983. A biochemical genetic evaluation of the northern and Florida subspecies of largemouth bass. *Transactions of the American Fisheries Society*, **112**, 1–20.

Philipp, D.P., Epifanio, J. M. & Jennings, M.J. 1993. Conservation genetics and current stocking practices: are they compatible? *Fisheries*, **18**, 14–16.

Philipp, D.P., Claussen, J.E., Kassler, T.W. & Epifanio, J.M. 2002. Mixing stocks of largemouth bass reduces fitness through outbreeding depression. *American Fisheries Society Symposium*, **31**, 349–370.

Quinn, T.P., Unwin, M.J. & Kinnison, M.T. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding in introduced populations of Chinook salmon. *Evolution*, **54**, 1372–1385.

Reid, D.P., Szanto, A., Glebe, B., Danzmann, R.G. & Ferguson, M.M. 2005. QTL for body weight and condition factor in Atlantic salmon (*Salmo salar*): comparative analysis with rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*). *Heredity*, **94**, 166–172.

Reisenbichler, R.R. & McIntyre, J.D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gardneri*. *Journal of the Fisheries Research Board of Canada*, 34, 123–128.

Rhymer, J.M. & Simberloff, D. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, **27**, 83–109.

Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias in estimates of growth, mortality, production, and yield. *Journal of the Fisheries Board of Canada*, **26**, 479–541.

Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1636–1656.

Robichaud, D. & Rose, G.A. 2001. Multiyear homing of Atlantic cod to a spawning ground. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2325–2329.

Rockett, J.C. & Dix, D.J. 1999. Application of DNA arrays to toxicology. *Environmental Health Perspectives*, **107**, 681–685.

Rogers, A.R. & Harpending, H. 1992. Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution*, **9**, 552–569.

Ruzzante, D.E., Taggart, C.T. & Cook, D. 1996. Spatial and temporal variation in the genetic composition of larval cod (*Gadus morhua*) aggregation: cohort contribution and genetic stability. *Canadian Journal of Fisheries and Aquatic Sciences*. **53**, 2695–2705.

Ruzzante, D.E., Taggart, C.T. & Cook, D. 1998. A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. *Molecular Ecology*, **7**, 1663–1680.

Ruzzante, D.E., Taggart, C.T. & Cook, D. 1999. A review of the evidence for genetic structure in cod (*Gadus morhua*) populatoins in the NW Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St. Lawrence. *Fisheries Research*, **43**, 79–97.

Ryman, N.& Laikre, L. 1991. Effects of supportive breeding on the genetically effective population size. *Conservation Biology*, **5**, 325–328.

Ryman, N. & Ståhl, G. 1980. Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). *Canadian Journal of Fishery and Aquatic Sciences*, **37**, 82–87.

Ryman, N., Utter, F. & Laikre, L. 1994. Protection of aquatic biodiversity. In: *The State of the World's Fisheries Resources: Proceedings of the World Fisheries Congress plenary sessions,* Voigtlander, C. W. (ed.), pp. 92–115. Oxford & IBH Publishing, New Dehli.

Ryman, N., Utter, F. & Laikre, L. 1995. Protection of intraspecific biodiversity of exploited fishes. *Reviews in Fish Biology and Fisheries*, **5**, 417–446.

Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. *Journal of Fish Biology*, **59**, 90–108.

Scheffer, M., Carpenter, S. & de Young, B. 2005. Cascading effects of overfishing marine systems. *Trends in Ecology and Evolution*, **20**, 579–581.

Sekino, M., Hara, M. & Taniguchi, N. 2002. Loss of microsatellite and mitochondrial DNA variation in hatchery strains of Japanese flounder *Paralichthys olivaceus*. *Aquaculture*, **213**, 101–122.

Senkowsky, S. 2004. Fear of fish: the contaminant controversy. *Bioscience*, **54**, 986–988.

Shaklee, J.B. & Tamaru, C.S. 1981. Biochemical and morphological evolution of Hawaiian bonefishes (*Albula*). *Systematic Zoology*, **30**, 125–146.

Shelton, P.A. & Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences*. **56**, 1521–1524.

Shelton, P.A., Sinclair, A. F., Chouinard, G.A., Mohn, R. & Duplisea, D.E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*. **63**, 235–238.

Sheridan, A.K. 1995. The genetic impacts of human activities on wild fish populations. *Reviews in Fish Science*, **3**, 91–108.

Sherman, K. & Duda, A.M. 1999. Large marine ecosystems: an emerging paradigm for fishery sustainability. *Fisheries* **24**, 15–26.

Sherman, K., Alexander, L.M. & Gold, B.D. (eds) 1993. *Large marine ecosystems: stress, mitigation and sustainability*. AAAS Press, Washington, D.C.

Sinclair, M. 1988. *Marine populations: an essay on population regulation and speciation*. Sea Grant, University of Washington Press, Seattle, WA.

Slate, J. 2005. Quantitative trait locus mapping in natural populations: progress, caveats and future directions. *Molecular Ecology*, **14**, 363—379.

Smith, C.T., Templin, W.E., Seeb, J. E. & Seeb, L.W. 2005. Single nucleotide polymorphisms provide rapid and accurate estimates of the proportions of U.S. and Canadian Chinook salmon caught in Yukon River fisheries. *North American Journal of Fisheries Management*, **25**, 944–953.

Smith, P.J. 1994. *Genetic diversity of marine fisheries resources: possible impacts of fishing*. FAO Fisheries Technical Paper No. 334, FAO, Rome. 53 p.

Spencer, P.D. & Collie, J.S. 1997. Patterns of population varibility in marine fish stocks. *Fisheries Oceanography*, **6**, 188–204.

Stergiou, K.I. 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. *Fisheries Research*, 55, 1–9.

Stokes, T.K. & Law, R. 2000. Fishing as an evolutionary force. *Marine Ecology Progress Series*, **208**, 307–309.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**, 585–595.

Taniguchi, N., Sumantadinata, K. & Iyama, S. 1983. Genetic change in the first and second generations of hatchery stock of black seabream. *Aquaculture*, **35**, 309–320.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**, 185–207.

Taylor, B.L. & Dizon, A.E. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. *Molecular Ecology*, **8**, S11–S16.

Teel, D., Van Doornik, D.M., Kuligowski, D.R. & Grant, W.S. 2003. Genetic analysis of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington reveals few Columbia River wild fish. *Fishery Bulletin*, **101**, 640–652.

Thorpe, J.E., Gall, G., Lannan, J.E., Nash, C. & Ballachey, B. 1995. The conservation of aquatic resources through management of genetic risk. In: *Conservation of Fish and Shellfish Resources: Managing Diversity*, J. Thorpe, J. Lannan, C. Nash (eds). pp. 33–46. Academic Press, San Diego.

Turner, T.F., Wares, J.P. & Gold, J.R. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics*, **162**, 1329–1339.

Utter, F. 2001. Patterns of subspecific anthropogenic introgression in two salmonid genera. *Reviews in Fish Biology and Fisheries*, **10**, 265–279.

Utter, F. 2004. Population genetics, conservation and evolution in salmonids and other widely cultured fishes: some perspectives over six decades. *Reviews in Fish Biology and Fisheries*, **14**, 125–144.

Vecchione, M., Mickevich, M.F., Fauchald, K., Collette, B.B., Williams, A.B., Munroe, T.A. & Young, R.E. 2000. Importance of assessing taxonomic adequacy in determining fishing effects on communities. *ICES Journal of Marine Science*, **57**, 677–681.

Verspoor, E. 1988. Reduced genetic variability in first generation hatchery populations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1686–1690.

Waples, R.S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. *Marine Fisheries Review*, **53**, 11–21.

Waples, R.S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *American Fisheries Society Symposium*, **17**, 8–27.

Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, **89**, 438–450.

Waples, R.S. & Do, C. 1994. Genetic risk associated with supplementation of Pacific salmonids: captive broodstock programs. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 310–329.

Waples, R.S. & Gaggioti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, **15**, 1419–1439.

Waples, R.S., Teel, D.J., Myers, J.M. & Marshall, A.R. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. *Evolution*, **58**, 386–403.

Waples, R.S., Gustafson, R. G., Witkamp, L.A., Myers, J.M., Johnson O. W., Busby, P. J., Hard, J.J., Bryant, G.J., Waknitz, F.W., Neely, K., Teel, D., Grant, W.S., Winans, G.A., Phelps, S., Marshall, A. & Baker, B.M. 2001. Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology*, **59**, 1–41.

Ward, R.D., Woodward, M. & Skibinski, D.O.F. 1994. A comparison of genetic diversity levels in marine, freshwater and anadromous fishes. *Journal of Fish Biology*, **44**, 213–227.

Watson, R. & Pauly D. 2001. Systematic distortions in world fisheries cat trends. *Nature*, **414**, 534–536.

Wheeler, Q.D., & Cracraft, J.1996. Taxonomic preparedness: are we ready to meet the biodiversity challenge? In: *Biodiversity II*, Reaka-Kudla, M.L., Wilson, D.E., Wilson, E. O. (eds), pp. 435–446. Joseph Henry Press, Washington, D.C.

Whitlock, M.C. & McCauley, D.E. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity*, **82**, 117–125.

Wilcox, B.A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. In: *National Parks, Conservation, and Development: The role of protected areas in sustaining society*, pp. 639–647. McNeeley, J. A., Millers, K. R. (eds), Washington, D.C.: Smithsonian Institution Press.

Williams, G.C., Koehn, R.K. & Mitton, J.B. 1973. Genetic differentiation without isolation in the American eel, *Anguilla rostrata*. *Evolution*, **27**, 192–204.

Williot, P., Arlati, G., Chebanov, M., Gulyas, T., Kasimov, R., Kirschbaum, F., Patriche, N., Pavlovskaya, L.P., Poliakova, L., Pourkazemi, M., Kim, Y., Zhuang, P. & Zholdasova, I.M. 2002. Status and management of Eurasian sturgeon: an overview. *International Review of Hybrobiology*, **87**, 483–506.

Wirgin, I., Waldman, J.R., Rosko, J., Gross, R., Collins, M.R., Rogers, S.G. & Stabile, J. 2000. Genetic structure of Atlantic sturgeon populations based on mitochondrial DNA control region sequences. *Transactions of the American Fisheries Society*, **129**, 476–486.

Wirth, T. & Bernatchez, L. 2001. Genetic evidence against panmixia in the European eel. *Nature*, **409**, 1037–1040.

Wirth, T. & Bernatchez, L. 2003. Decline of North Atlantic eels: a fatal synergy? *Proceedings of the Royal Society, London* B, **270**, 681–688.

Witte, F., Goldschmidt, T., Goudswaard, P.C., Ligtvoet, W., van Oijen, M.J. P.& Wanink, J.H. 1992. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology*, **42**, 214–232.

York, R. & Gossard, M.H. 2004. Cross-national meat and fish consumption: exploring the effects of modernization and ecological context. *Ecological Economics*, **48**, 293–302

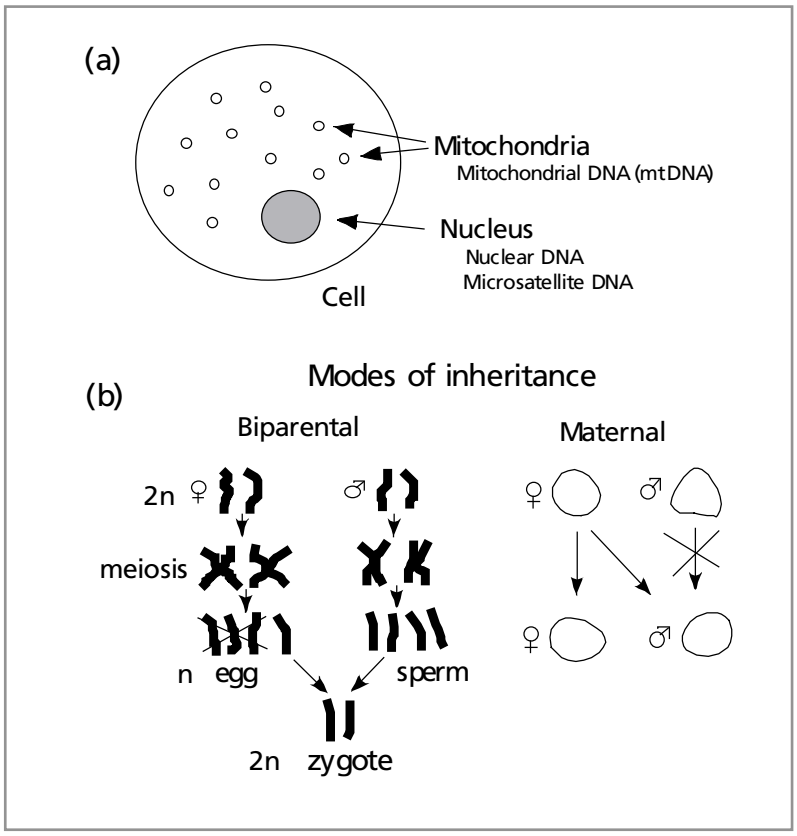
ANNEX 1

METHODS AND CONCEPTS FOR SURVEYING GENETIC RESOURCES

1. GENETIC BASIS FOR MOLECULAR VARIABILITY

The genetic information needed for the development and physiological maintenance of an individual is stored in a long polymeric molecule called DNA. DNA is found in two organelles in a cell: over 99% of DNA is located in the nucleus, but a small fraction occurs as a plasmid-like circular structure in mitochondria (Figure a). Genes encoded by nuclear DNA are inherited from both parents, and hence occur in pairs to form a diploid genotype (Figure b). Genes encoded by mitochondrial (mt) DNA, however, are maternally inherited in most species and hence occur as a single haplotype in an individual. The analysis of mtDNA, which also lacks recombination, can provide unique insights into population structure that is not possible with nuclear DNA (Avise, 1994). The entire complement of DNA is denoted by the term genome, and various parts of the genome serve different functions.

One important function is to encode information that can be translated into proteins. The coding parts (exons) of many genes are often interspersed by noncoding (introns) sections of DNA. Introns are less constrained by natural selection and hence mutate at a higher rate than the protein coding portions of a gene. Other parts of the genome encode regulatory information, important in development and gene expression. A large portion of the genome appears to serve no coding function, but may be important in the physical arrangement of DNA in the nucleus. These sections of DNA often have large numbers of short repeats called microsatellites.



2. TRENDS IN THE DEVELOPMENT OF MOLECULAR GENETIC MARKERS

Early methods of surveying genetic variability, such as immunological assays and allozyme electrophoresis, examined the products of DNA coding genes. A large amount of information on the genetics of natural and cultured populations of aquatic organisms has been produced since the early 1970s, when protein electrophoresis was first used on a large scale to the survey genetic variability in and among natural populations. However, technological developments since the 1980s have produced methods that assay DNA polymorphisms directly (Palsbøll, 1999). The most important population markers include direct sequencing, restriction enzyme fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs) and single nucleotide polymorphisms (SNPs). The application of these methods has been greatly aided by the development of the polymerase chain reaction (PCR), which amplifies targeted DNA sequences from small amounts of tissue. These various techniques provide complementary information about natural populations and are variously suited to answering different questions. When molecular population markers are under natural selection, caution must be used to infer movement between subpopulations from the geographical distributions of allele or haplotype-frequencies. Although selection on allozymes can occur because they encode proteins (Mitton, 1997), DNA cannot always be assumed to be free of selection (Avise, 1994; Bazin *et al.*, 2006; Nielsen *et al.*, 2006). Biogeographical and laboratory evidence indicates that selection may shape the geographical distributions of protein (Powers *et al.*, 1991; Powers and Schulte, 1998), mitochondrial DNA (Árnason, 2004; Bazin *et al.*, 2006; Grant *et al.*, 2006) and nuclear DNA variants (Pogson and Mesa, 2004; Canino and Bentzen, 2004; Case *et al*., 2005). The nature and intensity of selection must be understood when using selected population markers to infer population structure. Patterns of divergence for adaptive and neutral markers may not coincide (McKay and Latta, 2002). Although selectively neutral molecular markers will continue to be important, Vrijenhoek (1998) argues that adaptive traits should also be examined to help resolve conservation and management problems.

3. ESTIMATING EFFECTIVE POPULATION SIZE

One promising use of genetic data is to estimate the effective sizes of fishery populations. The genetic concept of effective population size is the number of individuals that actually contribute genetic information to the next generation. Not all individuals in a population produce offspring that reach reproductive maturity. In the marine environment, many species show a large variance in family size because of variability in the physical and biological factors influencing larval survival (Hedgecock, 1994). Fishery resource managers, on the other hand, focus on the actual number of individuals in a population (census size). The difference between these two numbers can be large for the same stock. Census population sizes are generally at least ten times the effective sizes (Frankham, 1995; Nunnery and Elam, 1994). In some cases, census size can be as much as three orders of magnitude larger than effective population size (Turner *et al.*, 2002). The loss of genetic diversity has been detected in some species, even though census numbers may still be large (Hauser *et al.*, 2002). Effective population size can be estimated in several ways. One way is to estimate the drift effective size by examining temporal changes in gene frequencies. The concept behind this approach is that effective population size influences the amount of genetic drift in a population. Small populations experience a greater amount of genetic drift, and hence greater gene frequency changes, than do larger populations. This method requires gene frequencies estimates from different generations. For some species, the analysis of archived fish scales from collections in the last few decades has provided estimates of historical gene frequencies (Miller and Kapuscinski,

1997; Nielsen *et al.*, 1997, 1999). Different statistical approaches have been used to extract unbiased estimates of effective population sizes from gene frequency data (Luikart *et al.*, 1999; Wang, 2001; Berthier *et al.*, 2002), These methods provide estimates of effective population sizes of contemporary or very recent populations. Other methods of estimating effective population size use equations from evolutionary theory that incorporate long-term effective population size. One approach is to use observed heterozygosity, which is expected to be a function of effective population size and the neutral mutation rate (Waples, 1991). Another approach is to estimate the coalescence times for mtDNA haplotypes when recombination is absent (Avise *et al.*, 1988). Coalescence time (the time until haplotype lineages trace to a common ancestral haplotype) is expected to be a function of population size. While these estimates may be reveal long-term features of the population biology of a species, they are not always useful for making management decisions, because they may not represent current population sizes.

4. REFERENCES

Árnason, E. 2004. Mitochondrial cytochrome *b* DNA variation in the high-fecundity Atlantic cod: trans-Atlantic lines and shallow gene genealogy. *Genetics*, **166**, 1871–1885.

Avise, J.C., Ball, R.M. & Arnold, J. 1988. Current versus historical population sizes in vertebrate species with high gene flow: A comparison based on mitochondrial DNA lineages and inbreeding theory for neutral mutations. *Molecular Biology and Evolution*, **5**,331–344.

Avise, J.C. 1994. *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York.

Bazin, E., Glémin, D. & Galtier, N. 2006. Population size does not influence mitochondrial genetic diversity in animals. *Science*, **312**, 570–572.

Berthier, P., Beaumont, M.A., Cornuet, J.-M. & Luikart, G. 2002. Likelihood-based estimation of the effective population size using temporal changes in allele frequencies: a genealogical approach. *Genetics*, **160**, 741–751.

Canino, M.F. & Bentzen, P. 2004. Evidence for positive selection at the pantophysin (*Pan* I) locus in walleye pollock, *Theragra chalcogramma*. *Molecular Biology and Evolution*, **21**, 1391–1400.

Case, R.A.J., Hutchinson, W.F., Hauser, L., van Oosterhout, C. & Carvalho, G. 2005. Macro- and micro-geographic variation in pantophysin (*Pan* I) allele frequencies in NE Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, **301**, 267–278.

Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: A review. *Genetical Research*, **66**, 95–107.

Grant, W.S., Spiess, I.B. & Canino, M.F. 2006. Biogeographic Evidence for Selection on Mitochondrial DNA in North Pacific Walleye Pollock *Theragra chalcogramma. Journal of Heredity*, in press.

Hauser, L., Adcock, G.J., Smith, P.J., Bernal-Ramírez, J.H. & Carvalho, G.R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Science, United States of America*, **99**, 11742–11747.

Hedgecock, D. 1994. Does variance in reproductive success limit effective population size of marine organisms? pp 122–134, In: *Genetics and evolution of aquatic organisms*. A. Beaumont (ed.), London: Chapman & Hall.

McKay, J.K. & Latta, R.G. 2002. Adaptive population divergence: markers, QTL and traits. *Trends in Ecology and Evolution*, **17**, 285–291.

Miller, K.M. & Kapuscinski, A.R. 1997. Historical analysis of genetic variation reveals low effective population size in a northern pike (*Esox lucius*) population. *Genetics*, **147**, 1249–1258.

Mitton, J. B. 1997. *Selection in Natural Populations*. Oxford University Press, Oxford.

Nielsen, E.E., Hansen, M. M. & Loeschke, V. 1997. Analysis of microsatellite DNA from old scale samples of Atlantic salmon *Salmo salar*: a comparison of genetic composition over 60 years. *Molecular Ecology*, **6**, 487–492.

Nielsen, E.E., Hansen, M.M. & Loeschcke, V. 1999. Analysis of DNA from old scale samples: technical aspects, applications and perspectives for conservation. *Hereditas*, **130**, 265–276.

Nielsen, E.E., Hansen, M. M. & Meldrup, D. 2006. Evidence of microsatellite hitch-hiking selection in Atlantic cod (*Gadus morhua* L.): implications for inferring population structure in nonmodel organisms. *Molecular Ecology*, **15**, 3219–3229.

Nunnery, L. & Elam, D. R. 1994. Estimating the effective population size of conserved populations. *Conservation Biology*, **8**, 175–184.

Palsbøll, P.J. 1999. Genetic tagging: contemporary molecular ecology. *Biological Journal of the Linnean Society*, **68**, 3–22.

Pogson, G.H. & Mesa, K. A. 2004. Positive Darwinian selection at the pantophysin (*Pan I*) locus in marine gadid fishes. *Molecular Biology and Evolution*, **21**, 65–75.

Powers, D.A. & Schulte, P. 1998. Evolutionary adaptations of gene structure and expression in natural populations in relation to a changing environment: a multidisiplinary approach to address the million-year saga of a small fish. *Journal of Experimental Zoology*, **282**, 71–94.

Powers, D.A., Lauerman, T., Crawford, D. & DiMichele, L. 1991. Genetic mechanisms for adapting to a changing environment. *Annual Review of Genetics*, **25**, 629–659.

Turner, T.F., Wares, J. P. & Gold, J. R. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics*, **162**, 1329–1339.

Vrijenhoek, R.C. 1998. Conservation genetics of freshwater fishes. *Journal of Fish Biology*, **53** (Supplement A), 394–412.

Wang, J. 2001. A pseudo-likelihood method for estimating effective population size from temporally spaced samples. *Genetical Research*, **78**, 243–257.

Waples, R.S. 1991. Genetic methods for estimating the effective population size of cetacean populations, pp. 279–300, In: *Report of the International Whaling Commission*, Special Issue 13, A. R. Hoezel, (ed.), Cambridge, UK: International Whaling Commission.

ANNEX 2

1. COMPUTER PROGRAMMES FOR GENETIC ANALYSIS

The development of new technologies to detect molecular variation and automation of several steps in these laboratory analyses have led to the production of large amounts of genetic data. The availability of these data has stimulated the development of new statistics and computer programmes, which provide insights from data not previously possible (Zhang and Hewitt, 2003). The use of computers provides the opportunity to test hypothesis with bootstrapping and coalescent simulations, in addition to standard parametric, non parametric and exact tests.

Most, if not all, the computer programmes available for genetic analysis can be downloaded from the web sites of academic institutions without charge. Several groups of programmes are available. Multipurpose progammes are generally used to examine genotype or sequence data and to describe gene diversities within and among samples. These programs include ARLEQUIN (Excoffier *et al.*, 2005), DnaSP (Rozas *et al.*, 2003), FSTAT (Goudet, 1995); GENEPOP (Raymond and Rousset, 1995), GENETIX (in French only; Belkhir *et al.*, 2000), and MEGA (Kumar *et al.*, 2004), among others. The basic facilities offered in these programs are reviewed in Excoffier and Heckel (2006).

In addition to these basic programmes, many other programmes incorporate algorithms that attempt to assign individuals to particular populations. These include BAPS (Corander *et al.*, 2004), GeneClass (Piry *et al.*, 2004) and GeneLand (Guillot *et al.*, 2005), STRUCTURE (Pritchard *et al.*, 2000), among others. Also in this group are programs written for fishery management to estimate the origins of individuals in areas of stock mixing (BAYES, Pella and Masuda, 2001; WHICHRUN, Banks and Eichert, 2000). Hansen *et al.,* (2001) reviews the utilities of these and other mixed-stock computer programmes for microsatellite DNA markers.

Another group includes specialized programme performing a variety of tests of past demographies (ARLEQUIN; DnaSP; BATWING, Wilson *et al.*, 2003, among others). Algorithms in these programmes search for evidence of population growth or bottlenecks in population size. Molecular markers are often assumed to be neutral to the effects of selection. This assumption can be tested by gene- or haplotype-frequency districtuions (MEGA; FDIST2, Beaumont and Nichols, 1996). Migration is also an important factor shaping the genetic population structure of a species. Estimates of migration between populations (gene flow) are often used in devising conservation and management strategies (COLONISE, Foll and Gaggiotti, 2005; MIGRATE, Beerli, 2006, among others).

Inferring phylogenetic relationships among species can also be important to the management of a multispecies fishery. Phylogenetic trees were first constructed from genetic distances estimated from gene frequencies. The widespread availability of DNA sequences, however, allow more sophisticated approaches to tree construction (see Felsenstein, 2003). These methods include parsimony, maximum likelihood and Baysian algorithms (Nei & Kumar, 2000). Many of the general programmes listed above provide options to use some of these methods. However, several specialized programmes can be downloaded from the internet. Some of the more commonly used programmes include PHYLIP (J. Felsenstein: http://evolution.gs.washington.edu/phylip.html), PAUP* (D. Swofford: Sinauer Associates), MacClade (W. Maddison: http://phylogeny.arizone.edu/macclade/macclade.html) and DAMBE (X. Xia: http://aix1.uottawa.ca/~xxia/software/software.htm), among others.

Many situations encountered by fishery biologists do not easily fit the assumptions of some biological and statistical models, which are often simplified for easier use. For example, equal population sizes and equal migration rates between populations are assumed in several genetic population models, but in nature are seldom equal to one

another. A refinement in the use of statistical models to interpret genetic data is the use of simulation programs to model particular situations (e.g. SIMCOAL, Excoffier *et al.*, 2000; EASYPOP, Balloux, 2001; METASIM, Strand, 2002; MESQUITE, Madison and Madison, 2004; among others). Future approaches to DNA data analysis will use maximum likelihood and Bayesian methods tailored to particular situations (e.g. Whitlock and McCauley, 1999; Pritchard *et al.*, 2003; Dawson and Belkhir, 2001; Wilson and Rannala, 2003).

These computer programmes should be used cautiously. The use of some programmes is complicated by the different input formats. This requires reformatting of datasets manually or with programmes designed for data conversion (see Excoffier and Hackel, 2006). Another caution is that different programmes may produced different values of the same statistics for the same set of data. This is likely due to differences in how the programmes are written. Lastly, these programmes offer numerous options for analyzing data and produce a wealth of statistical output. A researcher should always take the time to read the background literature on how a statistic is calculated and its interpretation. User documentation of some programmes (e.g. ARLEQUIN) presents some explanations. However, the successful application of many programmes requires that the user read the original literature.

2. REFERENCES

Balloux, F. 2001. EASYPOP (version 1.7): a computer program for population genetics simulations. *Journal of Heredity*, **92**, 301–302.

Banks, M. A. & Eichert, W. 2000. WHICHRUN (version 3.2): a comuter program for population assignment of individuals based on multilocus genotype data. *Journal of Heredity*, **91**, 87–89.

Beaumont, M.A. & Nichols, R. A. 1996. Evaluating loci for use in the genetic analysis of population structure. *Proceedings of the Royal Society, London B*, **263**, 1619–1626.

Belkhir, K., Borsa, P., Raufaste, N., Chikhi, L. & Bonhomme, F. 2000. GENETIX version 4.02, logiciel sous WINDOWS™ pour la génétique des populations. Laboratoire Génome et Populations, Université Montpellier 2, Montpellier.

Corander, Waldmann, P., Marttinen, P. & Sillanpaa, M. M. 2004. BAPS 2: enhanced possibilities for the analysis of genetic population structure. *Bioinformatics*, **20**, 2363–2369.

Dawson, K. & Belkhir, K. 2001. A Bayesian approach to the identification of panmictic populations and the assignment of individuals. *Genetical Research (Cambridge)*, **78**, 59–77.

Excoffier, L. & Heckel, G. 2006. Computer programs for population genetic data analysis: a survival guide. *Nature Reviews Genetics*, online doi:10.1038/nrg1904.

Excoffier, L., Novembre, J. & Schneider, S. 2000. SIMCOAL: a general coalescent program for the simulation of molecular data in interconnected populations with arbitrary demography. *Journal of Heredity*, **91**, 506–509.

Excoffier, L., Laval, G. & Schneider, S. 2005. Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

Felsenstein, J. 2003. *Inferring phylogenies*. Sunderland, MA: Sinauer Associates.

Gillot, G., Mortier, F. & Estoup, A. 2005. Geneland: a computer package for landscape genetics. *Molecular Ecology Notes*, **5**, 712–715.

Goudet, J. 1995. FSTAT version 1.2: a computer program to calculate *F*-statistics. *Journal of Heredity*, **86**, 485–486.

Hansen, M.M., Kenchington, E. & Nielsen, E.E. 2001. Assigning individual fish to populations using microsatellite DNA markers. *Fish and Fisheries*, **2**, 93–112.

Kumar, S., Tamura, K. & Nei, M. 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. *Briefings in Bioinformatics*, **5**, 150–163.

Maddison, W.P. & Maddison, D.R. 2004. *Mesquite: A Modular System for Evolutionary Analysis*. Version 1.01. http://mesquiteproject.org

Pella, J. & Masuda, M. 2001. Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin*, **99**, 151–167.

Pritchard, J.K., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Piry, S., Alapetite, A., Cornuet, J.-M., Paetkau, D., Baudouin, L. & Estoup, A. 2004. GeneClass2: A software for genetic assignment and first-generation migrant detection. *Journal of Heredity*, **95**, 536–539.

Raymond, M. & Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumnicism. *Journal of Heredity*, **86**, 248–249.

Rozas, J., Sanchez-Del Barrio, J.C., Messeguer, X. & Rozas, R. 2003. DnaSP, DNA polymorphisms analyses by the coalescent and other methods. *Bioinformatics*, **19**, 2496–2497.

Strand, A.E. 2002. METASIM 1.0: an individual-based environment for simulating population genetics of complex population dynamics. *Molecular Ecology Notes*, **2**, 373–376.

Whitlock, M.C. & McCauley, D.E. 1999. Indirect measures of gene flow and migration: F_{ST} not equal 1/(4Nm+1). *Heredity*, **82**, 117–125.

Wilson, G.A. & Rannala, B. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, **163**, 1177–1191.

Wilson, I.J., Weale, M.E. & Balding, D.J. 2003. Inferences from DNA data: population histories, evolutionary processes and forensic match probabilities. *Journal of the Royal Statistical Society* A, **166**, 155–188.

Zhang, D.-E. & Hewitt, G.M. 2003. Nuclear DNA analysis in genetic studies of populations: practice, problems and prospects. *Molecular Ecology*, **12**, 563–584.

ANNEX 3

USE OF GENETIC DATA IN FISHERY MANAGEMENT

1. DEFINING POPULATIONS FOR MANAGEMENT

One problematic issue has been a lack of consensus on the definition of a population, even though the 'population' is a fundamental unit in ecology, evolution and fishery management. In fishery management, few definitions of a population are operational enough to be used objectively by researchers or policy makers (Waples and Gaggiotti, 2006). Yet, how populations are connected to one another through migration has important consequences for devising management plans. Fishery managers usually agree that management units should coincide with natural population partitions, but how natural populations are defined is a subject of continuing debate (Ryder, 1986; Moritz, 1994; Waples and Gaggiotti, 2006; Schaefer, 2006; Palsbøll *et al.*, 2006).

Two contrasting, but overlapping, views appear in conservation biology and fishery management. In one perspective, the conservation of populations representing major evolutionary lineages is thought to be important. Beyond the conservation of evolutionary legacy is the attempt to maintain the population processes that produce deep levels of diversity in a species (Moritz, 2002). Genetic variability has to be conserved to allow a species to adapt to environmental changes taking place on decadal and millennial time scales. On the other hand, the needs of fishery management are short term and require a greater resolution of population structure on smaller geographical and temporal scales. To this end, traits responding rapidly to environmental variability such as morphology, meristic counts and life history patterns have frequently been used most to define populations and stocks.

A major problem arises in the use of genetic methods for conservation and fisheries resource management, because evolutionary and ecological definitions of a population are mistakenly used interchangeably (Figure 4). Both kinds of populations are defined by the degree of connectivity among populations through the exchange of migrants (population structure). However, far less migration is required to maintain genetic cohesiveness among populations on evolutionary time scales than is required to produce demographic homogeneity among populations. The evolutionary population concept predominates in conservation biology, in which a major concern is the protection of genetic lineages, which allows a species to adapt to environmental changes. In fishery management, an ecological population may not be genetically distinctive, but may still show life history differences or geographical isolation requiring separate management.

Ecological definitions of a population, however, focus on interactions between individuals that influence the demographic characteristics of a population, including competition, age structure and birth and death rates. These kinds of variables are used to define stocks for the biomass assessments used to set harvest limits. From this ecological viewpoint, demographic independence between populations can still persist with much large amounts of immigration (Figure 4). A limited amount of data indicates that demographic independence between populations occurs when the proportion of immigrants (m) falls below 10% (Hastings, 1993). The key variable for management considerations, especially of marine species, is the proportion of migrants, m. However, models used to interpret genetic data yield only estimates of Nm, the number of migrants between populations. Another difficulty is that N represents population size integrated over recent evolutionary time and not necessarily the size of a contemporary population. Estimates of census size are also not useful for estimating N, because effective population sizes may be an order of magnitude smaller than census size (see below). Future research will focus on the development of simulation and modelling tools that integrate ecological and genetic data for particular situations.

2. MODELS OF GENETIC POPULATION STRUCTURE

The origins of genetic population structure in freshwater and riverine organisms are fairly well known. Both demographic and genetic populations are usually delimited by lake shorelines and watercourses that represent strong physical barriers to migration. Unexpected genetic similarities between populations can usually be explained by historical events, such as headwater captures, altered river drainages or gene flow in proglacial lakes after the last ice age. Some of the classic models of population structure [e.g. island model of migration (Wright 1940)] have been used effectively to estimate contemporary levels of migration in many species from molecular markers (Neigel, 1997). Populations of marine fishes, on the other hand, are not generally bounded by strong barriers to migration. Nevertheless, the genetic structures of marine populations can be influenced by spawning migrations (Ruzzante *et al.*, 2006), sea surface temperature gradients (Beare *et al.*, 1995; Attrill and Power, 2002) and currents and ocean frontal systems (Rocha-Olivares and Vetter, 1999; Shaw *et al.*, 2004).

Two contrasting models of population structure have been posed for marine fishes. Under a local, self-sustaining model (vagrant-member hypothesis, Sinclair, 1988), populations are adapted to local environmental settings and persist only when conditions allow uninterrupted cycles of spawning, growth and reproduction. The magnitude of gene differences between populations depends on effective population size, which influences genetic drift and gene flow, which tends to reduce population differences. An extension of this model incorporates the ephemeral nature of some populations by recognizing that regional extinctions and colonization occur in marine populations (Smith and Jamieson, 1986; McQuinn, 1997). This model predicts that subpopulation extinctions and recolonizations should lead to a mosaic pattern of genetic diversity and gene frequency heterogeneity.

Under the 'basin model' (MacCall, 1990), the most favourable habitats lie toward the centre of a species' geographical range. During ocean-climate instability, subpopulations at the edges of the species' range disappear by contracting toward the central favourable basin. Abundances in the centre of the range remain constant, even though the species as a whole is declining. This model is also echoed in the classical biogeographical models of Mayr (1970), who found that environmental factors were most important in regulating abundances at the periphery of a species' range. When these species represent 'straddling stocks', international cooperation is especially important in setting harvest limits. Subpopulations following this model might show gradients in gene diversity with the highest diversities in the centre of the range, where populations have been most stable. Considerations of these two models are important to formulating management policies and planning locations of marine protected areas.

Genetic data generally fail to show the high degree of isolation in open-ocean marine fishes predicted by Sinclair (1988). Genetic estimates of gene flow are high in most marine species (Table 1), implying the movements of tens and hundreds of individuals between subpopulations. Mitochondrial DNA data appear to support the basin model for California anchovy (Lecomte *et al.*, 2004), but support a mosaic model for European anchovy (Grant, 2005; Magoulas *et al.*, 2006). However, finer-scale differences have been detected among populations that are not isolated by obvious physical or hydrographic barriers (Hedgecock *et al.*, 1994; Ruzzante *et al.*, 1999). This chaotic variability is likely due to large reproductive variances among families (Hedgecock, 1994), rather than to isolation or adaptations to particular open-water habitats. The instability of marine waters on annual, decadal and millennial time scales likely prevents adaptations to specific areas. On a decadal scale, anchovy populations, for example, respond rapidly to small climate changes with range contractions and expansions (e.g. Cushing, 1982; Beare *et al.*, 2004).

3. LOSS OF GENETIC DIVERSITY

A major concern in conservation biology is the maintenance of genetic diversity (measured by average heterozygosity). Values of heterozygosity, however, are affected most by the frequencies of abundant genes in the general range of 0.10-0.90. Genes at low frequencies contribute little to heterozygosity. Ryman *et al.* (1994, 1995) pointed out that the store of gene variability represented by low-frequency genes may be important in adapting to changing environments. Large populations have a greater capacity for retaining low-frequency genes than small populations, but the relative loss of rare genes during a population crash is much greater in large populations. For example, consider two populations of sizes 10 000 and 100 000 000, which are at mutation drift equilibrium, but which are reduced to 1% of their original size (1 000 and 1 000 000). The loss of heterozygosity is negligible in both populations, but the small population retains 98% of the original gene number, while the large population retains only 1% of its genes.

4. REFERENCES

Attrill, M. J. & Power, M. 2002. Climatic influence on a marine fish assemblage. *Nature*, **417**, 275–278.

Beare, D., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E. & Reid, D. 2004. An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology*, **10**, 1209.

Cushing, D.H. 1982. *Climate and Fisheries*. Academic Press, London.

Grant, W.S. 2005. A second look at mitochondrial DNA variability in European anchovy (*Engraulis encrasicolus*): assessing models of population structure and the Black Sea isolation hypothesis. *Genetica*, **125**, 293–309.

Hastings, A. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology*, **74**, 1362–1372.

Hedgecock, D., Hutchinson, E.S., Li, G., Sly, F.L. & Nelson, K. 1994. The central stock of northern anchovy is not a randomly mating population. *California Cooperative Oceanic Fisheries Investigation Reports*, **35**, 121–136.

Lecomte, F., Grant, W.S., Dodson, J.J., Rodriguiez-Sanchez, R. & Bowen, B.W. 2004. Living with uncertainty: genetic imprints of climate shifts in east Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). *Molecular Ecology*, **13**, 2169–2182.

MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. Sea Grant, University of Washington Press, Seattle, WA.

Magoulas, A., Castilho, R., Caetano, S., Marcato, S. & Patarnello, T. 2006. Mitochondrial DNA reveals a mosaic pattern of phylogeographical structure in Atlantic and Mediterranean populations of anchovy (*Engraulis encrasicolus*). *Molecular Phylogenetics and Evolution*, **39**, 734-746.

Mayr, E. 1970. *Populations, Species and Evolution*. Harvard University Press, Cambridge, MA.

McQuinn, I. 1997. Metapopulations in Atlantic herring. *Reviews in Fish Biology and Fisheries*, **7**, 297–329.

Moritz, C. 1994. Defining evolutionarily-significant-units for conservation. *Trends in Ecology and Evolution*, **9**, 373–375.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, **51**, 238–254.

Neigel, J.E. 1977. A comparison of alternative strategies for estimating gene flow from genetic markers. *Annual Review of Ecology and Systematics*, **28**, 105–128.

Palsbøll, P.J., Bérube, M. & Allendorf, F.W. 2006. Biologically and statistically sound delineation of management units. *Trends in Ecology and Evolution*, In press.

Rocha-Olivares, A. & Vetter, R.D. 1999. Effects of oceanographic circulation on the gene flow, genetic structure, and phylogeography of the rosethorn rockfish (*Sebastes helvomaculatus*). *Canadian Journal of Fishery and Aquatic Sciences*, **56**, 803–813.

Ruzzante, D.E., Taggart, C.T. & Cook, D. 1999. A review of the evidence for genetic structure in cod (*Gadus morhua*) populations in the NW Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St. Lawrence. *Fisheries Research*, **43**, 79–97.

Ruzzante, D.E., Mariani, S., Bekkevold, D., André, C., Mosegaard, H., Clausen, L.A. W., Dahlgren, T. G., Hutchinson, W. F., Hatfield, E. M. C., Torstensen, E., Brigham, J., Simmonds, E.J., Laikre, L., Larsson, L.C., Stet, R.J.M., Ryman, N. & Carvalho, G.R. 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proceedings of the Royal Society, London* B, **273**, 1459–1464.

Ryder, O.A. 1986. Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution*, **1**, 9–10.

Ryman, N., Utter, F. & Laikre, L. 1995. Protection of intraspecific biodiversity of exploited fishes. *Reviews in Fish Biology and Fisheries*, **5**, 417–446.

Ryman, N., Utter, F. & Laikre, L. 1994. Protection of aquatic biodiversity. In: *The State of the World's Fisheries Resources: Proceedings of the World Fisheries Congress plenary sessions,* Voigtlander, C. W. (ed.), pp. 92–115. Oxford & IBH Publishing, New Dehli.

Schaefer, J. A. 2006. Towards maturation of the population concept. *Oikos*, **112**, 236–240.

Shaw, P.W., Arkhipkin, A.I. & Al-Khairulla, H. 2004. Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology*, **13**, 3293–3303.

Sinclair, M. 1988. *Marine populations: an essay on population regulation and speciation*. Sea Grant, University of Washington Press, Seattle, WA.

Smith, P.J. & Jamieson, A. 1986. Stock discreteness in herrings: a conceptual revolution. *Fisheries Research*, **4**, 223–234.

Waples, R.S. & Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, **15**, 1419–1439.

Wright, S. 1940. Breeding structure of populations in relation to speciation. *American Naturalist*, **74**, 232–248.

Issues, status and trends in deep-sea fishery genetic resources

Peter J. Smith
National Institute of Water and Atmospheric Research (NIWA), New Zealand

1. SUMMARY

The deep sea is the largest habitat on earth, covering around 53% of the sea's surface, from the poles to the tropics. The deep-sea region starts at the shelf break at the continental margins, around 200 m, and extends down the continental slope and the continental rise to the abyssal plain at around 6 000 m, and the deep trenches. Deepwater fisheries occur on the continental slopes and on seamounts and exploit resources down to ~2 000 m. The continental slopes cover about 8.8% of the world's surface, an area greater than all the continental shelves and shallow seas, and include the most variable habitats in the deep-sea with canyons, ridges, seamounts, hydrothermal vents, and cold seeps.

Definitions of deepwater fisheries vary geographically, but generally occur at depths greater than 400-500 m; trawl fisheries for orange roughy (*Hoplostethus atlanticus*) and oreos (*Pseudocyttus maculatus, Allocyttus niger* and *Neocyttus rhomboidalis*) occur between 600-1 800 m, while long-line fisheries for toothfish (*Dissostichus* spp.) in the Southern Ocean operate down to ~1 800 m. Landings of deepwater fishes have risen from <0.5 m tonnes a year in the 1960s to >3 m tonnes by the late 1990s, with more than half of the annual catch taken from the Atlantic Ocean, but account for only ~5% of the total fish catch. The landing statistics are likely to be under estimates due to illegal, unreported and unregulated (IUU) fishing operations, and discards of bycatch species. Several deepwater fisheries have been characterized by "boom and bust" cycles. Catches of the armourhead (Pseudopentaceros wheeleri) on the North Hawaiian Ridge were estimated to have exceeded 150 000 tonnes a year during the late 1960s to 1970s where today no fishery exists. During the late 1990s a new fishery developed for orange roughy and alfonsino (*Beryx* spp.) in the South Indian Ocean with annual landings rising from <1 000 tonnes, peaking at 39 400 tonnes in 2000, and declining to <5 000 tonnes by 2002. In other regions orange roughy fisheries have been closed to commercial fishing, following a cycle of rapidly rising and declining catches. High catches of orange roughy in some areas have been maintained, at least temporarily, through local scale serial depletion as neighbouring seamounts and hills are fished down.

Deep-sea fishes include a large number of diverse species. Not all deepwater fishes are well described and molecular tools are being used to resolve taxonomic questions of species identity. Species exploited by deepwater fisheries include both shelf species, that extend down the continental slopes, and species restricted to depths >400-500 m. Most species are caught by trawls on seamounts and ridges, although line fishing and gillnets, and traps for invertebrates are used; toothfish (*Dissostichus* spp.) in the Southern Ocean are taken by trawl and long-line fisheries. An artisanal long-line fishery has existed for the black scabbard fish Aphanopus carbo for more than a century off Maderia, but most deepwater fisheries are relatively new and capital-intensive. A few small-scale

deepwater fisheries occur where the shelf is narrow and the fishery areas are accessible by small vessels using drop lines. The sustainable yields from such fisheries maybe only a few hundred tonnes a year, but are important for small island states.

Deepwater fisheries generally target teleosts, with sharks taken as bycatch; only a few target invertebrates. In the North Atlantic deepwater fisheries, 22 species of teleosts 10 species of shark and two invertebrates (the red crab *Chaecon affinis* and the shrimp *Aristeomorpha foliacea)* make up the most important commercial species. Major species associated with seamounts include orange roughy, oreos, alfonsinos, and the roundnose greanadier (*Coryphaenoides rupestris*). A high degree of endemism has been reported for seamount invertebrates and fishes, but many of the targeted fish species have extensive ocean-wide and even cosmopolitan distributions.

As with coastal and shelf fisheries, conserving genetic diversity at the population, species, and ecosystem levels should be major goals for managing genetic resources in wild populations. Genetic issues identified for shelf species are likely to be magnified for deepwater species. Many slope and seamount species exhibit traits such as high longevity, slow growth rate, and late maturity, that make them more vulnerable to exploitation than most shelf species.

Marine fish tend to have higher levels of intraspecific genetic diversity than anadromous species, which in turn are more variable than freshwater species; a trend relating to larger evolutionary effective population sizes in marine fishes. Low levels of genetic diversity have been reported in the Antarctic toothfish *Dissostichus mawsoni*. Marine fishes show less spatial genetic differentiation than anadromous and freshwater species, due to the fewer barriers to gene flow in the marine environment. A negative relationship reported between genetic differentiation and dispersal potential in coastal fishes appears to apply to deepwater fishes. Recent developments with new molecular tools, coupled with new analytical approaches, have revealed finer scale population structure within ocean basins for the Patagonian toothfish *D. eleginoides*, but for many deepwater fishes there is little or no information on genetic diversity within and among regions, and the scale of appropriate management units remain uncertain. Local declines among orange roughy fisheries on neighbouring seamounts suggest that they maybe independent units in the ecological time frame of fisheries management, in the absence of detectable genetic differentiation at small spatial scales.

Directional selection, through size-selective harvesting, has been implicated in changes in life history traits in heavily exploited stocks of shelf species, but has not been demonstrated in deepwater fishes, in part due to the limited time series of appropriate data. The genetic composition of a population can also change over generations due to random events. Changes due to genetic drift are most likely in small populations and are expected to be weak in marine fishes with large populations ($N > 10^7$). However 'sweepstake' events, due to high larval mortalities, can result in a small effective population size (N_e) several orders of magnitude smaller than the census population (N). Low N_e / N ratios have been demonstrated in several shelf species and are equally likely to occur in some deepwater species, and potentially lead to loss of genetic diversity in collapsed stocks

There is a general perception that the risk of extinction is low for commercially important marine fishes due to their large population sizes and wide geographical distributions. Only a few marine fishes have been listed as endangered and fewer appear to be close to extinction. Several traits of deepwater species (long life span, large body size, low natural mortality, and late sexual maturity) make them more vulnerable to extinction than shelf species, in particular those species that aggregate on seamounts. Deepwater fisheries have only been operating in the Northwest Atlantic Ocean since the 1970s, but already several species appear to meet the criteria of being critically endangered. Non-target species, that include teleosts endemic to

seamount complexes and elasmobranchs with low reproductive potentials, are also likely to be endangered.

Currently discarded fish waste from processing is used for low value products such as fish-oils, meals, pet foods, and silage. Bioactive compounds may be extracted from left-over fish-frames, internal organs, and invertebrate bycatch species for biotechnological and pharmaceutical applications, offering the opportunity to add value to fisheries. Some compounds derived from fish waste have been identified as potential nutraceuticals. Marine invertebrates that occur around hydrothermal vents may provide enzymes and biochemicals for the biotechnology industries and become target species in the future, raising further issues over exploitation of specialised deepwater habitats.

Genetic resources at the species and ecosystem levels are equivalent to ecological resources for which the management issues are well documented in the fisheries literature. The rapid development, and in some cases rapid depletion, of deepwater fisheries is of major concern to fisheries managers around the world, and has been identified repeatedly at local, regional, and international meetings. ICES have recognised that most exploited deepwater fishes are harvested unsustainably and radical reductions in fleets, in particular trawlers, are required to reduce effort and to conserve vulnerable habitats.

NGOs have expressed concern over the mortality of macro invertebrates taken as bycatch in deepwater trawl fisheries on seamounts, and for seabirds taken in toothfish trawl and long-line fisheries, although mitigation measures have been put in place to reduce the bird catch. The fragile and ancient coral "forests" found on seamounts that are amenable to trawling are quickly reduced to rubble by heavy trawl gear. Improvements to trawl gear and monitoring may allow the operation of deepwater pelagic trawls that avoid contact with bottom features. In the short term, one mitigation measure to protect vulnerable and unique habitats is to close selected areas to bottom trawling.

Many deepwater fisheries occur in high-seas areas compounding the problem of management and regulation. IUU fishing has been widespread in high seas fisheries. Increased surveillance and the introduction of a catch documentation scheme have reduced IUU fishing for toothfish within and outside the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Area in the Southern Ocean. Removal of fisheries subsidies should relieve pressure on deepwater stocks to some extent, but will need to be considered in parallel with other management tools. Regional Fishery Management Organisations (RFMOs) are being developed that cover high seas fisheries, and urgent action is required at the global level, to avoid shifting the deepwater fishing problem from one region to another. The inertia in developing and implementing international fisheries legislation, has lead to NGOs calling for the designation of large scale protected areas, and for a moratorium on bottom trawling. Recent initiatives have seen the establishment of a high seas benthic protected area in the Southern Indian Ocean, with further proposals for a network of large Marine Protected Areas or Benthic Protected Areas in waters around Australia and New Zealand, and in the Southern Ocean.

2. INTRODUCTION

The impacts of large scale industrial fishing on coastal ecosystems are well known. In some shelf and open ocean fisheries the community biomass has been reduced by up to 80 per cent within 15 years of exploitation (Myers and Worm, 2003). For the recorded species of coastal and oceanic sharks in the Northwest Atlantic Ocean fisheries, all except one have shown declines in relative abundance of >50% since the mid 1980s (Baum *et al*., 2003). Extinctions of marine species were thought to be rare events, but two species of skate are near extinction in the North Atlantic (Brander, 1981; Casey and Myers, 1998); in coastal fisheries the Pacific abalone *Haliotis sorenseni* is in a

perilous condition (Davis *et al.,* 1998), and some populations of giant clams, *Tridacna,* are locally extinct (Awaya and Lee, 2005).

Compared to the rest of the planet, much of the deepsea appears to be relatively unimpacted by human activities. International regulations prohibit the dumping of structures and radioactive waste in the deep-sea; and oil and gas extraction has been limited (Glover, AGS, C R 2003). However, the expansion of commercial fisheries into deep waters (>400 m) especially those in high seas outside coastal jurisdictions has been a major development in world fisheries in recent years (Watson, R and Morato, T 2004). Landings of deeper water species have increased, driven by technological developments, that enable fishers to target localised feeding and spawning aggregations of fishes in deepwater, and by catch-limits imposed in coastal fisheries. The biological issues of overfishing deepwater species are well documented and there is general agreement that many deepwater fishes are exploited beyond sustainable levels (Koslow, *et al.*, 2000; Haedrich *et al*., 2001; Watson and Morato, 2004; FAO, 2005b; Devine, *et al.*, 2006; Morato *et al.,* 2006a and 2006b). Urgent action is required at the global level to reduce effort in deepwater fisheries and to protect fragile ecosystems from the impact of bottom trawling.

The impacts of fishing on deep-sea genetic resources are likely to be similar to those observed in shelf fisheries at the population, species, and ecosystem levels. In general, the effects of fishing on intra-specific genetic diversity are more difficult to detect than ecological impacts (Kenchington, E. 2003), but include loss of diversity through size-selective fishing favouring early maturity and slow growth (Dieckmann *et al.,* 2006 in press), and through reduction in numbers of breeding fish (Hauser *et al.*, 2002). Patterns of genetic diversity and population structure are not well known for most deepwater fishes. The life history traits of some deepwater fishes, in particular high longevity, slow growth, and late maturity, make them more vulnerable to fishing than coastal species (Morato *et al.*, 2006a and 2006b), such that they may require different management systems (Clarke, M. *et al*. 2003). Some deepwater fishes already qualify as endangered species following <20 years of exploitation (Devine *et al.*, 2006).

3. THE DEEP-SEA AND DEEPWATER FISHERIES

The deep-sea is the largest habitat on earth, covering around 53% of the sea's surface from the poles to the tropics. The deep-sea region is generally recognised as starting at the shelf break at the continental margins (around 200 m) and extending down the continental slopes and the continental rises to the abyssal plains at around 6 000 m, to include the trenches. Much of the continental slope and the abyssal plain regions are covered by soft mud substrates, but the slopes include the most variable habitats in the deep-sea with canyons, ridges, seamounts, hydrothermal vents, and cold seeps. Four depth zones are recognised in the deep-sea: mesopelagic (200-1 000 m); bathypelagic (1 000-4 000m); abyssopelagic (4 000-6 000 m); and the hadalpelagic below 6000 m depth, in the deep ocean trenches.

The deep-sea is a dark, cold environment. There is no primary productivity via photosynthesis; even at depths of 150m light levels are just 1% of those at the surface and are insufficient to support photosynthesis. Concentrations of organic material decrease exponentially with depth, but the deep-sea is fuelled by a rain of sinking dead phytoplankton and nekton, and by many species that perform extensive vertical migrations, transferring surface production into deeper waters. Specialist habitats are maintained by organic material derived from sinking wood and from whale carcases and have lead to the evolution of unique fauna (Distel *et al*., 2000) which along with fauna on hydrothermal vents and cold seeps are dependent on chemoautotrophic primary production (VanDover, 2000).

Limited resources in shelf fisheries lead to an expansion of fishing effort into deeper waters during the 1980s. Some shelf fisheries expanded into deeper waters on the continental slope as technologies developed, e.g. the North Atlantic fishery for Greenland halibut *Reinharditus hippoglossoides*. Other deepwater fisheries are relatively new and target species that are restricted to deepwater, e.g. the orange roughy Hoplostethus atlanticus found in the Atlantic, Indian and Pacific Oceans between 600-1 600 m.

Deepwater fisheries occur on the continental slope and on seamounts (see Box 1) and exploit resources down to ~2 000 m. The continental slopes cover about 8.8% of the world's surface, an area greater than all the continental shelf and shallow seas (~7.5% of the world's surface). Definitions of deepwater fisheries vary geographically; ICES uses the term deepwater fisheries for those in depths >400m; others define deepwater fisheries as those occurring deeper than ~500 m (Koslow *et al.,* 2000). Around New Zealand deepwater trawl fisheries occur between 750-1 500 m, while middle depths fisheries are recognised between 200-750 m.

Most deepwater species are caught by trawls on seamounts and ridges, although line fishing and gillnets are used, as are traps for invertebrates; toothfish *Dissostichus* spp. in the Southern Ocean are taken by trawl and long-line fisheries. An artisanal long-line fishery has existed for the black scabbard fish Aphanopus carbo for more than a century off Maderia, but most deepwater fisheries are relatively new, technology-dependent and capital-intensive. The Spanish deepwater fisheries are opportunistic with target species changing according to availability of other commercial species (Pineiro *et al*., 2001). A few small-scale deepwater fisheries occur where the shelf is narrow and the fishery areas are accessible by small vessels using drop lines. The sustainable yields from such fisheries maybe only a few hundred tonnes a year, but are important for small island states.

Several deepwater fisheries have been characterized by "boom and bust" cycles. Catches of the armourhead *Pseudopentaceros wheeleri* on the North Hawaiian Ridge were estimated to have exceeded 150 000 t a year during the late 1960s to 1970s (Boehlert, 1986; Boehlert and Sasaki, 1988; Somerton and Kikkawa, 1992): today no fishery exists. Catches of the Pacific Ocean perch (*Sebastes alutus*) peaked at around 450 000 tonnes in the mid 1960s and have since fluctuated at 5-30 000 tonnes a year (Ianelli and Zimmerman, 1998). During the late 1990s a new fishery developed for orange roughy and alfonsino (*Beryx* spp.) on the Southwest Indian Ridge with annual landings rising from <1 000 tonnes, peaking at 39 400 tonnes in 2000, and declining to <5 000 tonnes by 2002 (FAO, 2002). In other regions orange roughy fisheries have been closed to commercial fishing, following a cycle of rapidly rising and declining catches. High catches of orange roughy in some areas are maintained, at least temporarily, through local scale serial depletion as neighbouring seamounts and hills are fished down.

The top fish species by landings (>1 m tonnes a year) that account for 30% of the total world capture fisheries are shelf and pelagic species, and of these 7 are fully exploited or overexploited (FAO 2005c). Furthermore, the top 71 species of fish and invertebrates, which account for ~50% of capture production by tonnage are shelf and pelagic species, with only two middle depths (300-700 m) species , the grenadiers, *Macruronus novaezelandiae* and *M. magellanicus* (both >200 000 tonnes in 2003). China's landings of deepwater fishes are dominated by the largehead hairtail *Trichiurus lepturus* (which accounted for 1.5% of the total world marine fish landings in 2002), and although sometimes listed as a deepwater species, is more correctly a shelf species found in depths <400 m.

Landings of deepwater fishes have risen from <0.5 m tonnes a year in the 1960s to >3 m tonnes by the late 1990s, with more than half of the annual catch taken from the

BOX 1
Seamounts

Seamounts, steep sided undersea mountains, are widely distributed in the world's oceans and usually associated with volcanic activity (Rogers, 1994). Some definitions describe seamounts as features with an elevation greater than 1 000 m, but in practice "seamount" is applied to knolls (elevation 500-1 000 m) and hills (elevation <500 m) that contrast with the surrounding seafloor. Seamounts often occur in clusters along ridges leading to island groups or chains that are physically isolated from other island chains. Seamounts (and oceanic islands) enhance productivity, due to Taylor columns and upwelling of nutrient rich water (Rogers, 1994), and provide a unique deep-sea environment for fishes and invertebrates that are not found in the open ocean (Boehlert and Mundy, 1993; Koslow *et al*., 2000; Richer-de-Forges *et al*., 2000). Several teleosts spawn above seamounts where they form dense seasonal aggregations (Koslow *et al.*, 2000).

A high degree of endemism has been reported for benthic invertebrates (~30%) and fishes (12%) on seamounts (Wilson and Kaufman, 1987; Richer-de-Forges *et al.,* 2000; Froese and Sampang, 2004). The macro invertebrates on seamounts tend to be dominated by suspension feeding corals (Rogers, 1994) which are most abundant along the sides and ridges of seamounts and provide habitat for a diverse facultative fauna (Jensen and Frederikesn, 1992). Recent exploration using acoustics and submersibles has revealed unexpectedly widespread and diverse coral ecosystems in deepwaters on continental shelves, slopes, seamounts, and ridge systems around the world (Roberts *et al.,* 2006). In the New Zealand Exclusive Economic Zone macro-invertebrates in trawl samples are made up of Cnidaria (black corals, hard corals, and sea fans), Echinodermata (starfish, sea lilies, and brittlestarfish), Arthropoda (stone crabs and true crabs), and Mollusca (gastropods, octopus and squid); but the greatest invertebrate biomass has been corals (Probert *et al.*, 1997). These large epibenthic organisms are vulnerable to trawling, and corals have been the dominant bycatch in the development of trawl fisheries on some newly discovered seamounts (Anderson and Clark, 2003). On Tasmanian seamounts major impacts were recorded within a few years of the development of the orange roughy *Hoplostethus atlanticus* fishery; on heavily trawled seamounts (>1 000 trawls) reef aggregate was removed or reduced to rubble, and the invertebrate biomass was 83% lower than on lightly fished seamounts (Koslow and Gowlett-Holmes, 1998). The recovery of these deep-sea corals that may live for centuries (Andrews *et al*., 2005) is likely to be extremely slow.

Fisheries for teleosts and to a lesser extent for crustacea occur on and around seamounts in the North Pacific Ocean along the southern Emperor and northern Hawaiian Ridge in the North Pacific, in the southwest Pacific Ocean around New Zealand, New Caledonia and Tasmania, and the SE Pacific off Chile, in the North Atlantic around the Azores and on the Mid Atlantic Ridge, and in the South Atlantic. Fisheries have expanded for toothfish around sub Antarctic islands and seamounts in the Southern Ocean and for orange roughy and alfonsino on the Southwest Indian Ocean Ridge.

Atlantic Ocean, but still accounts for only ~5% of the total fish catch. The landing statistics are likely to be under estimates due to illegal, unreported and unregulated (IUU) fishing operations, and discards of bycatch species.

Currently discarded fish waste from processing is used for low-value products such as fish-oils, meals, pet foods, and silage. Bioactive compounds may be extracted from left-over fish-frames, internal organs, and invertebrate bycatch species for biotechnological and pharmaceutical applications, offering the opportunity to add value to fisheries. Some compounds derived from fish waste have been identified as potential nutraceuticals (Kim, S-K. and Mendis, E. 2006). Marine invertebrates that occur around hydrothermal vents may provide enzymes and biochemicals for the biotechnology industries and become target species in the future, raising further issues over exploitation of specialised deepwater habitats.

Deepwater fisheries and genetic resources

Aquatic genetic resources have been defined by the 1993 UN Convention on Biological Diversity (CBD) as genetic material of actual or potential value. It has been assumed that such a broad definition encompasses the sum total of all aquatic plants and animals on the planet and that aquatic biodiversity and aquatic genetic resources are almost synonymous terms (Bartley and Pullin, 1999; Pullin, 2000). Fish stocks and bycatch that are exploited, or potentially exploited, by fisheries are all considered as genetic resources (Bartley and Pullin, 1999). However, unlike the terrestrial genetic resources based on plants (PGR), livestock (AnGR), and even aquaculture genetic resources (FiGR, after Pullin, 2000), the deep-sea genetic resources are based on capture from natural ecosystems.

Much of fisheries management has been and continues to be directed towards population and ecosystems management and incorporates genetic resources by default (FAO, 2005b).

The specific application of genetic tools in the management of capture fisheries has been limited to stock identification. Awareness is growing of the genetic structure of fish stocks and the impact of fishing on genetic diversity (Pullin, 2000), but for many marine species the patterns of genetic diversity are poorly understood. The short term pragmatic stock assessment goals to estimate maximum sustainable yields, by necessity have overlooked the long term goals of conserving genetic diversity.

Deepwater fishes

Deepwater fishes comprise three major groups: pelagic fish living largely in midwater, with no dependence on the bottom; demersal fish, living close to and depending on the bottom; and benthopelagic fish, living close to the bottom but undertaking vertical migrations in the water mass (e.g. for feeding). Much remains unknown about the biology and distribution of deepwater fishes and new species continue to be discovered (Roberts and Paulin, 1997; Roberts *et al*., in press). Species exploited by deepwater fisheries include both shelf species, that extend down the continental slopes, and species restricted to depths >400-500 m, and have been grouped into those that aggregate on seamounts and ridges and those more generally dispersed on the continental slope (see Box 2). Many of the commercially targeted species are widespread horizontally, but zoned by depth (e.g. alfonsino and orange roughy), and exhibit specialist adaptations for dispersal and recruitment (Boehlert and Mundy, 1993).

Species diversity is high in the deep-sea and many fishes exhibit unique adaptations, such as bioluminescent organs, modified swim bladders, jaws, and eyes for the deep-sea environment. FishBase lists 1276 bathypelagic species and 2103 bathydemersal species; 798 species of fish have been classified as seamount species (Froese and Sampang, 2004; Morato *et al*., 2006a). Not all deepwater fishes are well described and molecular tools

BOX 2
Deepwater fishes

Species associated with seamounts

The **orange roughy** *Hoplostethus atlanticus* has a wide distribution in the Atlantic, Indian and South Pacific Oceans, where it is found between 500-1 800 m, but is most abundant from 750 to 1 100m. Fisheries have developed around New Zealand, south-east Australia, in the southwest Indian Ocean, off Namibia, Chile, and on the Mid Atlantic Ridge, but the bulk of the catch has been made in the southern hemisphere. The New Zealand fisheries initially concentrated on flat bottom and slope edges, but technical developments, such as GPS navigation, net monitoring, and swathe mapping, coupled with increasing experience in the deepwater fisheries lead to the targeting of orange roughy spawning aggregations on seamounts The catch of orange roughy from seamounts has increased from about 30% of the total catch in 1985 to 80% by 1995 and has stabilized at 60-70% (Clark, 1999; Clark, and O'Driscoll, 2001).

In spite of the extensive distribution, adults are not highly migratory and movement, inferred from seasonal catches and changes in distribution, is only hundreds of kilometres. Orange roughy eggs remain in the plankton for only about 10 days before descending and hatching near the bottom and the larvae are assumed to be epibenthic (Zeldis *et al.*, 1994). Relatively few juveniles (<1 000) have been caught in bottom trawls around New Zealand (Mace *et al.*, 1990) where the fishery peaked at more than 50 000 tonnes a year (Annala *et al.*, 2000). The species is slow-growing, reaching maturity at 25-30 years of age, and may live for more than 100 years (Smith *et al.*, 1995).

The Oreosomatids, the **black oreo** (*Allocyttus niger*) and the **smooth oreo** (*Pseudocyttus maculatus*), support fisheries in the New Zealand and Australian EEZs. In the New Zealand EEZ black and smooth oreo, together with the less abundant **spiky oreo** (*Neocyttus rhomboidalis*), have been managed under a combined quota. The proportion of oreo catch derived from seamount fisheries increased from ~20% in the 1980s to 65% in the 1990s. Oreos aggregate in the mid slope region and above seamounts at 600-1800 m, and are long lived with estimated maximum ages of 86 years for *P. maculatus* and 150 years for *A. niger* (Doonan *et al.,* 1995). Smooth oreo adults are generally found north of 52° S, but most of the few recorded juveniles have been found between 60 and 68° S (James *et al.*, 1988); only 23 black oreo juveniles have been recorded from the New Zealand EEZ (McMillan, NIWA, unpub.obs.), despite annual catches >25 000 t within the New Zealand EEZ (Annala *et al.*, 2000). Juveniles of both black and smooth oreos are pelagic (James *et al.*, 1988) and settle at approximately 4 and 6 years respectively. The pelagic features and their low $\Delta^{14}C$ levels were interpreted as indicating a high latitude origin for black and smooth oreo juveniles (Morison *et al.*, 1999). It is possible that there are single genetic stocks of both species, and that juveniles recruit northwards, after which they show little dispersal and may form discrete ecological stocks.

Alfonsino (*Beryx splendens*) has a wide distribution in tropical and temperate waters of the Atlantic, Indian and Pacific Oceans and the Mediterranean Sea (Kotylar 1996), and occurs over seamounts and the continental slope in depths between 25–1300 m, but is most abundant between 300–500 m. Maximum age is 20 years and age at maturity is from 6 to 8 years. The adults do not appear to make extensive adult migration to spawning areas (Lehodey *et al.*, 1997), but the larvae and juveniles disperse widely in the pelagic environment for several months before settling on shallow seamounts (Boehlert and Sasaki, 1993). *B. decadactylus* has a wide distribution in tropical and temperate waters of except the eastern Pacific Ocean (Kotylar 1996), and occurs on the continental slope and ridges. Relative proportions of *B. splendens* and *B. decadactylus* are unknown.

BOX 2 *(cont.)*

Black cardinalfish (*Epigonus telescopus*) is widely distributed in the North Atlantic from Iceland to the Canary Islands, in the western Mediterranean, and in the South Atlantic, Indian, and southwest Pacific Oceans. The species occurs between 200–1400 m but is most common between 600–900 m. The juveniles are pelagic and undergo major ontogenetic changes; little is known of adult movements. Unvalidated otolith readings indicate slow growth and longevity, with maximum ages ~100 years. Around half the New Zealand catch (~2 000 tonnes year) has been taken as bycatch, with 80% taken in the orange roughy fisheries. In the North Atlantic black cardinalfish are taken as bycatch in trawl and long-line fisheries (Pineiro *et al.*, 2001).

Toothfish are large notothenoids living in Antarctic and sub-Antarctic waters. The two species are circumpolar, the **Antarctic toothfish** (*Dissostichus mawsoni*) is found at high latitudes south of the Antarctic Convergence around 60° S, while the **Patagonian toothfish** (*D. eleginoides*) ranges from about 50° S to 65° S, around sub Antarctic Islands and seamounts, between 50-60° S, and on the Patagonian Shelf and the southern coast of Chile to 30°S (Gon and Heemstra, 1990). *D. eleginoides* reaches a large size >200 cm and age of 50 years (Horn, P. 2002). It is targeted by trawl and long-line fisheries between 70 -1 800m, and was lightly exploited until the mid 1980s, with catches around several hundred tonnes a year. Catches increased rapidly during the 1990s; unofficial estimates suggested that catches reached more than 80 000 tonnes in 1996-97, with large IUU fishing activities (ISOFISH 1998), which have subsequently declined following the introduction of a catch documentation scheme. *D. mawsoni* reach a length of 175 cm and age of ~35 years (Horn, 2002) and have become the target of a number of new and exploratory fisheries since the mid 1990s, with TACs determined by CCAMLR.

Large catches of the **pelagic armourhead** *(Pseudopentaceros wheeleri)* were taken from seamounts (with summits 250-600 m) along the Emperor-Northern Hawaii Ridge in the central North Pacific during the 1970s. Annual catches were estimated at 50 000-200 000 tonnes, but were reduced to a few thousand tonnes in the late 1970s (Boehlert, 1986; Somerton and Kikkawa, 1992). The species is fast growing with a long pelagic juvenile phase and maximum age of 4 years.

Roundnose grenadier (*Coryphaenoides rupestris*) is abundant in the North Atlantic north of 50° N, from Newfoundland Banks to Rockall at 600-800 m, and occurs down to 2 000 m; long lived > 60 years; matures at agea 8-10 years. *C. rupestris* is caught in mixed trawl fisheries with black scabbard fish in the NE Atlantic. Geographically distinct populations exist on the Mid-Atlantic ridge and the Hatton Bank, but its genetic relationships are unknown. A fishery developed in the Northeast Atlantic in the mid 1970s peaked at ~80 000 tonnes and declined rapidly to ~6 000 tonne a year by 1980; the fishery began in the north of the range and moved southwards in the NW Atlantic (Atkinson, 1995). *C. rupestris* has recently been identified as critically endangered (Devine *et al.*, 2006).

Sebastes spp. (**redfish** and **ocean perch**) have supported the longest deepwater fisheries in both the Atlantic and Pacific Oceans. Many species are long lived (up to 100 years), with slow growth rates and late maturity (> 20 years). *Seabastes alutus* is found <50-825 m in the North Pacific, from Honshu, Japan through the Bering Sea to California, with a maximum age of 100 years (Leaman, 1991). The primary focus of deepwater fisheries has been on the upper slope off North America, with catches peaking in the 1960s at around 450 000 tonnes, and since fluctuating at 5 000-30 000 tonnes (Ianelli and Zimmerman, 1998). The fishery has extended into deepwater and exploits several other species of scorpaenids (Ianelli and Zimmerman, 1998)

The *Sebastes* fishery in the Northwest Atlantic is based on the redfish complex *S. fasciatus*, *S. mentella*, and *S. marinus*, which are caught on the shelf edge and the upper

BOX 2 *(cont.)*

slope. The species are characterized by longevity, episodic recruitment, and low fecundity due to ovoviparous reproduction (Leaman, 1991). The Northwest Atlantic fishery peaked at 400 000 tonnes in the late 1950s and has recently declined. In the Northeast Atlantic the fishery has fluctuated between 150 000-300 000 tonnes since the early 1950s; this figure might mask serial depletion as *S. marinus* has been replaced in the landings by the deepwater *S. mentella*.

Continental slope species

The **ling** (*Molva molva*) is found in the Northwest and Northeast Atlantic on the continental shelf, and is common between 100-400 m; it is found down to 1000 m. The only significant fisheries are in the Northeast Atlantic, where landings have been around 50-60 000 tonnes since the 1970s, but recent CPUE data indicate severe depletion (ICES, 2005a). Ling reach 30 years of age and grow to 200 cm in length.

The **blue ling** (*Molva dypterygia*) is common between 350-500 m, and ranges between 150-1 000 m in the Northeast and Northwest Atlantic. Landings peaked at 35 000 tonnes in the 1980s, but declined to <10 000 tonnes. It reaches 20 years of age and 155 cm in length. Recent CPUE data indicate a severe depletion. Its growth rate is unknown (ICES, 2005a).

The **tusk** (*Bromse bromse*) is found in the Northwest and Northeast Atlantic on the continental shelf to 1 000 m, but the only fisheries are in the Northeast Atlantic. It reaches a maximum size 120 cm and a reported age of 20 years. Its landings are in decline and CPUE indicates a severe depletion. Its growth rates are unknown (ICES, 2005a).

Hoki or blue grenadier (*Macruronus novaezelandiae*) support the largest fishery in the New Zealand EEZ and are caught between 300-700 m. It occurs from 10-900 m, matures at 4-5 years and has a maximum age of 20-25 years. It is found around New Zealand and Tasmania. Annual catches in New Zealand peaked at 269 000 tonnes in 1997-98; the current TAC has been reduced to 100 000 tonnes. The **whiptail hake** (*Macruronus magellanicus*) supports trawl fisheries in the South Atlantic and South Pacific around South America from Punta Medanos Argentina to Valparaíso Chile. It is caught by the purse-seine fleet off central-south Chile. It reaches maximum age of ~20 years.

Greenland halibut (*Reinhardtius hippoglossoides*) is found in the North Pacific and North Atlantic Ocean on the shelf down to 2000 m; it reaches a maximum age of 30 years and length of 120 cm. The Northwest Atlantic fishery for *R. hippoglossoides* remained high over the 1960s to 1990s, but grew rapidly during the early 1990s with the entry of Spanish vessels into the fishery, leading to the much publicised Canada-Spain "turbot war" in 1993. The mean size of fish has declined rapidly and the bulk of the catch is made up of fish smaller than the size at maturity. A major collapse of the fishery appears likely (Haedrich *et al.*, 2001).

Black scabbardfish (*Aphanopus carbo*) has a wide distribution in the Northeast Atlantic in 200-1 600 m. There are longline fisheries off Madeira and Portugal and more recently *A. carbo* has become an important species in the mixed bottom-trawl fishery that developed in the Rockall Trough in the 1990s where it is caught with *C. rupestris*. Age estimates vary from 8-25 years with a maximum length of 110 cm. The stock composition of this species is unknown, but element composition of its otoliths indicates differences between the northern and southern areas of the Mid-Atlantic Ridge (Swan *et al.*, 2003). The eggs, larvae and small juveniles are unknown.

The sablefish *(Anoplopoma fimbria)* is found in the North Pacific: Bering Sea coasts of Kamchatka, Russia and Alaska southward to southern Japan and central Baja California.

BOX 2 *(cont.)*

It supports major fisheries in the NE and NW Pacific and reaches a maximum size of 200 cm, and maximum reported age of 114 years. It is found from the surface to 2 700 m: the juveniles are pelagic and migratory.

Deepwater sharks

In the Northeast Atlantic 12 species of shark are caught in the deepwater fisheries. The wide distribution of deepwater sharks means that fishers in deepwater areas cannot avoid catching them and the catch has risen from <100 t a year in the late 1980s to ~11 000 tonnes by 2003. The **Portuguese dogfish** (*Centroscymnus coelolepis*) and the **leafscale gulper shark** (*Centrophorus squamosus*) are target species in long-line and gill net fisheries but they, and other sharks, are taken as bycatch in trawl fisheries targeting orange roughy, roundnose grenadier, blue ling and longline fisheries for black scabbard fish. As trawlers have started to fish further down the continental slope the species mix of sharks has changed from that dominated by leafscale gulper shark in the early stages of the fishery to the Portuguese dogfish (ICES 2005b); more than 95% of the ICES shark catch probably consists of these two species; the other shark species have low commercial value and are discarded. A combined TAC applies to all deepwater shark species for 2006-07 (ICES, 2005b). The lack of species-specific catch data may have disguised an extreme decline of vulnerable species. Although it has been difficult to advise on a sustainable catch with limited information, the current fishing effort in the North Atlantic is recognised as too high (ICES, 2005b).

Both *C. squamosus* and *C. coelolepis* have wide distributions and depth ranges. *C. squamosus* is found between 150–2 400 m in the Eastern Atlantic, the Western Indian Ocean and Western Pacific, and although caught on the bottom 600–1 000 m it is pelagic above deepwater (4 000 m). It reaches a maximum age of 60–70 years and size of 160 cm. *C. coelolepis* is caught between 500-1 500 m and are found between 270-3 600 m in the Western and Eastern Atlantic, the Mediterranean and Western Pacific. It reaches a maximum size of 120 cm; Its maximum age is unknown, and it is near threatened.[1]

Deepwater sharks in other fisheries are vulnerable, whether taken as targeted species or as bycatch. The dumb gulper shark (*Centrophorus harrissoni*), which is possibly restricted to Western Australia, Tasmania and New South Wales and caught in a deepwater trawl fishery off New South Wales, is critically endangered (FishBase).

[1] A general term used to cover taxa whose survival is uncertain (FishBase).

are being used to resolve taxonomic questions of species identity. DNA barcoding initiatives (Hebert *et al.*, 2003) will provide tools for the rapid identification of species in processed products.

Some of the commercially important deepwater fishes exhibit extreme life history traits with slow growth rates, high longevity (~100 years) and late maturity (15-25 years), see Box 2. In addition some species appear to exhibit long periods of low recruitment (Koslow *et al.,* 2000). For species with episodic recruitment the removal of older fishes may reduce the ability of populations to withstand extended periods of very low recruitment (Koslow *et al.*, 2000); for example the Pacific Ocean perch (*Sebastes alutus*) in lightly and heavily fished populations shows 73% and 7% respectively of fish older than 20 years (Leaman, B.M. 1991).

4. STATUS AND TRENDS OF THE GENETIC RESOURCES

Genetic resources and stock structure

A knowledge of the stock structure of marine fishes is important for the management and conservation of genetic resources. Several approaches are used to measure relationships among spatially isolated populations, most are based on ecological measures, such a parasite load (McKenzie, 2002) or accumulation of trace elements (Thresher, 1999), or environmentally sensitive characters such as morphometrics and meristics (Cadrin, 2000). Molecular tools provide an alternative, indirect measure of dispersal and gene flow. Genetic diversity measured with most molecular methods is assumed to be selectively neutral and non-adaptive with respect to fitness. In general marine fishes have higher levels of genetic diversity than anadromous species, which in turn have higher levels than freshwater species (Gyllenstein, 1985; Ward *et al.*, 1994), a trend that probably results from larger evolutionary effective population sizes in marine fishes (Dewoody and Avise, 2000).

Marine fishes on average show less spatial genetic differentiation than anadromous and freshwater species, due to the fewer barriers to gene flow in the marine environment. Marine dispersal is constrained by the length of time of the pelagic larval and juvenile stages, by behavioural mechanisms, and by physical barriers such as gyres and ocean fronts. An inverse relationship has been reported between genetic differentiation and dispersal potential in small shelf fishes (Waples, 1987; Doherty *et al.*, 1995), but many of the larger shelf fishes show little genetic differentiation over ocean wide scales (Hauser, and Ward, 1998), possibly due to a combination of large population sizes and high mobility.

Deepwater species with potential for extensive dispersal through pelagic juvenile stages, such as the Pacific armourhead, (*Pseudopentaceros wheeleri*) (Martin *et al.*, 1992), the alfosino (*Beryx splendens*) (Hoarau and Borsa, 2000; Aboim, 2005), the wreckfish (*Polyprion americanus*) (Sedberry *et al.*, 1996; Ball *et al.*, 2000), and the silver roughy (*Hoplostethus mediterraneus*) (Smith unpublished observations) exhibit ocean-wide genetic population structures. In the wreckfish, microsatellite allele frequencies were homogeneous in the eastern and western North Atlantic and Mediterranean, but heterogeneous between the North and South Atlantic Ocean (Ball *et al.*, 2000), a genetic discontinuity supported by differences in mitochondrial (mt) DNA haplotype frequencies; and by implication there is little contemporary gene flow across the tropics (Sedberry *et al.*, 1996). In the redfish (*Sebastes mentella*) genetic homogeneity observed over 6 000 km probably results from larval gene flow in the cyclonic circulation of the central North Atlantic, although at wider spatial scales there is evidence for three genetically differentiated groups around the Gulf of St Lawrence/Newfoundland; the Grand Banks to the Faroes; and the eastern Atlantic and the Barents Sea (Roques *et al.*, 2002). In the hoki (*Macruronus novaezelandiae*) there is no genetic differentiation among spawning stocks within the New Zealand EEZ (Smith *et al.*, 1996), but there is genetic differentiation across the Tasman Sea (Milton and Shaklee, 1987).

Likewise for the black oreo (*Allocyttus niger*) and smooth oreo (*Pseudocyttus maculatus*) which have extensive pelagic dispersal during the juvenile stages, no significant genetic differentiation was found among black oreo and among smooth oreo samples from the New Zealand EEZ (Smith *et al.*, 2002). At wider scales a lack of genetic differentiation was reported in smooth oreo samples from Western Australia, Tasmania, and New Zealand, with a different suite of allozyme and mtDNA markers, and little evidence for genetic differentiation between black oreo samples from New Zealand and Tasmania (Ward *et al.*, 1998).

Mitochondrial DNA haplotype data indicated a strong genetic differentiation between populations of the viviparous blackbelly rosefish (*Helicolenus dactylopterus*) from the NE and NW Atlantic Ocean (Aboim, 2005; Aboim *et al.*, 2005). The

application of microsatellite DNA markers has revealed finer population structure within the central NE Atlantic Ocean off Portugal and around the Azores archipelago (Aboim, 2005).

Contrasting patterns of genetic differentiation have been reported in some congeneric pairs of species. In the Patagonian toothfish (*D. eleginoides*) a study of allozyme markers showed no significant regional differentiation among samples from the Southern Ocean, while microsatellite DNA markers showed significant heterogeneity, rejecting the null hypothesis of a single stock (Smith and McVeagh, 2000). Samples from the Indian Ocean were homogeneous for both mitochondrial DNA and microsatellite markers (Appleyard and Williams, 2004), but heterogeneity was found among samples from Macquarie Island, Heard and MacDonald Islands (Appleyard *et al.*, 2002). A major genetic break has been reported north and south of the convergence zone in the Atlantic Ocean (Smith and Gaffney, 2000a; 2000b; Shaw *et al.*, 2004). Recent studies with single nucleotide polymorphsisms (SNPs) in *D. eleginoides* have revealed finer population structure with differentiation within ocean basins (Gaffney, University of Delaware pers.com.). In contrast, populations of the Antarctic toothfish (*D. mawsoni*) appear to be characterized by very low mitochondrial sequence diversity, and homogeneous frequencies of nuclear alleles and mitochondrial haplotypes among sea areas. These preliminary genetic data provide little support for the hypothesis of separate regional stocks of (*D. mawsoni*) (Smith and Gaffney, 2005).

In the congeneric alfonsinos (*Beryx splendens*) and (*B. decadactylus*) analyses of mtDNA haplotype data revealed major differences in the structure and history of the populations of the two species. *B. splendens* appears to have one population in the Northeast Atlantic, while *B. decadactylus*, exhibits lower genetic diversity but strong genetic differentiation between Cape Verde and the other populations in the NE Atlantic Ocean (Aboim, 2005).

The orange roughy (*Hoplostethus atlanticus*) and silver roughy (*H. mediterraneus*) have wide distributions in the North Atlantic, Indian and Pacific Oceans, but different dispersal potentials. Orange roughy have weak dispersal potential: their pelagic eggs sink and hatch near the bottom (Zeldis *et al.*, 1994) and exhibit genetic differentiation at small spatial scales in the SW Pacific Ocean and Tasman Sea (Smolenski *et al.*, 1993; Smith *et al.*, 1996; Smith and Benson, 1997; Smith *et al.*, 1997). In contrast silver roughy have a long pelagic phase and show little genetic differentiation at the oceanic scale (Smith, unpublished results). Local declines among orange roughy fisheries on neighbouring seamounts suggest that they may be independent units in the ecological time frame of fisheries management, in the absence of detectable genetic differentiation.

Genetic diversity in deep-sea soft sediment invertebrates and deep-sea corals

The deep-sea soft-sediment environment hosts a diverse and often highly endemic fauna of uncertain origins. Little is known of the genetic resources and the impact of trawling on these soft substrates, but some broadly distributed invertebrates exhibit genetically divergent populations in the absence of morphological divergence, and may represent cryptic species (Etter, 1999; Zardus *et al.*, 2006). High levels of genetic diversity were found in the protobranch bivalve (*Deminticula atacellana*), which is widespread throughout the Atlantic Ocean in soft sediments at bathyal and abyssal depths. Samples from localities in the North American, West European and Argentine basins were divided into four major clades, with DNA haplotypes unique to each basin (Zardus *et al.*, 2006). Genetic divergence was greater among populations at different depths within basins, than among those at similar depths in separate basins, indicating population differentiation at small (100s kms) spatial scales (Chase *et al.*, 1998; Zardus *et al.*, 2006). Depth-related divergence has also been reported in the deepwater amphipod (*Eurythenes gryllus*) (Bucklin *et al.*, 1987; France and Kocher, 1996), and this general finding may reflect historical patterns of colonization, or strong environmental

selective gradients, or horizontal dispersal in the deep-sea (Bucklin *et al.*, 1987; Etter *et al.*, 2005; Zardus *et al.*, 2006).

There have been few genetic studies on deepwater corals to identify dispersal and connectivity among seamounts (Baco *et al.*, 2006); yet such data are required for the development of management strategies for these species that dominate the fragile ecosystems. Low-sequence divergences were found among some deep-sea octocorals, but preliminary results for the bamboo corals (Keratoisidinae) in the SW Pacific suggest that some species are widespread and are not restricted to seamounts (France, and Hoover, 2002; Smith *et al.*, 2003). Genetic data for the scleractinian coral (*Lophelia pertusa*), the main framework-building species in the Northeast Atlantic at depths between 200 and 1 000 m, have revealed distinct offshore and fjord populations. The levels of genetic diversity in *L. pertusa*, and the contribution of asexual reproduction to the maintenance of the subpopulations were highly variable among sites (Goff-Vitry *et al.*, 2004).

Potential loss of genetic diversity in small populations

The genetic composition of a population can change over generations due to random events. Changes due to genetic drift are most likely in small populations and are expected to be weak in marine fishes with large populations ($N > 10^7$). However, sweepstake events driven by very high larval mortalities can reduce N_e (the number of individuals contributing to the next generation) by several orders of magnitude from the census population size, N (Hedgecock, 1994). Estimates of N_e in several shelf fishes are considerably smaller then census sizes (Bagley *et al.*, 1999; Chapman *et al.*, 2002; Hauser *et al.*, 2002; Turner *et al.*, 2002). Long-lived fishes with overlapping generations and annual spawning events are protected from loss of genetic variability due to drift, through the "storage effect" of year classes that buffer annual decreases in N_e (Gaggiotti and Vetter, 1999). However, additional pressures from fishing practices that lead to population declines and loss of juvenile habitat, imposed on sweepstake recruitment events, may lead to loss of genetic diversity (Chapman *et al.*, 1999b; Hauser *et al.*, 2002). Temporal genetic variation maybe enhanced in deepwater fishes, because the low productivity environment may restrict individual fish from spawning annually, leading to low and patchy recruitment (Leaman and Beamish, 1984).

Within-area temporal variation has been reported in orange roughy (Smolenski *et al.*, 1993; Smith and Benson, 1997); grouper (*Mycteroperca microlepis*) (Chapman *et al.*, 1999b); and hake (*Merluccius merluccius*) (Lundy *et al.*, 2000); and may result from stochastic events in progeny survival (Chapman *et al.*, 1999a). The low N_e/N ratios demonstrated in several shelf species are equally likely to occur in some deepwater species, and potentially lead to loss of genetic diversity in collapsed stocks.

Genetic diversity and selective fisheries

Substantial changes in life history traits, in particular age and size at maturity, have been reported in heavily exploited stocks on the continental shelves in the North Atlantic (Smith, 1994; Stokes and Law, 2000; Dieckmann *et al.*, 2006 in press). These changes may result from environmental change, the direct selective effects of fishing, or a compensatory response to reduced stock densities (Law, 2000). The compensatory response to a reduction in stock size promotes growth rate, resulting in a decrease in the age at maturity but an increase in the size at maturity, and may conceal long-term selection effects that would favour early maturing genotypes (Rochet, 1998). These responses may be non-exclusive making it difficult to untangle the compensatory and evolutionary components of these observed changes (Law, 2000).

Reaction norms for age and size at maturation have been used to estimate the probability of maturing at each relevant age and size, and thereby separate the genetically determined character from the plasticity in maturation that results

from changes in growth rate (Heino *et al.,* 2002; Engelhard and Heino, 2004). Growth-related phenotypic plasticity appears to have been largely responsible for recorded changes in early maturity in the Norwegian spring herring (*Clupea harengus*) (Engelhard and Heino, 2004), but in Atlantic cod (*Gadus morhua*) (Heino, 2002) and plaice (*Pleuronectes platessa*) (Rijnsdorp *et al.*, 2005) evolutionary changes appear to have occurred in response to heavy fishing (Law, 2000). These evolutionary changes are supported by controlled selection experiments that have demonstrated that fisheries have the potential to cause rapid evolution in life history traits (Conover, 1998; Conover *et al.*, 2005). Life history traits in populations of Atlantic cod off southern Labrador and eastern Newfoundland continually shifted towards maturation at earlier ages and smaller sizes, before the fishery finally collapsed in the 1990s. These changes in life history could provide a tool to give warning signals before more overt changes occur to populations (Olsen *et al.*, 2004).

Directional selection, through size-selective harvesting has not been demonstrated in deepwater fishes, in part due to the lack of long term data sets and, for long-lived species the long response time of the population to fishing. A number of changes were observed in a major orange roughy fishery on the Chatham Rise (New Zealand) over a 19-year period. The species distribution showed a marked contraction, with aggregations becoming centred around seamounts, or localised areas of the slope, and the biomass declined substantially to about 20% of virgin levels (Clark *et al.*, 2000). However size structure and size or age at maturity did not change markedly over the same period. Biological changes may not have been apparent because orange roughy is a long-lived, slow-growing species, with low productivity (Clark *et al.*, 2000).

Deepwater fisheries have only been operating in the Northwest Atlantic Ocean since the 1970s, but already four out of five species (the roundnose grenadier [*Coryphaenoides rupestris*], the onion-eye grenadier [*Macrourus berglax*], the blue hake [*Antimora rostrata*], and the spinytail skate [*Bathyraja spinicauda*]) have declined by 25-57% in mean size over 17 year period, so that fewer fish reach maturity and breed (Devine *et al.*, 2006). In the Northwest Atlantic fishery for Greenland halibut *R. hippoglossoides* the mean size of fish has declined rapidly and the bulk of the catch is made up of fish smaller than the size at maturity, and a major collapse of the fishery is likely (Haedrich *et al.*, 2001).

Endangered species

Only a few marine fishes have been listed as endangered (although the list is growing) and fewer appear to be close to extinction, e.g. skates (Brander, 1981; Casey and Myers, 1998). Traits of several deepwater species, such as long-life span, large body size, low natural mortality and late sexual maturity, are likely to make them more vulnerable to extinction than shelf species, in particular species that aggregate above seamounts. A review of the extinction risk in marine fish found that large body size and late maturity were the best predictors of vulnerability to fishing; there was no evidence that high fecundity conferred increased resilience (Reynolds *et al.*, 2005). Much of the evidence for extinction risk comes from shelf species, where inshore sub-populations of Atlantic cod and herring have been driven to extinction or have had insufficient time to recover from severe depletions (Smedbol and Stephenson, 2001).

Different criteria have been used to express the risk of extinction. The widely used IUCN system uses the graded terms vulnerable, endangered, and critically endangered and is applied to all organisms regardless of life history strategy. The IUCN criteria may overestimate the extinction risk for many marine fishes with their high intrinsic rates of increase, and for which management plans allow for stock biomass targets of 20-30% of the virgin biomass (Musick, 1999). Stocks of some pelagic shelf fishes have collapsed with severe reductions (1/3000) in population size, but have shown evidence of recovery. In general these species are characterized by small body size and early

maturity, the converse of traits that were the best predictors of vulnerability to fishing (Reynolds *et al.*, 2005). Pelagic species showing the greatest declines have shown the slowest recoveries (Beverton, 1990). The American Fisheries Society (AFS) developed a precautionary set of criteria to predict the risk of extinction in marine fishes, which includes rarity, specialization in habitat requirements, endemicity or small range, and population decline, and also aims to recognise distinct population segments (DPS) when data are available (Musick, 1999). Rare species, because of evolutionary or ecological factors or crypsis, would be classified as vulnerable until further data were available. Species that are endemic or occur over a small range where the habitat is under threat from degradation would be classified as vulnerable, and where habitat loss has occurred they would be classified as endangered or threatened. Species with specialised habitat requirements, but that occur over wide geographic ranges, may also be vulnerable when the specialised habitat is subject to degradation or destruction (Musick, 1999). However the lack of knowledge about critical minimum population size and possibility of depensation create the greatest problems in assessing the extinction risk in marine fishes (Musick, 1999). Consequently the AFS proposed evaluating the resilience of the DPS using four levels of productivity: high, medium, low, and very low. Fish with late maturity (5-10 years), a long life span (>30 years), and high fecundity (>10^4), typical of some deepwater fishes (and some show even later maturity and greater longevity), would be classified as very low productivity and would have a lower threshold to extinction than a species with medium or high productivity (Musick, 1999). Non-target species, that include teleosts endemic to seamount complexes and elasmobranchs with very low productivity, are likely to be vulnerable. For the few seamount fishes for which there are adequate biological data, most species have a low or very low productivity, and low resilience to exploitation (Froese and Sampang, 2004). It has been predicted that more seamount populations will be depleted and some will be extirparted if fishing continues at current levels (Morato *et al.*, 2006a).

Five deepwater species (the roundnose grenadier *C. rupestris*, the onion-eye grenadier *M. berglax*, the blue hake *A. rostrata*, the spinytail skate *B. spinicauda*, and the spiny eel *Notocanthus chemnitzi*) in Northwest Atlantic fisheries appear to meet the IUCN and AFS criteria of being critically endangered (80% decline in 10 years or three generations, or whichever is longer), showing overall declines in relative abundance of 87-98% in <20 years of exploitation, and higher estimated declines over three generations (Devine *et al.*, 2006). If the IUCN criteria are applied, the Dumb gulper shark (*Centrophorus harrissoni*) caught in the deepwater fishery of New South Wales is critically endangered; the deepwater bluntnose sixgill shark (*Hexanchus griseus*), circumglobal in tropical and temperate seas, is vulnerable (20% decline in 10 years or three generations or whichever is longer) while the kitefin shark (*Dalatias licha*) and the leafscale gulper shark (*Centrophorus squamosus*) are at lower risk, near threatened (i.e., survival is uncertain), along with several other species of shark in shelf waters (IUCN Red List).

The blue skate (*Dipturus batis*) is endangered and extirpated by trawling over much of its range in the eastern North Atlantic. The shallow water bocaccio *(Sebastes paucispinis)* found on seamounts in the eastern Pacific is critically endangered, while the deepwater shortspine thornyhead (*Seabastolobus alascanusis*) in the North Pacific is endangered. The Atlantic halibut (*Hippoglossus hippoglossus*) caught in shelf and slope fisheries in the North Atlantic is also endangered (see FishBase).

5. MAJOR INTERNATIONAL INITIATIVES, AGREEMENTS AND INSTRUMENTS

Genetic resources at the species and ecosystem levels are equivalent to ecological resources for which the management issues are well documented in the fisheries literature. The rapid development, and in some cases rapid depletion, of deepwater fisheries is of major concern to fisheries managers around the world, and has been

identified repeatedly at the local, regional and international levels (Koslow *et al.*, 2000; Haedrich *et al.*, 2001; Molenaar, 2004; FAO, 2005b; Morato *et al.*, 2006b). ICES have recognised that most exploited deepwater fishes are harvested unsustainably and radical reductions in fleets, in particular bottom trawlers are required to reduce effort and to conserve vulnerable habitats (ICES, 2005a).

Many deepwater fisheries occur in high seas areas adding to the problem of management and regulation. Urgent action is required at the global level, to avoid shifting the deepwater fishing problem from one region to another. Concerns about the apparent inertia in developing and implementing fisheries legislation, especially in the international arena, have lead to NGOs calling for the designation of large-scale protected areas, and for a moratorium on bottom trawling until area management regimes can be implemented. Several countries have small-scale closures for deepwater fisheries within their territorial waters.

1995 UN Fish Stocks Agreement (FSA)

The 1995 UN Fish Stocks Agreement sets out the principles for the conservation and management of straddling fish stocks and highly migratory fish stocks and establishes that management be based on the precautionary approach and the best available scientific information (UN, 1995). The Agreement builds on the fundamental principle, established in the 1982 UN Convention of the Law of the Sea that States should cooperate to ensure conservation and promote the objective of the optimum utilization of fisheries resources both within and beyond the EEZs. The 1995 UN Fish Stocks Agreement was signed by 59 States and entities, but some major fishing nations, such as China and the Republic of Korea have not yet ratified the Agreement. The Agreement does not cover deepwater stocks found exclusively outside the 200 mile EEZs (i.e. discrete high seas stocks), but in practice States have been applying it to discrete high seas stocks (e.g. the South East Atlantic Fisheries Organisation).

A review meeting of the FSA in May 2006 identified a series of actions for States individually, and collectively through regional fisheries management organizations, to ensure the conservation and sustainable use of straddling fish stocks and highly migratory fish stocks, and that these principles should be applied to fish stocks in the high seas.[1]

1995 FAO Code of Conduct for Responsible Fisheries

The 1995 FAO Code of Conduct for Responsible Fisheries (FAO, 1995) is a voluntary comprehensive instrument that sets out the principles and standards for the conservation and management of all fisheries and aquaculture including processing and trade in fish and fishery products, research and the integration of fisheries and aquaculture into coastal management areas. The Code refers to the role of Regional Fisheries Bodies to establish responsible international fisheries regimes.

Regional fisheries management organizations or arrangements (RFMOs)

There are 44 regional fisheries bodies that cover three categories: RFMOs, Advisory bodies, and Scientific bodies (FAO, Fisheries). Of these, 17 RFMOs are responsible for establishing management measures and some have regulatory powers in their jurisdictions, although many have a purely advisory role. Major problems for the current RFMOs relate to decision making, the allocation of resources to new entrants (principally developing countries that do not have a historical catch record) and the impacts of IUU fishing.[2]

[1] http://www.un.org/Depts/los/convention_agreements/review_conf_fish_stocks.htm
[2] http://www.fao.org/docrep/008/a0098e/a0098e06.htm

Most RFMOs have common responsibilities (Devaney, PL 2005) to:

- collect and distribute fishery statistics,
- provide evaluations of the state of fish stocks in their area of jurisdiction,
- determine the total allowable catch (TAC) quotas,
- set limits on the number of vessels allowed to exploit the fishery,
- control fishing opportunities by RFMO participants using such measures as area and seasonal closures and bycatch limits,
- regulate the types of gear used and conduct inspections to ensure compliance,
- monitor and enforce adherence to the rules of the RFMO and
- oversee the scientific research conducted within the fishery.

Australia, Chile, and New Zealand are promoting the development of a South Pacific Regional Fisheries Management Organisation (SPRFMO) to address governance of high-seas fisheries from the eastern Southern Indian Ocean, across the Tasman Sea and South Pacific Ocean to the Pacific EEZ's of South America. Several other countries have fishery interests in the area, notably Russian Federation, Ukraine, China, the Republic of Korea and the European Union. Currently there is little or no control over fishing methods or the management of fish stocks, other than for highly migratory tunas, in this extensive region. Other RFMOs, such the Western and Central Pacific Fisheries Convention (WCPFC) and the Inter-American Tropical Tuna Convention (IATTC) cover parts of this region, but their mandates relate only to highly migratory species.

The High Seas Task Force

The High Seas Task Force was established in 2003 to develop an action plan to combat IUU fishing (see below) on the high seas; membership consists of a group of fisheries ministers from Australia, Canada, Chile, Namibia, New Zealand, and the UK; and international NGOs – WWF, the World Conservation Union (IUCN) and the Earth Institute. Although established in 2003 the first report was not released until 2006. The High Seas Task Force aims, inter alia, to develop a Global Information System (GIS) on high seas fishing vessels that will make available information on the characteristics, ownership, and operations of all high seas fishing vessels. The GIS will also identify vessels previously black-listed by RFMOs, with the intention to make it difficult for IUU operators.

The Marine Stewardship Council (MSC) and ecolabelling of fish products

The MSC is an independent non-profit organisation that aims to use consumer purchasing power to enhance responsible management of seafood resources to ensure the sustainability of global fish stocks and the health of the marine ecosystem. The MSC has developed an environmental standard for sustainable and well-managed fisheries and uses a product label to reward responsible fishery management and practices. Certification is only granted if there is consensus amongst independent assessors that the fishery meets the MSC standard. Consumers, concerned about overfishing and its environmental impacts are able to choose seafood products which have been given MSC certification. The New Zealand hoki (*Macruronus novaezelandiae*) was the first large whitefish and only deepwater fishery to achieve MSC certification, for a period of five years.

Other NGOs have developed eco-labels that rank fish species by the sustainability of the fisheries so as to provide information to consumers. Eco-labels may be in conflict with the MSC, for example the New Zealand Forest and Bird Society's *Best Fish Guide* advises consumers to avoid eating hoki, and lists this as a worst choice species, due to the bycatch of fur seals, albatrosses and petrels and management practices in the fishery.

Guidelines for ecolabelling fish products have been developed by the FAO Committee of Fisheries (COFI) for governments and organizations that maintain, or

are establishing, labelling schemes for fish and fishery products from well-managed marine capture fisheries (FAO, 2005a). The general principles for ecolabelling schemes include the need for reliable and independent auditing, transparency of standard-setting and accountability and the need for the standards to be based on good science.

6. KEY SCIENTIFIC AND MANAGEMENT ISSUES TO BE ADDRESSED

Many deepwater species differ from shelf species in that they exhibit high longevity and late maturity; some have extensive but localised distributions in a low productivity environment. However there are limited scientific data available for many species. Working Groups at the Deep-sea 2003 conference identified several scientific areas where additional data are desirable for the management of deepwater species (FAO 2005b):

- accurate catch data,
- time series of abundance,
- stock identity and distribution information,
- life-history information,
- population biology statistics and age-frequency data,
- ability to make use of the most recent developments in fisheries resource management

Fishery subsidies

One component of reducing fishing capacity is the reduction or removal of subsidies (Pauly *et al.,* 2002). In general, the provision of subsidies increases the net returns from fishing and leads to an increased pressure on deepwater fish stocks, although simply removing subsidies will be ineffective in the absence of other management regimes (Cox, 2005). Subsidies, and other incentives such as accelerated depreciation for vessels, that encourage the expansion of capacity, such as vessel construction, may lead to increased pressure on deepwater fisheries that are technology driven. The converse, subsidies for vessel decommissioning, will only be effective if the vessels are scrapped (to avoid transfer to another fishery) and not replaced by new vessels (Cox, 2005). Rising fuel prices might also contribute to the restriction of some deepwater fishing operations.

Illegal, unreported and unregulated (IUU) fishing

The global excess of fishing capacity has contributed to illegal, unreported and unregulated (IUU) fishing and is recognized as a major threat to the long term sustainability of the world's fish stocks (FAO, 2004a). IUU fishing on the high seas is generally described as any fishing that takes place within the jurisdiction of a RFMO, but not in compliance with its regulations. IUU fishing is more broadly defined by the FAO as fishing activities in the area of application of a relevant RFMO that are conducted by vessels without nationality, vessels flagged to a State not party to that organization, or by a fishing entity, in a manner that is not consistent with, or contravenes, the conservation and management measures of that organization (FAO 2004a).

A number of measures aimed at combating IUU fishing, have been adopted by States and RFMOs, but despite these measures IUU fishing appears to continue because mobile fishing fleets are able to move rapidly between areas. FAO have developed a voluntary instrument within the framework of the Code of Conduct, the 2001 FAO International Plan of Action to Prevent, Deter and Eliminate Illegal, Unreported, and Unregulated Fishing (IPOA-IUU).[3]

[3] http://www.fao.org/docrep/005/y3554e/y3554e00.HTM

IUU fishing for toothfish has consisted largely of illegal fishing within the EEZs of sub-Antarctic island territories within the CCAMLR Area and unregulated and unreported fishing both within and outside the CCAMLR Area. Most IUU fishing is thought to have occurred in the Indian Ocean sector around Crozet, Heard, Kerguelen and Prince Edward Islands. Increased surveillance activity in these areas has forced illegal operators to more remote areas, such as the waters around Ob and Lena Banks, and the waters around South Georgia.[4]

CCAMLR introduced a catch documentation scheme (CDS)[5] that became binding on its members in May 2000. The Scheme tracks the landings and trade flows of toothfish caught in the CCAMLR Area by requiring landings and trans-shipments of toothfish to be accompanied by a valid CCAMLR Catch Document. The CDS identifies the origin of toothfish entering the markets of all participants in the Scheme. CDSs are a promising tool for other RFMOs to encourage legal fishing, and certify that fish entering the markets were caught in compliance with regional fishing regulations. However IUU fishers who land their catch into non-member port states will continue to undermine conservation measures.

In addition, CCAMLR maintains a list of vessels with a history of IUU fishing and has passed a resolution to avoid flagging and licensing non-Contracting Party vessels to fish in CCAMLR waters when the vessels have a history of IUU fishing. Several RFMOs have also instituted a system of black listing IUU fishers as a cost effective enforcement tool and prohibit black listed vessels from landing their catches in member ports.

New technologies are creating opportunities for RFMOs to better monitor vessels and catches and applications are supported by the High Seas Task Force. Vessel Monitoring Systems (VMSs) installed on fishing vessels allow RFMOs to receive up-to-the-minute data on the locations of member vessels. DNA barcoding of marine fish will provide tools for the rapid identification of species in processed products.

Protected areas

The international community, including NGOs, have expressed concern over the loss of macro invertebrates taken as bycatch in deepwater trawl fisheries on seamounts and for seabirds taken in toothfish trawl and long-line fisheries, although mitigation measures have been implemented to reduce the bird catch (FAO, 2004b). The fragile and ancient coral "forests" found on seamounts are reduced to rubble by heavy trawl gear and consequently habitat for numerous other invertebrate species is lost. Improvements to trawl gear and monitoring may eventually allow the operation of deepwater pelagic trawls that avoid contact with bottom features, but in the short term the most effective mitigation measure to protect vulnerable and unique habitats is to close relevant areas to bottom trawling. The application of marine protected areas is controversial, especially in areas outside national jurisdiction, and the subject is under debate within the IUCN and CBD;[6] notably, IUCN Recommendation 3099 calls for the protection of seamounts, deep-sea corals and other vulnerable deep-sea habitats from destructive fishing practices, including bottom trawling, on the high seas.[7] Zoning the oceans into unfished marine reserves and areas with limited levels of fishing effort is one mechanism that might allow sustainable fisheries to be maintained within the diverse deep-sea ecosystems (Pauly *et al.,* 2002). The inertia in developing and implementing international fisheries legislation has lead to NGOs calling for the designation of large-scale protected areas and for a moratorium on high seas bottom trawling until area management regimes can be implemented.[8]

[4] http://www.ccamlr.org/pu/E/sc/fish-monit/iuu-intro.htm
[5] http://www.ccamlr.org/pu/E/cds/intro.htm
[6] http://www.iucn.org/en/news/archive/2006/03/31_high_seas.htm
[7] http://www.iucn.org/en/news/archive/2006/02/22_unga_high_seas.htm
[8] http://www.savethehighseas.org/display.cfm?ID=136

A recent survey estimated that 47% of seamounts fall inside EEZs and 53% in international waters (Alder and Wood, 2004). Several countries have limited closures in place within their territorial waters. The Tasmanian seamounts reserve was voluntary established in the Australian EEZ in 1996 and formally declared in 1999. Below 500 m the reserve has a protected area (IUCN management category 1a) and represents ~20% of the total seamounts in the local region. In the Tasman Sea, the Lord Howe Marine Park covers all the waters around Lord Howe Island down to 1800 m. Nineteen seamounts around New Zealand were closed to bottom trawling in 2000 (Clark *et al.*, 2000). The closed seamounts were identified as being either representative of seamounts in their area or unique features in the EEZ. The faunal compositions of many seamounts are not known and selection of seamounts was based on geographical location and depth, rather than biodiversity. In the North Pacific the Bowie Seamount has a marine protected status that includes the conservation and protection of commercial and non-commercial fisheries. In Australia, the Department of Environment and Heritage have proposed establishing a network of large scale Marine Protected Areas (MPAs) in the SE marine region, that would cover 171 000 km^2 and close the major orange roughy fisheries (Buxton *et al.*, 2006). Recent initiatives have lead to the establishment of a high seas Benthic Protected Area (BPA) in the Southern Indian Ocean,[9] while representatives from the New Zealand fishing industry have proposed closing 31% of the seafloor (~1.2 m km^2) in the New Zealand EEZ to bottom trawling,[10] although the areas selected for closure need scientific review[11] to ensure that the areas that are representative of marine environments in the EEZ.

7. SUMMARY

The expansion of fisheries into deepwaters, especially those in high seas outside coastal jurisdictions, has been the most significant development in world fisheries in recent years. Several of the important deepwater species are characterised by high longevity and late age at maturity; these species have ocean-wide distributions within a depth range and exhibit weak genetic differentiation within oceans. Several species, especially elasmobranchs taken as bycatch, are endangered; some teleost species in the NW Atlantic appear to have become endangered following 20 years of heavy exploitation. There is general agreement that many deepwater fishes are exploited beyond sustainable levels and that urgent action is required at the global level to reduce effort and to protect fragile ecosystems from the impact of bottom trawling. Difficulties in managing deepwater fishes are compounded by the high seas nature of many fisheries and the limited regimes available for management in international waters.

8. ELECTRONIC BIBLIOGRAPHY

CCAMLR	http://www.ccamlr.org
Census of Marine Life	http://censeam.niwa.co.nz/
DNA barcoding, fish	http://www.fishbol.org/
FAO, Fisheries	http://www.fao.org/fi/default.asp
FishBase	http://filaman.ifm-geomar.de/home.htm
High Sea Task Force	http://www.high-seas.org/
ICES	http://www.ices.dk/advice/icesadvice.asp
ICES, sharks	http://www.ices.dk/marineworld/jaws.asp
IUCN Red List	http://www.redlist.org/
RFMOs	http://www.pon.org/downloads/ien14_4Devaney.pdf.
South Pacific RFMO	http://www.southpacificrfmo.org
Toothfish	http://www.traffic.org/toothfish/tooth2.html

[9] http://www.iucn.org/en/news/archive/2006/07/2_qa_fishing_high_seas.htm
[10] http://www.seafood.co.nz/newscentre/press/2006pressreleases/closures.asp
[11] http://www.eco.org.nz/campaigns/benthicprotectedareas.htm

9. REFERENCES

Aboim, M.A. 2005. *Population genetics and evolutionary history of some deep-sea demersal fishes from the Azores - North Atlantic*. PhD thesis University of Southampton, Faculty of Enginering Science and Mathematics, School of Ocean and Earth Science, PhD Thesis: 167 p.

Aboim, M.A., Menezes, G.M., Schlitt, T. & Rogers, A.D. 2005. Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. *Molecular Ecology*, 14:

Alder, J. &Wood, L. 2004. *Managing and protecting seamount ecosystems*. In Seamounts: Biodiversity and Fisheries (ed) T. Morato and D. Pauly. Fisheries Centre Research Report: 67-73.

Anderson, O.F. & Clark, M.R. 2003. Analysis of bycatch in the fishery for orange roughy, *Hoplostethus atlanticus*, on the South Tasman Rise. *Marine and Freshwater Research,* 54: 643-652.

Andrews, A.H., Cailliet, G., Kerr, L.A., Coale, K.H., Lundstrom, C. & DeVogleare, A. 2005. *Investigations of age and growth for three species of deep-sea coral from the Davidson Seamount off central California. Cold-water Corals and Ecosystems*. A. Freiwald and J.M. Roberts eds. Proceedings of the Second International Symposium on Deep-sea Corals. Erlangen, Germany. 965-982.

Annala, J.H., Sullivan, K.J., O'Brien, C.J. & Iball, S.D. 2000. Report from the Fishery Assessment Plenary, May 2000: *Stock Assessments and Yield Estimates.*

Appleyard, S., Ward, R. and Williams, R. 2002. Population structure of the Patagonian toothfish around Heard, McDonald and Macquarie Islands. *Antarctic Science*, 14: 364-373.

Appleyard, S. & Williams, R. 2004. Population genetic structure of Patagonian toothfish in the West Indian ocean sector of the Southern Ocean. *CCAMLR. Science,* 1: 21-32.

Atkinson, D.B. 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the northwest Atlantic. In Deepwater fisheries of the North Atlantic Oceanic Slope Kluwer Academic Publsihers, Dordrecht the Netherlands: 51-112.

Awaya, K.L. & Lee, C-S. 2005. *Giant Clam*. American Fisheries Society Symposium, 46: 111-124.

Baco, A.R., Clark, A.M. & Shank, T.M. 2006. Six microsatellite loci from the deep-sea coral *Corallium lauuense* (Octocorallia: Coralliidae) from the islands and seamounts of the Hawaiian archipelago. *Molecular Ecology Notes* 6: 147-153.

Bagley, M.J., Lindquist, D.G. & Geller, J.B. 1999. Microsatellite variation, effective population size, and population genetic structure of vermillion snapper *Rhomboplites aurorubens*, off the southeastern United States of America. *Marine Biology*, 134: 609-620.

Ball, A.O., Sedberry, G.R., Zatcoff, M.S., Chapman, R.W. & Carlin, J.L. 2000. Population structure of the wreckfish *Polyprion americanus* determined with microsatellite genetic markers. *Marine Biology*, 137: 1077-1090.

Bartley, D.M. & Pullin, R.S.V. 1999. *Towards policies for conservation and sustainable use of aquatic genetic resources.* ICLARM Conference Proceedings, 59: 1-16.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. 2003. Collapse and Conservation of Shark Populations in the Northwest Atlantic. *Science*, 299: 389-392.

Beverton, R.J.H. 1990. Small marine pelagic fish and the threat of fishing: are they endangrered? *Journal of Fish Biology*, 37 (Suppl A): 5-16.

Boehlert, G. & Mundy, B. 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Science*, 53: 336-361.

Boehlert, G. & Sasaki, T. 1988. Pelagic biogeography of the armorhead *Pseudopentaceros wheeleri*, and recruitment to isolated sea mounts in the north Pacific Ocean. *Fishery Bulletin*, 86: 453-466.

Boehlert, G. & Sasaki, T. 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Science* 53: 336-361.

Boehlert, G.W. 1986. Productivity and population maintenance of seamount resources and future research directions. NOAA Technical Report National Marine Fisheries Service, 43: 95-101.

Brander, K. 1981. Disappearance of common skate Raia batis from Irish Sea. *Nature*, 290: 48-49.

Bucklin, A., Wilson, R.R. and Smith, K.L. 1987. *Genetic differentiation of seamount and basin populations of the deep-sea amphipod Eurythenes gryllus*. Deep-sea Research, 34: 1795-1810.

Buxton, C., Haddon, M. & Bradshaw, M. 2006. *Regional impact assessment for the marine protected areas proposed for the south-east region.* Fisheries Research and Development Corporation Final Report 2005/083: 141 p.

Cadrin, S.X. 2000. *Advances in morphometric identification of fishery stocks.* Reviews in Fish Biology and Fisheries 10: 91-112.

Casey, J.M. & Myers, R.A. 1998. Near extinction of a large, widely distributed fish. *Science* 281: 690-692.

Chapman, R.W., Ball, A.O. & Marsh L.R. 2002. Spatial homogeneity and temporal heterogeneity of red drum (Sciaenops ocellatus) microsatellites: effective population sizes and management implications. *Marine Biotechnology,* 4: 589-603.

Chapman, R.W., Sedberry, G.B. & McGovern, J.C. 1999a. The genetic consequences of reproductive variance: studies of species with different longevities. American Fisheries Society Symposium 23: 169-181.

Chapman, R.W., Sedberry, G.R., Koenig, C.C. & Eleby, B.M. 1999b. Stock identification of gag, Mycteroperca microlepis, along the southeast coast of the United States, 1: 137-146.

Chase, M.R., Etter, R.J., Rex, M.A. & Quattro, J.M. 1998. Bathymetric patterns of genetic variation in a deep-sea protobranch bivalve, *Deminucula atacellana*. *Marine Biology*, 131: 301-308.

Clark, M. 1999. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. *Oceanologia Acta* 22: 593-602.

Clark, M. & O'Driscoll, R. 2001. Deepwater fisheries and aspects of their impact on seamount habitat in New Zealand. *Journal Northwest Atlantic Fisheries Science*, 31: 441-458.

Clark, M., O'Shea, S., Wood, B. & Wright, I. 2000. Seamount management. A report on seamounts potentially suitable for consideration under the MFish seamount management strategy. Report prepared for the New Zealand Ministry of Fisheries April 2000: 82 p.

Clark, M.R., Anderson, O.F., Francis, C. & Tracey, D. 2000. The effects of commercial exploitation on orange roughy (Hoplostethus atlanticus) from the continental slope of the Chatham Rise, New Zealand, from 1979 to 1997. *Fisheries Research*, 45: 217-238.

Clarke, M., Kelly, C., Connolly, P. & Molloy, J. 2003. A life history approach to the assessment and management of deepwater fisheries in the Northeast Atlantic. *Journal Northwest Atlantic Fisheries Science*, 31: 401-411.

Conover, D., Arnott, S., Walsh, M. & Munch, S. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Canadian Journal of Fisheries & Aquatic Sciences*, 62: 730-737.

Conover, D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. Bulletin of Marine Science 62: 477-493.

Cox, A. 2005. Subsidies and deep-sea fisheries management: policy issues and challenges. www.oecd.org/dataoecd/10/27/24320313.pdf 23 p.

Davis, G.E., Haaker, P.L. & Richards, D.V. 1998. The perilous condition of white abalone *Haliotis sorenseni*, Bartsch, 1940. *Journal of Shellfish Research*, 17: 871-875.

Devaney, P.L. 2005. Regional Fisheries Managenent Organizations. Papers on International Negotiation XIV: 18 pp.

Devine, J.A., Baker, K.D. & Haedrich, R.L. 2006. Deep-sea fisheries qualify as endangered. *Nature*, 439: 29.

Dewoody, J.A. & Avise, J.C. 2000. Microsatellite variation in marine, freshwater and anandromous fishes compared with other animals. *Journal of Fish Biology*, 56: 461-473.

Dieckmann, U., Godo, O.R. & Heino, M. (Eds) JM 2006 in press. Fisheries induced adaptive change. International Institute for Applied Systems Analysis

Distel, D.L., Baco, A.R., Chaung, E., Morrill, W., Cavanaugh, C & Smith, C.R. 2000. Do mussels take wooden steps to deep-sea vents? *Nature*, 403: 725-726.

Doherty, P.J., Planes, S. & Mather, P. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier reef. *Ecology*, 76: 2373-2391.

Doonan, I., McMillan, P., Kalish, J. & Hart, A. 1995. *Age estimates for black oreo and smooth oreo.* New Zealand Fisheries Assessment Report 95/14: 26p.

Engelhard, G.H. & Heino, M. 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary response? *Marine Ecology Progress Series,* 272: 245-256.

Etter, R., Rex, M., Chase, M. & Quattro, J. 2005. Population Differentiation Decreases With Depth In Deep-Sea Bivalves. *Evolution*, 59: 1479-1491.

Etter, R.J., Rex, M.A., Chase, M.C. & Quattro, J.M. 1999. A genetic dimension to deep-sea biodiversity. *Deep-sea Research*, 46: 1095-1099.

FAO. 1995. *Code of Conduct for Responsible Fisheries.* Rome, FAO. 41p.

FAO. 2002. *Report of the Second Ad Hoc Meeting on Management of Deepwater Fisheries Resources of the Southern Indian Ocean. Fremantle, Western Australia. 20–22 May 2002*. FAO Fisheries Report. No. 677. Rome, FAO. 106p.

FAO. 2004a. *Report of the Expert Consultation on Fishing Vessels Operating under Open Registries andtheir Impact on Illegal, Unreported and Unregulated Fishing. Miami, Florida, United States of America, 23–25 September 2003.* FAO Fisheries Report. No 722. Rome, FAO. 168p.

FAO. 2004b. *Report of the FAO/BirdLife South American Workshop on Implementation of NPOA–Seabirds and Conservation of Albatrosses and Petrels. Valdivia, Chile, 2–6 December 2004,* by Lokkeborg, S. and Thiele, W. (eds.). FAO Fisheries Report. No. 751. Rome, FAO. 2004. 32p.

FAO. 2005a. *Report of the Technical Consultation on International Guidelines for the Ecolabelling of Fish and Fishery Products from Marine Capture Fisheries. Rome, 19–22 October 2004.* FAO Fisheries Report. No. 760. Rome, FAO. 99p. (Trilingual)

FAO. 2005b. *Report on DEEP SEA 2003, an International Conference on Governance and Management of Deep-Sea Fisheries. Queenstown, New Zealand 1–5 December 2003.* FAO Fisheries Report. No. 772. Rome, FAO. 84p.

FAO. 2005c. *Review of the state of world marine fishery resources*, by Marine Resources Service, Fishery Resources Division. FAO Fisheries Technical Paper. No. 457. Rome, FAO. 235p.

France, S. & Hoover, L. 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). *Hydrobiologia*, 471: 149-155.

France, S. & Kocher, T. 1996. Geographic and bathymetric patterns of mitochondrial 16S rRNA sequence divergence among deep-sea amphipods, *Eurythenes gryllus*. *Marine Biology*, 126: 633-643.

Froese, R. & Sampang, A. 2004. *Taxonomy and biology of seamount fishes.* In Seamounts: Biodiversity and Fisheries (ed) T. Morato and D. Pauly Fisheries Centre Research Report: 25-31.

Gaggiotti, O. & Vetter, R. 1999. Effect of life history strategy, environmental variability, and overexploitation on the genetic diversity of pelagic fish populations. *Canadian Journal of Fisheries & Aquatic Sciences*, 56: 1376-1388.

Glover, A.G.S., C R. 2003. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environmental Conservation,* 30: 219-241.

Goff-Vitry, M.L., Pybus, O. & Rogers, A. 2004. Genetic structure of the deep-sea coral *Lophelia pertusa* in the northeast Atlantic revealed by microsatellites and internal transcribed spacer sequences. *Molecular Ecology*, 13: 537-549.

Gon, O. & Heemstra, P. 1990. Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown

Gyllenstein, U. 1985. The genetic structure of fish: differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater species. *Journal of Fish Biology*, 26: 691-699.

Haedrich, R., Merrett, N. & O'Dea, N. 2001. Can ecological knowledge catch up with deep-water fishing? A North Atlantic perspective. *Fisheries Research*, 51: 113-122.

Hauser, L., Adcock, G., Smith, P., Bernal-Ramirez, J.H. & Carvalho, G.R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). Proceedings National Academy of Sciences 99: 11742-11747.

Hauser, L. & Ward, R.D. 1998. Population identification in pelagic fish: the limits of molecular markers. In Carvalho G (ed) Advances in Molecular Ecology. IOS, Amsterdam pp 191-224.

Hebert, P., Cywinska, A., Ball, S. & deWaard, J. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B 270: 313-322.

Hedgecock, D. 1994. Temporal and spatial genetic structure of marine animal populations in the California Current. Reports of California Cooperative Oceans Fisheries Investigations 35: 73-81.

Heino, M., Dieckmann, M.U. & Godo, O. 2002. Reaction norm analysis of fisheries induced adapative change and the case of the Northeast Arctic cod. ICES CM2002/Y:14

Hoarau, G. & Borsa, P. 2000. Extensive gene flow within sibling species in the deep-sea fish Beryx splendens. *Life Sciences*, 323: 315-325.

Horn, P. 2002. Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the subantarctic to the Ross Sea, *Antarctica. Fisheries Research*, 56: 275-287.

Ianelli, J, & Zimmerman, M. 1998. Staus and future prospects for the Pacific Ocean perch resource in waters off Washington and Oregon as assessed in 1998. In Status of the Pacific coast groundfish fishery through 1998 and recommended acceptable biological catches for 1999 Pacific Fishery Management Council, Portland Oregon: 53 p.

ICES. 2005a. Advice on deepwater stocks (EC FISH). ICES Report on Deepwater Fisheries Resources 10: 10-20.

ICES. 2005b. Deepwater sharks in the northeast Atlantic (ICES Sub-areas V-XIV, mainly Portuguese dogfish and leafscale gulper shark. ICES Report on Deepwater Fisheries Resources 10: 21-27.

ISOFISH. 1998. The Vikings: the involvement of Norwegian fishermen in illegal and unregulated longline fishing for Patagonian toothfish in the Southern Ocean. ISOFISH Occasional Report , Hobart Australia 3:

James, G., Inada, T.& Nakamura, I. 1988. Revision of the oreosomatid fishes (Family Oreosomatidae) from the southern oceans, with a description of a new species. *New Zealand Journal of Marine & Freshwater Research*, 15: 291-326.

Jensen, A. & Frederikesn, R. 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe Shelf. Sarsia 77: 53-69.

Kenchington, E. 2003. The effects of fishing on species and genetic diversity. Responsible fisheries in the marine ecosystem Conf. on Responsible Fisheries in the Marine Ecosystem, Reykjavik (Iceland), 1-4 Oct 2001. Sinclair, M and Valdimarsson, G (ed): 235-253.

Kim, S-K. & Mendis, E. 2006. Bioactive compounds from marine processing byproducts - a review. *Food Research International*, 39: 383-393.

Koslow, J., Boehlert, G., Gordon, J., Haedrich, R., Lorance, P. & Parin, N. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science,* 57: 548-557.

Koslow, J. & Gowlett-Holmes, K. 1998. The seamount fauna off southern Tasmania: benthic communities, their conservation and impacts of trawling. Report to the Environmental Australia Fisheries Commission 95/058: 104 p.

Law, R. 2000. Fishing, selection, and phenotypic plasticity. ICES Journal of Marine Science 57: 659-668.

Leaman, B., Beamish, R. 1984. Ecological and management implications of longevity in some Northeast Pacific groundfishes. International North Pacific Fisheries Commission Bulletin 42: 85-97.

Leaman, B.M. 1991. Reproductive styles and life history variables relative to exploitation and management of Sebastes stocks. *Environmental Biology of Fishes*, 30: 253-271.

Lehodey, P., Grandperrin, R. & Marchal, P. 1997. Reproductive biology and ecology of a deep-demersal fish, alfonsino *Beryx splendens* over the seamounts off New Caledonia. *Marine Biology*, 128: 17-27.

Lundy, C., Rico, C. & Hewitt, G. 2000. Temporal and spatial genetic variation in spawning grounds of European hake (*Meluccius merluccius*) in the Bay of Biscay. *Molecular Ecology*, 9: 2067-2079.

Mace, P., Fenaughty, J., Coburn, R. & Doonan, I. 1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the North Chatham Rise. New Zealand Journal of Marine & Freshwater Research 24: 105-119.

Martin, A., Humphreys, R. & Palumbi, S. 1992. Population genetic structure of the armourhead *Pseudopentaceros wheeleri* in the North Pacific Ocean: application of the polymerase chain reaction to fisheries problems. Canadian Journal of Fisheries & Aquatic Sciences 49: 2386-2391.

McKenzie, K. 2002. Parasites as biological tags in population studies of marine organisms: an update. Parasitology 124: 153-163.

Milton, D. & Shaklee, J. 1987. Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandiae* (Hector) (Pisces: Merluccidae), from Australian waters. Australian Journal of Marine and Freshwater Research 38: 727-742.

Molenaar, E. 2004. Unregulated deep-sea fisheries: a need for a multi-level approach. International journal of marine and coastal law 19: 223-246.

Morato, T., Cheung, W. & Pitcher, T. 2006a. Vulnerability of seamount fish to fishing: fuzzy analysis of lifehistory attributes. Journal of Fish Biology 68: 209-221.

Morato, T., Watson, R., Pitcher, T. & Pauly, D. 2006b. Fishing down the deep. Fish and Fisheries 7: 24-34.

Morison, A., Kalish, J., Green, C. & Johnston, J. 1999. Estimation of orange roughy, black oreo and smooth oreo and natural mortality of black and smooth oreo. Final Research report to the New Zealand Ministry of Fisheries, project DEE9702

Musick, J. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24: 6-14.

Myers, R. & Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, 423: 280-283.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932-935.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R & Zeller, D. 2002. Towards sustainability in world fisheries. *Nature*, 418: 689-695.

Pineiro, C.G., Casas, M. & Banon, R. 2001. The deep-water fisheries exploited by Spanish fleets in the Northeast Atlantic: a review of the current status. Fisheries Research 51: 311-320.

Probert, P.K., McKnight, D.G. & Groove, S.L. 1997. Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 7: 27-40.

Pullin, R.S.V. 2000. Management of Aquatic Biodiversity and Genetic Resources. Reviews in Fisheries Science 8: 379-393.

Reynolds, J.D., Dulvy, N.K., Goodwin, N.B. & Hutchings, J.A. 2005. Biology of extinction risk in marine fishes. Proceedings of the Royal Society of London B 272: 2337-2344.

Richer-de-Forges, B.R., Koslow, J.A. & Poore, G.C.B. 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405: 944-947.

Rijnsdorp, A.D., Grift, R.E. & Kraak, S.B.M. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? Canadian Journal of Fisheries & Aquatic Sciences 62: 833-843.

Roberts, C., Paulin, C., Stewart, A., McPhee, R. & McDowall, R. in press. Appendix. Checklist of living lancelets, jawless fishes, cartilaginous fishes and bony fishes. In: D. P. Gordon (ed.). The New Zealand Inventory of Biodiversity. Volume 1. Kingdom Animalia. Canterbury University Press, Christchurch.:

Roberts, C.D. & Paulin, C.D. 1997. Fish collections and collecting in New Zealand. Ichthyology and Herpetology 207-229.

Roberts, J.M., Wheeler, A.J. & Freiwald, A. 2006. Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. *Science*, 312: 543-547.

Rochet, M-J. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55: 371-391.

Rogers, A.D. 1994. The Biology of seamounts. Advances in Marine Biology 30: 305-350.

Roques, S., Sevigny, J.M. & Bernatchez, L. 2002. Genetic structure of deepwater redfish, *Sebastes mentella*, populations across the North Atlantic. Marine Biology 140: 297-307.

Sedberry, G.R., Carlin, J.L., Chapman, R.W. & Eleby, B. 1996. Population structure in the pan-oceanic wreckfish *Polyprion americanus* (Teleostei: Polyprionidae), as indicated by mtDNA variation. Journal of Fish Biology 49: 318-329.

Shaw, P., Arkhipkin, A. & Al-Khairulla, H. 2004. Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology,* 13: 3293-3303.

Smedbol, R.K. & Stephenson, R. 2001. The importance of managing within-species diversity in cod and herring fisheries of the north-wetsern Atlantic. *Journal of Fish Biology,* 59: 109-128.

Smith, D.C., Fenton, G.E., Robertson, S.G. & Short, S.A. 1995. Age determination growth of orange roughy (*Hoplostethus atlanticus*): A comparison of annulus counts with radiometric ageing. Canadian Journal of Fisheries & Aquatic Sciences 52: 391-401.

Smith, P. 1994. Genetic diversity of marine fisheries resources: possible impacts of fishing. FAO Fisheries Technical Paper 344: 53 pp.

Smith, P. & Benson, P. 1997. Genetic diversity in orange roughy from the east of New Zealand. Fisheries Research 31: 197-213.

Smith, P., Benson, P. & McVeagh, S. 1997. A comparison of three genetic methods for stock discrimination of orange roughy, *Hoplostethus atlanticus*: allozymes, PCR amplified mitochondrial DNA and random amplified polymorphic DNA. Fishery Bulletin 94: 800-811.

Smith, P. & Gaffney, P. 2000a. Population genetics of Patagonian toothfish (*Dissostichus eleginoides*) and fillet identification of Patagonian toothfish and Antarctic toothfish *D.mawsoni*. CCAMLR WG-FSA-00/53 13pp.

Smith, P. & Gaffney, P. 2000b. Toothfish. Water & Atmosphere 8: 17-18.

Smith, P. & Gaffney, P. 2005. Low genetic diversity in the Antarctic toothfish *Dissostichus mawsoni* observed with mitochondrial and intron DNA markers. CCAMLR Science 12: 43-51.

Smith, P., McMillan, P., Bull, B. & McVeagh, S. 2002. Genetic and meristic variation in black and smooth oreos in the New Zealand EEZ. New Zealand Journal of Marine & Freshwater Research 36: 737-750.

Smith, P. & McVeagh, M. 2000. Allozyme and microsatellite DNA markers of toothfish population structure in the Southern Ocean. Journal of Fish Biology 57: 72-83.

Smith, P.J., McVeagh, S.M. & Ede, A. 1996. Genetically isolated stocks of orange roughy (*Hoplostethus atlanticus*) but not hoki (*Macruronus novaezelandiae*) in the Tasman Sea and Southwest Pacific Ocean around New Zealand. *Marine Biology,* 125: 783-793.

Smith, P.J., McVeagh, S.M., Mingoia, J.T. & France, S.C. 2003. Mitochondrial DNA sequence variation in deep-sea bamboo coral (Keratoisidinae) species in the southwest and northwest Pacific Ocean. *Marine Biology*, 144: 253-261.

Smolenski, A.J., Ovenden, J.R. & White, R.W.G. 1993. Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus*), Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. *Marine Biology*, 116: 219-230.

Somerton, D.A. & Kikkawa, B.S. 1992. Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on southeast Hancock seamount. Fishery Bulletin 90: 756-769.

Stokes, K. & Law, R. 2000. Fishing as an evolutionary force. Marine Ecology Series 208: 307-309.

Swan, S.C., Gordon, J.D.M. & Shimmield, T. 2003. Preliminary investigations on the uses of otolith microchemistry for stock discrimination of the deep-water black scabbardfish (*Aphanopus carbo*) in the Northeast Atlantic. Journal Northwest Atlantic Fisheries Science 31: 221-231.

Thresher, R.E. 1999. Elemental composition of otoliths as a stock delineator in fishes. Fisheries Research 43: 165-204.

Turner, T.F., Wares, J.P. & Gold, J.R. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarein dependent marine fish (Sciaenops ocellatus). *Genetics*, 162: 1329-1339.

UN. 1995. Agreement for the implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks. United Nations Conference on Straddling Fish Stocks and Highly Migratory Fish Stocks Sixth session New York, 24 July-4 August 1995. http://daccessdds.un.org/doc/UNDOC/GEN/N95/274/67/PDF/N9527467.pdf?OpenElemen

VanDover, C.L. 2000. The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton, NJ.

Waples, R.S. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution 41: 385-400.

Ward, R.D., Elliott, N.G., Grewe, P., Last, P.R., Lowry, P.S., Innes, B.H. & Yearsley, G.K. 1998. Allozyme and mitochondrial DNA variation in three species of oreos (Teleostei: Oreosomatidae) from Australasian waters. New Zealand Journal of Marine & Freshwater Research 32: 233-245.

Ward, R.D., Woodwark, M & Skibinski, D.O.F. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *Journal of Fish Biology*, 44: 213-232.

Watson, R. & Morato, T. 2004. Exploitation patterns in seamount fisheries: a preliminary analysis. In Seamounts: Biodiversity and Fisheries (ed) T. Morato and D. Pauly Fisheries Centre Research Report: 61-65.

Wilson, R. & Kaufman, R. 1987. Seamount biota and biogeography. *Geophysics Monographs,* 43: 355-377.

Zardus, J.D., Etter, R.J., Chase, M.R., Rex, M.A. & Boyle, E.E. 2006. Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). *Molecular Ecology*, 15: 639-651.

Zeldis, J.R., Grimes, P.J. & Ingerson, J.K.V. 1994. Ascent rates vertical distribution, and a thermal history model of development of orange roughy *Hoplostethus atlanticus* eggs in the water column. *Fishery Bulletin,* 93: 373-385.

Genetic resources for aquaculture: status and trends

Roger S.V. Pullin
7A Legaspi Park View, 134 Legaspi Street, Consultant, Philippines

1. SUMMARY

Aquaculture, the farming of aquatic plants and animals, has grown consistently since 1970, when it provided only 3.9 percent of world fish supply. In 2004, global production of farmed fish (mainly crustaceans, molluscs and finfish) was over 45 million tonnes, comprising about 32 percent of total world fish supply, while the total production of farmed seaweeds for food and extraction of chemicals, was about 13.9 million t. Aquaculture also provides increasing proportions of the world's supply of ornamental aquatic organisms. Over 90 percent of aquaculture takes place in developing countries, where it has high importance for poor people in terms of nutrition and livelihoods and where further responsible development of aquaculture, integrated with other natural resource use, has high potential for future growth. Based upon statistics submitted to FAO by its member States, about 84 percent of farmed fish production comes from Asia, with 67 percent coming from the Peoples' Republic of China. However, aquaculture is increasing in importance in all developing regions and is expected to provide about 50 percent of world food fish supply within the next 20 years.

The future of aquaculture will depend in large measure upon the effective management of the genetic resources for farmed aquatic plants (PGR) and farmed fish (FiGR), as well as those for the organisms that provide their food and ecosystem services. Fish farms are agroecosystems and aquatic genetic resources for aquaculture on farms are part of agrobiodiversity. For example, microalgae and small invertebrates are mass cultured as live feeds for production of the early life history stages ("seed") of farmed fish in hatcheries and natural feeds such as plankton are produced in fish farm waters. For some live feeds (e.g. the brine shrimp, *Artemia salina*) there is extensive information on genetic resources, but the genetic resources of most of the flora and fauna that support farmed fish production have been little explored.

The main difference between the status of most FiGR and aquatic PGR for aquaculture and all PGR and livestock ("farm animal") genetic resources (FAnGR) for agriculture is that, with few exceptions, substantial domestication and genetic improvement of farmed aquatic species lag far behind the long history of purposeful breeding and genetic gains achieved for crops and livestock. This is now changing rapidly for some widely farmed aquatic species, such as tilapias, but much of the world's production of seed for aquaculture and subsequent farm harvests remain documented mainly at the species level. Among the 80 species of livestock that are used for farming and ranching, over 6 000 different breeds have been recognized. The total number of aquatic animal species that have been farmed, experimentally or in actual production systems, is probably about 500, but the total number of farmed fish breeds has not yet been documented.

Many of the aquaculture statistics collected by governments and submitted to FAO are flawed; for example, by incomplete coverage of small-scale rural and

peri-urban aquaculture; by omission of data for some farmed aquatic species, such as freshwater macrophytes; by variable and incorrect nomenclature; and by aggregating and recording data by taxa higher than the species level. The relative importance of many genetic resources for aquaculture has still to be deduced in general terms from statistics that describe them as species, genera, families, commodity groups, and others "not elsewhere included (nei)". For example, "aquatic plants nei" have become one of the largest contributors to production statistics for farmed aquatic plants. With few exceptions (e.g. catfish and striped bass), the contributions of fish hybrids, distinct strains, and other genetically altered forms are not yet recorded in most national statistics, and therefore cannot yet be accommodated in the statistics disseminated by FAO.

Information about genetic resources for aquaculture is not yet adequately covered by major global and regional databases and online information systems, including those currently provided by FAO and those that cover in detail the biology of aquatic organisms; e.g. FishBase. Moreover, there is a widespread need for greater standardization of correct nomenclature and terminology with respect to aquatic genetic resources. Progress is, however, underway in both these areas, with operators of databases and information systems for aquatic plants, crustaceans, molluscs and finfish now striving for greater collaboration and interoperability.

Major aquaculture publications and statistics reviewed from 1972 to 2004 suggest the following approximate ranges of numbers of farmable and potentially farmable aquatic organisms identified to species: microalgae, about 5 named as species, but with 16 genera also named; freshwater macrophytes, 5-8; marine macroalgae (seaweeds), 13-24; crustaceans, 26-79; molluscs, 20-74; other invertebrates, 4-7; finfish, 122-294; amphibians and reptiles, 3-11. Further exploration and documentation of the genetic resources of such large numbers of species - as wild and captive populations, geographical races, distinct farmed strains, hybrids and other genetically altered forms - will be a large task. However, the genetic resources for farmed aquatic plants could be covered under existing arrangements for terrestrial PGR and the most important FiGR for aquaculture could be prioritized; for example, by choosing initially the top 50 to 100 species that contribute most to farmed fish production, though with flexibility to include others that have clear potential importance and/or any wild and farmed FiGR that appear most threatened with extinction.

Consumer preferences are the main driver for farmers' choices of which fish to farm. However, most of the world's aquaculture and culture-based fisheries production is based on seed produced from broodstock populations by the operators of fish hatcheries. Public and private seed producers, their breeding programmes and related research determine largely which types of seed are available for purchase by farmers, for subsequent growout to marketable size. Fish farms range in size from small-scale/backyard to large scale corporate ventures. Vertically integrated aquaculture, similar to broiler chicken production, is also expanding. Most aquaculture is undergoing intensification to boost production per unit area or volume of farm waters. This requires the development of strains, hybrids and other genetically altered forms that are tailored to intensive farming, especially with respect to commercial traits such as good feed conversion, disease resistance, fillet yield, colour, flavour, etc.

Because of the short history of domestication, breeding programmes and related research for most farmed aquatic organisms, the free-living populations of their wild and feral relatives and of other potentially farmable aquatic species have high importance as genetic resources. Many of these free-living populations, especially in freshwaters, are among the world's most seriously threatened biodiversity; for example, the wild genetic resources of farmed carps and tilapias. Moreover in aquaculture, as in agriculture, most private sector seed producers and farmers keep only the most profitable farmed species and types, leaving others under threat of extinction. The use

in aquaculture production and related research of alien species and of genetically altered forms (e.g. distinct strains, hybrids, polyploids, trangenes etc., whether developed from alien and/or indigenous species) is certain to increase. This will require more effective biosafety and biosecurity procedures than have been implemented to date, particularly with respect to thorough appraisal of the impacts of escapes and releases of farmed aquatic organisms before granting approvals for introductions and transfers, as well as strictly enforced quarantine.

These trends indicate an urgent need for better management – meaning fully integrated use and conservation – of aquatic genetic resources for aquaculture: *in situ/in vivo*, as free-living, wild and feral populations; *in situ/in vivo*, as captive populations on-farm; *ex situ/in vitro*, as collections of cryopreserved sperm, embryos and other tissues/DNA; and *ex situ/in vivo* as aquarium and research populations. This will require increased investment in the management of FiGR and aquatic PGR, commensurate with their high and growing contributions to world food security, Keeping representative, free-living wild populations of farmed fish species undisturbed in their natural habitats and off-limits to aquaculture and to contact with farmed fish, has operational and opportunity costs. Therefore, unless there is equitable sharing of costs and benefits among the stewards and potential users of such aquatic genetic resources for aquaculture, the conservation element in their management will not be achieved. Establishing and maintaining *ex situ, in vivo* and/or *in vitro,* fish gene banks is also expensive and will require public and private sector investment and partnerships. Attempts by the private sector to acquire intellectual property rights on genetically altered fish and related biotechnological processes in aquaculture have so far been limited, compared to the situation in plant breeding. It is unlikely that attempts to enforce proprietary rights on genetically altered fish will prosper in the near future. Rather, as public and private fish breeding programmes develop, returns to fish breeders will likely come from purchased access to pedigreed fish populations and eventually to pedigree individuals, as for livestock and pet animals. However, private sector research, especially for the development of biotechnological products and processes, is bound to increase in aquaculture, following the trends in agriculture.

The following strategic directions are suggested for improving the management of genetic sources for aquaculture: increased investment; management (i.e. fully integrated use and conservation) as part of agrobiodiversity; improved information systems; conservation in changing ecosystems; reconciliation of aquaculture with nature conservation; progressive linking of the management of aquatic PGR and FiGR with that for terrestrial PGR and FAnGR; and exploration of the application of an interactive governance approach, with assessments of the governability of aquatic genetic resources.

2. INTRODUCTION

Aquaculture is the farming of aquatic plants and animals. It comprises the mass production, usually in hatcheries, of "seed" (eggs, larvae, postlarvae, fry, fingerlings, juveniles etc.) of farmed aquatic organisms, and the subsequent growout of that seed to marketable size in aquatic farms or its release for culture-based fisheries (CBF) (e.g. see Bartley and Leber, 2004; Caddy and Defeo, 2004). Hatchery operations for CBF are generally considered part of aquaculture. The FAO Code of Conduct for Responsible Fisheries (FAO, 1995) and its guidelines for aquaculture development (FAO, 1997) refer throughout to "*aquaculture, including culture-based fisheries*". Seed is produced mainly from captive breeding populations. However, for the minority of farmed aquatic species where mass production of seed in captivity is not yet technically possible, or where its collection from wild populations still makes economic sense, wild seed or young adults are obtained from capture fisheries and then grown to marketable size in captivity. This can be termed capture-based aquaculture (e.g. Ottolenghi *et al.,* 2004).

This review is concerned mainly with the genetic resources of fish, meaning finfish and aquatic invertebrates (principally crustaceans and molluscs) that are farmed or potentially farmable. The genetic resources for CBF, as well as their genetic impacts on wild populations, are not considered here. Most farmed aquatic plants and animals are used for human consumption as food but some are farmed for other purposes; e.g. for extraction of industrial chemicals (seaweeds), as ornamental species (aquatic plants, invertebrates, finfish, amphibians and reptiles), for sport fisheries (finfish) and for cosmetic, jewelry, and medicinal products (molluscs, seahorses etc.). It is implicit in this review that policy and other provisions made for the genetic resources of aquatic organisms farmed as human food should apply also to those of aquatic organisms that are farmed for other purposes. Genetic resources for farmed aquatic plants are covered briefly here, emphasizing macroalgae (seaweeds) farmed for human food or for extraction of chemicals. All genetic resources for farmed aquatic plants are called PGR.

By convention, all fish genetic resources for aquaculture and capture fisheries are now termed FiGR. FAO aquaculture statistics include farmed macroalgae within a general definition of "fish", but their genetic resources are PGR, not FiGR. Farmed aquatic amphibians and reptiles also figure in FAO and some other farmed fish statistics, but can be considered as livestock ("farm animal") genetic resources (FAnGR), thereby restricting the use of the term FiGR for farmed aquatic vertebrates to finfish alone. Similarly, the farming of aquatic birds and mammals is not considered part of aquaculture, and their genetic resources are regarded as FAnGR, not FiGR. Farmed amphibians and aquatic reptiles are mentioned here only insofar as they are included in FAO aquaculture statistics and major texts.

This review builds upon recent publications that address conservation and use of aquatic genetic resources (e.g. Pullin *et al.,* 1999; Pullin, 2000, 2006b; Science Council Secretariat, 2005). The importance of aquaculture, its rapid growth and dynamic nature are summarized, with overviews of the main categories of genetic resources for aquaculture; i.e., for feeds and ecosystem services, aquatic plants and fish. Discussions follow on factors that affect the status of and trends in genetic resources for aquaculture: choosing what to farm; information and nomenclature; threats; management, defined as fully integrated use and conservation; and the sharing benefits and costs, including ownership and use issues. No order of priority is implied here. The review concludes by identifying some strategic directions for improving the management (i.e., the fully integrated use and conservation) of genetic resources for aquaculture.

3. THE GROWING IMPORTANCE OF AQUACULTURE

FAO is the source of all aquaculture statistics quoted here, unless otherwise stated. FAO began to publish statistics in 1950 but, up to 1984, aquaculture statistics were combined with those for fish catches. Despite their subsequent separate status and increasing importance, world aquaculture statistics are still beset with uncertainties. There is a widespread need to improve collection of data from small-scale, rural aquatic farms, especially in developing countries. The world's small-scale rural and peri-urban aquaculture production, as well as its value and importance in household food security and provision of incomes and employment are probably substantially under-recorded in many national statistics. Moreover the real, as opposed to perceived, contributions of many CBF to world fish supply are poorly known and will remain so unless data for their seed production and harvests are adequately disaggregated from those for growout on farms and capture of wild fish. Uncertainties concerning the current contributions and future potential of CBF have been mentioned by many authors (e.g. Lorenzen *et al.,* 2001; Leber *et al.,* 2004). There is also a need to analyse trends in aquaculture both with and without inclusion of the statistics reported by the Peoples' Republic of China (PRC) (e.g. New, 2003).

Despite these uncertainties, the present contributions of aquaculture to world food security and its future potentials are well recognized. Aquaculture has large potential for further growth, not only in the countries where it is well-established but also in many of those where it is relatively new, including sub-Saharan Africa and Latin America. Governments in all developing regions have framed and begun to implement policies that place reliance on expansion and intensification of aquaculture for sustaining and increasing their fish supply (e.g. see Brugère and Ridler, 2004).

In 2002, the status and future prospects of aquaculture were described as follows in a background paper for the first meeting of the FAO Sub-Committee on Aquaculture (FAO, 2002):

"Aquaculture is an important domestic provider of much needed, high quality, animal protein, generally at prices affordable to the poorer segments of society. It is also a valuable provider of employment, cash income, and foreign exchange, with developing countries contributing over 90 percent of the total global production. When integrated carefully, aquaculture also provides low-risk entry points for rural development and has diverse applications in both inland and coastal areas."

Annual rates of increase for aquaculture production and value have varied greatly with species and farming systems but, since the 1970s, almost all have been higher than those for other food production sectors and remain so. For example, shrimp farming in the late 1970s grew at 24 percent per year and FAO (2002) described its 6 percent average annual growth rate in the 1990s as "modest". Farmed fish currently provide about 32 percent of world food fish supply, compared to about 3.9 percent in 1970 and their contributions are widely expected to grow to about 50 percent, probably within the next 20 years. According to McHugh (2003), most of the world's production or macroalgae for human food and for extraction of chemicals (hydrocolloids) is derived from aquaculture. For 2004, FAO statistics indicate total world production of 13.9 million tonnes of farmed aquatic plants, worth about $6.8 billion. Aquaculture is also an increasingly important source of supply for ornamental freshwater and marine tropical fish, in developed and developing countries. Information on ornamental plants and animals is widely available through global databases (e.g. for marine fish and invertebrates, see www.unep-wcmc.org).

A nutrition transition, from diverse, traditional fish-, fruit- and vegetable-rich diets to fat-, sugar- and alcohol-rich diets, is underway in the developing world and is causing rapid growth of diet-related, chronic diseases (ischemic heart disease, diabetes, obesity, hypertension, stroke, and certain cancers), with high consequential costs. In 1995, these diseases accounted for 41.6 percent of all deaths and 22.5 percent of all hospital expenses in the PRC, equivalent in total to 2.1 percent of gross domestic product (GDP), while for Sri Lanka the corresponding figures were 18.3 percent, 16.7 percent and 0.3 percent of GDP (Popkin *et al.,* 2001). Gillespie and Haddad (2001) reviewed the "double burden" of malnutrition: undernutrition and overnutrition from overconsumption of unhealthy foods. Farmed fish will be increasingly important contributors in efforts to solve these problems, especially as they can provide substantial nutritional and livelihood benefits to the poor (e.g. ADB 2005a; FAO/NACA-STREAM 2005). For many developing countries, aquaculture is the main hope for sustaining and increasing contributions of affordable fish and fish products to healthy diets. Fish provide their consumers with animal protein, health promoting lipids and essential vitamins and minerals and are particularly important in human nutrition as sources of the omega-3 fatty acids necessary for brain development in the human foetus and its functioning throughout life (e.g. Elvevoll and James, 2000; Anon., 2006).

Aquaculture is often categorized according to the feeds available to farmed fish. In extensive aquaculture, fish depend entirely on the natural productivity of farm waters,

TABLE 1
Production (tonnes (t) and value (US$, thousands) in 2004 of farmed fish (mainly crustaceans, finfish and molluscs) for the top ten producer countries and the rest of the world.

Producer countries	Production (t)	Value ($ thousands)
1. People's Republic of China, excluding the Hong Kong SAR	30 614 998	30 869 609
2. India	2 472 335	2 936 479
3. Viet Nam	1 198 617	2 443 589
4. Thailand	1 172 866	1 586 626
5. Indonesia	1 058 042	2 130 004
6. Bangladesh	914 752	1 363 180
7. Japan	776 421	3 205 093
8. Chile	674 979	2 801 037
9. Norway	637 993	1 688 202
10. USA	606 549	907 004
Subtotal	**40127 552**	**49 930823**
Rest of the world	5 353 375	13 562 462
TOTAL	**45480 927**	**63 493 285**

Source: FAO Statistics

supplying natural feeds: plankton, detritus, vegetation etc. In semi-intensive aquaculture, relatively cheap supplementary feeds are given, and the production of natural food in farm waters is sometimes artificially increased by fertilization. In intensive aquaculture, farmed fish are entirely dependent upon provision of nutritionally complete feeds, which typically account for about 65 percent of the total variable costs of production. Intensification, through maximizing use of pond fertilizers and supplemental feeds to intensive feedlot systems, is now a major trend for most forms of aquaculture. This boosts production per unit area or volume of farm waters, but makes large ecological footprints beyond farming areas. The main exceptions to this are seaweed farming and most farming of bivalve molluscs, which remain largely extensive aquaculture operations, involving minimal husbandry from seed to harvest.

Table 1 summarizes the most recent aquaculture production and value statistics (2004), by the top 10 leading countries and the rest of the world, for fish farmed for human food. From these data, Asian countries accounted for 84 percent of world aquaculture production in 2004, with the PRC alone accounting for 67 percent. Note the higher values accorded to aquaculture produce in the more developed countries.

4. GENETIC RESOURCES FOR AQUACULTURE

4.1 Feeds and ecosystem services

All sources of human food production, including aquaculture, are interconnected as a global food web. The genetic resources for the cereal crops and other plants that provide ingredients for the feeds given to farmed fish are genetic resources for aquaculture. Similarly, the genetic resources for the low value/trash fish (LV/TF) and industrial fisheries that provide fish, fishmeal and fish oils for feeding farmed fish and livestock are genetic resources for both aquaculture and livestock production. However, Tacon *et al*., (2006), citing FAO (2005), pointed out that only 18.2 percent of global fishmeal production and 45 percent of fish oil production is currently attributable to named species. This means that many of the FiGR for fishmeal are fish oil production are undocumented, even at species level. From a world food security perspective, it is important to note that aquaculture production which remains based upon substantial use of wild caught fish, fishmeal and fish oil, cannot be claimed as a net gain in fish supply or as a net contribution to filling the gap in fish supply caused by declining capture fisheries. Tacon *et al.*, (2006) estimated that in 2003 the "aquaculture sector"

consumed as feeds the equivalent of 20 to 25 million tonnes captured fish, as live weight equivalents, in order to produce 30 million tonnes of farmed finfish and crustaceans. They identified the following groups of farmed fish as net consumers or producers of fish: net consumers – river eels, marine fish and shrimps, salmon and trout; net producers – carp, catfish, freshwater crustaceans, milkfish and tilapia.

Production of fish seed in aquaculture and for CBF often involves protein-, essential lipid- and micronutrient-rich starter fish feeds; supplied in fine particulate form or as live food organisms, cultured or collected specifically for this purpose; e.g. bacteria, microalgae, rotifers, crustaceans and molluscan larvae. The genetic resources for organisms that are used to produce these feeds and for live food organisms used in aquaculture are also genetic resources for aquaculture. The status and diversity of some of the latter are well-documented; for example, there are interlinked collections and information sources for cultured bacteria and microalgae and a reference centre for the brine shrimp *Artemia salina* and the rotifer *Brachionus plicatilis* (www.aquaculture.ugent.be).

Many other microbial, plant and animal species provide farmed fish with food and feed ingredients and with a wide range of ecosystem products and services, including oxygen, shelter, spawning substrates and waste processing. Their genetic resources are essential for the future of aquaculture, being broadly analogous to the genetic resources for organisms that contribute organic fertilizers for the production of crops and fodders for livestock. Inedeed, all species that provide feeds and ecosystem services to aquaculture are part of agrobiodiversity when found on-farm; i.e., in agroecosystems. These supportive genetic resources for aquaculture merit much wider recognition and documentation, and above all more effective management, than they have received to date.

4.2 Farmed aquatic plants

Farmed aquatic plants comprise green microalgae (e.g. Chlorella); blue-green algae, more properly termed cyanobacteria (e.g. Spirulina); macroalgae (brown, green and red seaweeds); and freshwater macrophytes (e.g. floating species, such as azolla and duckweeds, and emergent species such as lotus, water chestnut and water spinach). Table 2 gives numbers of farmed aquatic plants identified to species in some major aquaculture publications.

Farmed microalgae are not well covered in most aquaculture literature, except as live feeds for fish hatchery operations. FAO statistics give production of farmed Spirulina in 2004 as 41 750 tonnes. *Chlorella vulgaris* is listed, but with zero production recorded. Stickney (2000) mentioned 16 farmed microalgal genera.

TABLE 2
Numbers of farmed aquatic plants that are named as species in some major aquaculture publications, including species under experimentation and/or having potential for aquaculture as well as those used in actual production systems

Farmed aquatic plants	Numbers of species			
	A	B	C	D
Microalgae	5	2	-	1
Freshwater macrophytes	8	5	5	-
Marine macroalgae (seaweeds)	15	24	-	13
TOTAL	28	31	5	14

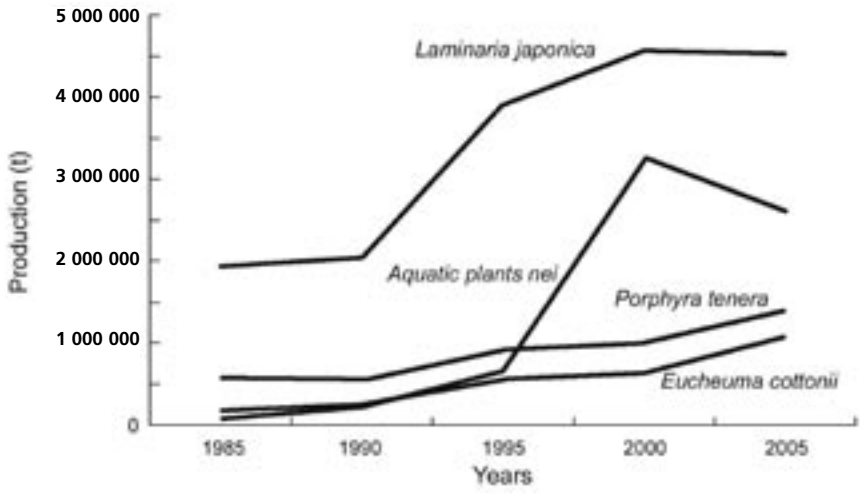
Source A: Bardach *et al.* (1972); B: Pillay (1990); C: Stickney (2000); D: FAO aquaculture statistics (2004)

Despite their high importance as human food, as fodders and fertilizers in agriculture and as components of waste treatment systems (e.g. Edwards, 1980; Van Hove, 1989; Kanungo *et al.,* 2001), farmed freshwater macrophytes are not well covered in mainstream aquaculture literature and FAO aquaculture statistics. Some freshwater macrophytes – for example, water spinach (*Ipomea aquatica*) are major crops, but information on their production and their genetic resources is not easily obtained, either from agriculture or aquaculture sources. Conversely, the wetland and deepwater rice, which are aquatic macrophytes, are well covered by mainstream crop genetics literature. Most of the available information on other freshwater macrophytes concerns control of nuisance species; for examples, see the Journal of Aquatic Plant Management; http://www.apms.org/japm/japmindex.htm. However, a new "forum" about peri-urban farming of freshwater macrophytes and fish is being established, based upon examples in Southeast Asian cities (contact: W. Leschen; wl2@stir.ac.uk).

FAO statistics for farmed aquatic plants focus on marine macroalgae (seaweeds) and are included with farmed fish statistics. They name only eight macroalgal species and group others together within seven genera and/or as higher taxa. The major contributors to world farmed seaweed production that are identified to species are *Laminaria japonica*, *Porphyra tenera*, and *Eucheuma cottonii*. Large contributions are said to come from "aquatic plants nei" (i.e. not elsewhere included), which are assumed to be macroalgae. Production of these aquatic plants nei has tended to increase, mainly because of the larger quantities reported from the PRC since 1998 (1 946 980 tonnes) as compared to 1997 (461 675 tonnes). Prior to 1998, production of farmed seaweeds in the PRC was reported on a live (wet) wet basis, whereas from 1998 it was recorded first as dry weight and then reported after applying conversion factors (A. Lowther, personal communication). Figure 1 shows the trends in production of the four major farmed species, plus aquatic plants nei, from 1985 to 2004.

McHugh (2003) forecast limited scope for expansion of seaweed farming as follows: to supply agar, limited; to supply alginates (typically from *Laminaria japonica*), about 2-3 percent per year; to supply carrageenan, about 5 percent per year; and as human food, highly variable prospects, dependent upon promotional efforts. However, seaweed farming undoubtedly has potential to improve the lives of some poor and marginalized

FIGURE 1
Production (tonnes; t) of major species of farmed macroalgae and others "not elsewhere included (nei)" from 1985 to 2003



Source: FAO statistics

coastal communities, especially in the tropics. For example, in the Philippines Autonomous Region in Muslim Mindanao, some poor coastal communities in the farm seaweed as contract growers, for exporters of seaweed products. In 2004, this region produced 472 514 tonnes of farmed seaweed: over 50 percent of the Philippine national total of that used for exportable seaweed products (Unson, 2006). Against the many actual and potential benefits of seaweed farming, there is serious cause for concern when alien macroalgal species are introduced for aquaculture to new coastal locations without through prior appraisal of their possible ecological impacts.

More detailed coverage of production and value data for farmed aquatic plants, with authoritative and correct names at species level, is an essential prerequisite for monitoring the status of and trends in their genetic resources. This merits high priority, not only for the major commercial species groups but also for those that are of high importance as contributors to the food and livelihood opportunities of poor communities; e.g. *Caulerpa* spp. in tropical Asia. The database www.algaebase.org is a good source of information on correct taxonomy and nomenclature of algae and could be supplemented to give information on the genetic resources of farmed algae. At present, however, most information about these PGR is scattered and is to be found mainly in the major phycological journals and occasionally in those that cover aquaculture in general (e.g. Cheney 1999). It could be collected and made accessible through existing arrangements for terrestrial PGR, given additional investments.

4.3 FARMED FISH

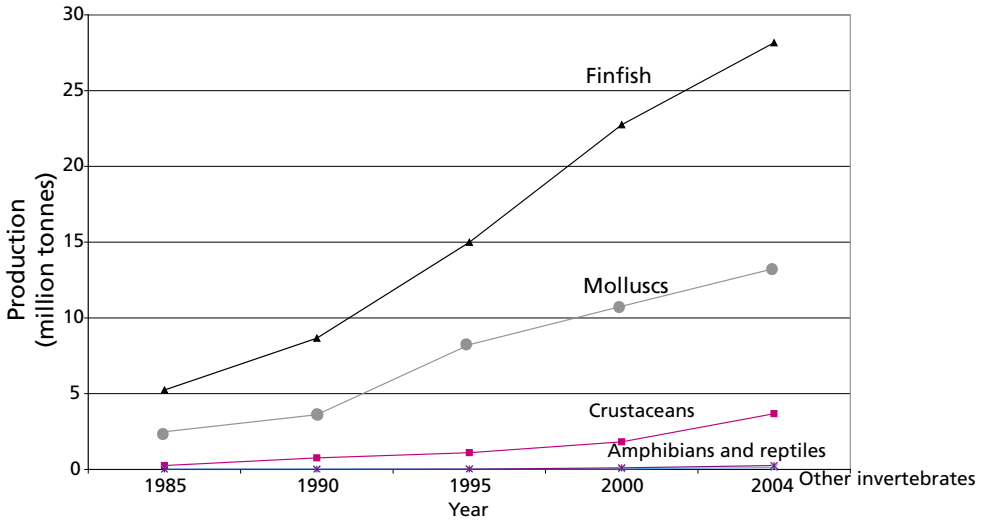
FiGR for aquaculture can categorized in a wide variety of ways: by taxonomy and genetic terminology (e.g. allele, selected strain, hybrid, artificial polyploid, transgene, species, genus, family, order, commodity group etc.); by location (area of production; natural and introduced geographic ranges; by free-living and/or farm environments, including migratory habits (brackishwater/diadromous; freshwater; marine) and production systems (cages, pens, ponds, raceways, recirculating systems, tanks, etc.); by relative current worth (production tonnages, monetary values, nutritional importance, poverty alleviation through livelihood provision and diversification, sociocultural value; sport and recreational value etc. However, the main basis for categorization of FiGR for aquaculture is their actual and potential use, as indicated by aquaculture statistics and research findings. Table 3 gives numbers of farmed aquatic animals identified to species in some major aquaculture publications.

TABLE 3
Approximate numbers of farmed aquatic animals that are named as species in some major aquaculture publications, including those having potential for farming

Farmed aquatic animals	Numbers of species				
	A	B	C	D	E
Invertebrates					
Crustaceans	79	38	45	26	38
Molluscs	61	43	74	20	64
Others (mainly echinoderms)	-	-	-	7	4
Subtotal	**140**	**81**	**119**	**53**	**106**
Vertebrates					
Finfish	294	130	201	122	212
Amphibians and reptiles	6	-	11	6	3
Subtotal	**300**	**130**	**212**	**128**	**215**
TOTAL	**440**	**211**	**331**	**181**	**321**

Sources A: Bardach *et al.* (1972); B: Pillay (1990); C: Nash (1993); Nash and Novotny (1995); D: Stickney (2000); E: FAO aquaculture statistics (2004)

FIGURE 2
Production (tonnes; t) of farmed fish (crustaceans, finfish and molluscs) from 1985 to 2003



Source: FAO statistics

FAO aquaculture statistics retain data entry lines for species and higher taxa for which zero production and value are recorded. For some, production has been zero for decades. This means that FAO's aquaculture statistics are records of all historical use of these species and higher taxa, not just records of recent and current farming. Figure 2 shows the production of farmed fish by major groups (crustaceans, finfish and molluscs) from 1985-2004, with production of other farmed aquatic invertebrates and of farmed aquatic amphibians and reptiles seen as very small by comparison.

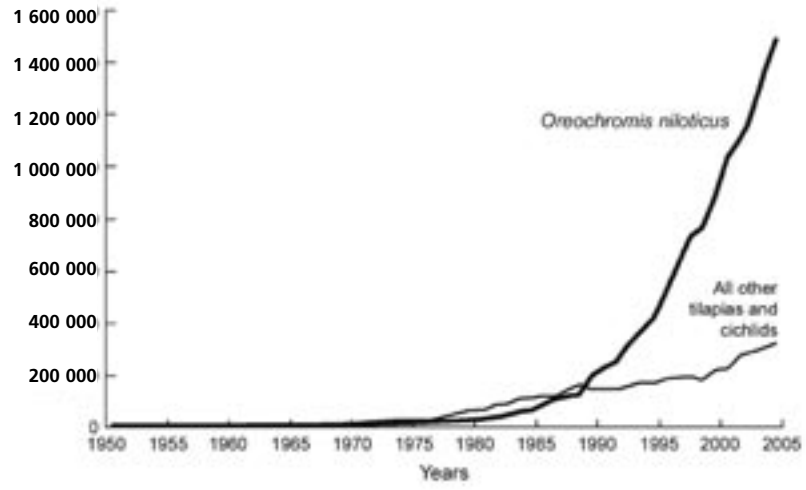
As Bartley *et al.*, (2001) have shown, interspecific fish hybrids are used in aquaculture, but their contributions to production go largely unrecognized and, with very few exceptions (e.g. hybrid catfish [*Clarias gariepinus* x *Clarias macrocephalus*] and hybrid striped bass [*Morone chrysops* x *Morone saxatilis*]), are not yet captured adequately in national or FAO statistics. The data from member countries, upon which FAO statistics are based, is given only at species level or at higher taxa comprising unspecified numbers of species; for example, genus + "spp." and "not elsewhere included". There is no information concerning any taxon below species level.

FAO statistics can be analysed in various ways to attempt to prioritize farmed aquatic species. Contributions not only to aquaculture production and value but also to availability of produce that is affordable by poor consumers would probably be the most equitable and best broad measure. Such prioritization would, however, be a lengthy exercise and is not attempted here. A good general idea of the approximate numbers of important farmed fish can be gained from recent analyses. For example, New (2003) lists the following numbers of clearly important species: 8 crustaceans; 10 molluscs; and 26 finfish (13 freshwater, 7 diadromous and 6 marine). This gives a total of 44 most important species, but more flexibility and inclusiveness are needed to prioritize FiGR for aquaculture because some species are of special importance to only one or a few countries.

The relative national and international importance of a farmed aquatic species can change rapidly; for example, farmed Nile tilapia (*Oreochromis niloticus*) production has shown extraordinarily rapid growth in recent years (Figure 3), though a substantial proportion of what is currently recorded as production of farmed Nile tilapia is

FIGURE 3

Production (tonnes; t) of the world's main farmed tilapia species *(Oreochromis niloticus)* and of all other farmed tilapias and other cichlids from 1950 to 2003



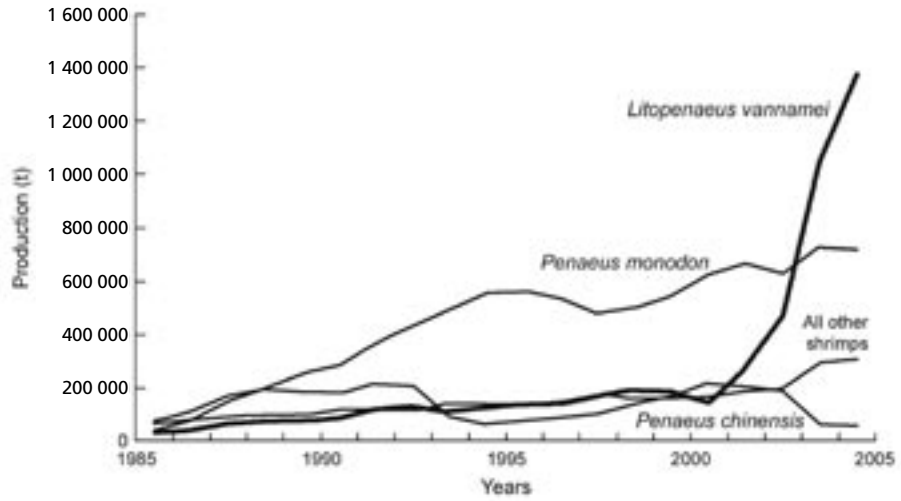
Source: FAO statistics

probably of tilapia hybrids having this species as one of the parents. The Pacific white shrimp (*Litopenaeus vannamei*) has rapidly become the main species of farmed penaeid shrimp. The data shown in Figure 4 are probably underestimates of its increasing contributions, because some countries reporting to FAO take time to adjust their reporting by species as the proportions of farmed species change. *L. vannamei* probably now accounts for over 80 percent of farmed penaeid shrimp production in Asia.

The world's FAnGR for livestock farming and ranching comprise about 80 species, of which 14 contribute most to world production and within which over 6 000 breeds have been recognized, whereas the world's FiGR for aquaculture probably comprise about 500 species that have recorded as having been farmed to some extent (including experimentally) at some time (Pullin, 2006b; Science Council Secretariat, 2005). FishBase (www.fishbase.org) has listed 344 species of farmed finfish. However, data currently available at species level in aquaculture statistics and aquaculture research literature suggest to this author that substantial coverage of FiGR for aquaculture could be achieved by prioritizing 50 to 100 species of farmed and potentially farmable fish, taking into consideration their international and national importance as well as their status, especially where they are threatened (see 7. below).

All major livestock species are considered fully domesticated. Their few remaining wild relatives are of low importance for future breeding programmes, and there are few new potential candidate species for farming. Most farmed fish species are not yet fully domesticated. Their wild relatives are of high importance for breeding programmes and related research, and there are many (possibly hundreds) of new potential candidate species for aquaculture. Balon (2004) argued that only the common carp (*Cyprinus carpio*) as a farmed food fish and as koi ornamental carp, the goldfish (*Carassius auratus*) and a few other ornamental species can be called true domesticates, with other farmed fish (including Chinese and Indian carp, catfish, salmon, sturgeon and trout species) qualifying only as "exploited captives", apart from their few colour variants, such as albino strains, that can be termed "domesticated". There is good evidence to support this view. For example, the diversity and stability of goldfish (*Carassius auratus*) breeds are comparable to those for dog breeds (e.g. Zhen, 1988), but most

FIGURE 4
Production (tonnes) of three major species of farmed penaeid shrimps and of all other farmed shrimp species from 1985 to 2003



Source: FAO statistics.

farmed fish strains and hybrids look alike and the consumer of farmed fish and farmed fish products does not yet have breed-specific choices, comparable to those available for many livestock products. At present, the world's farmed fish are represented by relatively few well-documented, distinct and stable breeds.

Prior to the big expansion of application of genetics in aquaculture that began in the late 1980s, development of and documentation about distinct and stable breeds and hybrids of farmed fish were poor. Even by the 1990s, fish breeds and hybrids had not been developed for particular farm environments and farming methods and for most farmed aquatic species, particularly in the developing countries, well-documented FiGR of known provenance were simply not available. This meant that the products of any well-reputed genetic improvement research were almost certain to enjoy high demand for use in a wide range of farming systems. GIFT and GIFT-derived Nile tilapia are a good example. Having been bred from initial research trials in a wide range of farm environments from ricefields to ponds and cages (Eknath *et al.,* 1993), GIFT and GIFT-derived Nile tilapia have been farmed in most tilapia farming systems and, in view of their broad genetic base, have become the main basis for national tilapia breeding programs in several countries (ADB, 2005b).

Parallel to the intensification of aquaculture, there is an ongoing quest to push many farmed aquatic species towards omnivory and acceptance of least-cost formulated feeds, irrespective of their natural feeding habits (Pullin, 2006a). Many farmed fish, especially marine species, are naturally carnivorous but are being constrained to accept feeds containing as much plant and microbial protein as is biologically possible, as well as a wide range of rendered livestock and other waste products. Conversely, many widely farmed and naturally herbivorous and omnivorous fish species (such as grass carp and Nile tilapia) are being farmed more and more intensively, using feeds containing fishmeal, rendered livestock products etc. In general, these trends require the development of fish strains, hybrids and other genetically altered forms that perform well in intensive farming systems, that show good feed conversion on low cost feeds, that yield attractive and well-flavoured products, and that enjoy high survival

and growth performance in adverse environments; for example, cold- and saline-tolerant tilapias. Breeding programmes and related research that compare these and other commercial traits among different farmed strains, hybrids and other genetically altered forms are therefore increasing (e.g. Rutten *et al.,* 2004a, 2004b) and will draw upon FiGR from farmed, wild and feral populations, including those established in adverse environments. Costa-Pierce (2003) recognized the importance of feral tilapia populations and recommended establishment of a registry using genetic markers. Over the past 30 years, fish breeding programmes and related research have been undertaken largely by public institutions and organizations, but will be increasingly pursued by public-private partnerships or by the private sector alone.

5. CHOOSING WHAT TO FARM

Genetic improvement of farmed fish lags far behind genetic improvement of crops and livestock but is taking similar approaches. Crop breeding and related research are increasingly driven by market assessments of demand for certain types of seed, with the development and importance of different genetic resources (varieties, hybrids, etc.) determined mostly by demand-led technical change, rather than supply-led proposals from scientists (P. Pardey, personal communication). The same trends are likely to develop in fish breeding.

Fish consumers determine the demand for different types of farmed fish at any given time, while aquaculture science works to develop and to introduce new options. Most fish consumers are, however, unaware of the existence and importance of FiGR. They usually buy, or receive (for example, in disaster relief operations) aquatic produce that they know only by common names. Their categorization and choices of produce usually approximate to species level, though they often know the names of the places of production of farmed fish (e.g. Scottish salmon in the United Kingdom; Batangas Province tilapia in the Philippines) and seek produce from a named location, based on their previous experience of buying it or on perceptions about its quality. The naming of places of production in fish markets, as in fish restaurant menus, is often a marketing ploy and does not usually provide reliable information about the genetic identity of produce. For example, some of the salmon farmed in Scotland and other countries were bred in Norway, and many farmed salmon look alike irrespective of origin and breeding history. In developing countries, there is rarely any independent certification that fish in the market place bearing the name of an area or farm of origin all came from there.

In many countries, though primarily at present in the developed world, consumers' choices of farmed fish are being made increasingly on ethical grounds. Ethics and responsibility in aquaculture have been reviewed by Kaiser (2002). For fish consumers, the main factors are whether farmed fish are treated humanely and whether they are produced in environment- and biodiversity-friendly farming systems; considering not only the obvious impacts of effluents from fish farms, abuse of antibiotics, etc., but also the choice of fish with feeding requirements – preferably herbivorous/omnivorous – that will not exacerbate pressures on capture fisheries that are already overexploited. Public perceptions of genetic modification of food species are also a major factor in ethically-based choices of what to eat, irrespective of considerations of biosafety and food safety. All such ethical considerations are being applied to farmed fish, particularly as organically farmed fish are becoming new entrants to organic agriculture (www.ifoam.org). Fish welfare issues, including those of farmed fish have been reviewed by Huntingford *et al*. (2006).

In most aquaculture, as in most agriculture, seed production and growout are separate enterprises, in different hands. Also in aquaculture, as throughout agriculture, seed producers' and farmers' choices of which aquatic organisms to farm are

determined by market demand, profitability, and technical feasibility. Assessments of all of these imply risk assessment and management, and these in turn require information as well as adequate knowledge and skills. Seed producers and farmers base their choices of fish upon their own experience and/or external advice concerning a wide range of commercial traits: e.g. for seed producers, fecundity of and egg quality from broodstock, and survival, growth rate and disease-resistance of seed; for farmers, survival, growth rate, feed conversion, disease resistance, dressing weight, color, flavour etc. Many farmers, especially small-scale farmers in developing countries, have to make choices about what to farm while lacking adequate science-based information and independent advice on the genetic diversity that is available and on the performance of different species, hybrids and strains. The links in the "chain of choice" concerning what to farm are at their strongest in modern, vertically integrated aquaculture and agriculture, where research, breeding, seed production, contract growing, processing and marketing are all or mostly undertaken within the same organization – usually a large food company which also manufactures feeds and supplies technical support services. Some forms of aquaculture, such as intensive farming of Nile tilapia, already resemble vertically integrated poultry farming though, like chickens, tilapia can also be farmed in a wide range of systems from free range through backyard feedlot to small, medium and large scale commercial farms (e.g. see Young and Muir, 2002).

Although choices about which fish are farmed are primarily consumer-driven, many other actors, including researchers, breeders, and fish processors, also influence these choices. Decision-making along this chain is a research area that has been little explored, but it is probable that some of its links are weak or even disconnected. Most fish consumers, and indeed fish farmers, feel that they know what need, while researchers, breeders and seed producers tend to promote their new ideas and products, often with strong political and commercial backing. Sometimes this results in large benefits to farmers and consumers, sometimes not. A good positive example was the development of new technology for the farming of genetically improved farmed tilapia (GIFT) (ADB, 2005b). However, interactions among aquaculture scientists, seed producers, farmers and fish consumers are often weak. Globalization is increasing the remoteness of some fish farmers from their markets. For others who remain closer to their markets, consumer demand and profit margins clearly dictate the choice of what to farm. An important recent example can be seen in the switch made by carp farmers in Andra Pradesh, India, from following long-established, scientist-derived polyculture formulae, that required stocking six (three indigenous and three alien) carp species in all ponds, to a much simpler system of stocking just two indigenous carp species, resulting in greater yields and profits (Nandeesha, 2001). This worked because of the high price of one of these species (*Catla catla*) and the opportunistic feeding behaviour of the other (*Labeo rohita*). The theoretical basis of multispecies polyculture – different species occupying separate feeding niches (benthos, detritus, phytoplankton, zooplankton, etc.) – tends to break down as aquaculture is intensified.

The other main actors whose activities influence current and future choices of what to farm, as well as where to farm it, are the conservationists at all levels (international, national and local/community) who recognize the need to conserve not only the genetic resources of farmed aquatic organisms, but also those of their wild relatives, of farmed types for which production has been discontinued, and of potential new candidate species for aquaculture. The overall goal here is to maximize options for future availability and use of FiGR and aquatic PGR. In agriculture, conservation of the wild relatives of farmed plants and animals and of traditional and rare varieties and breeds seems to be generally of less importance than it is in aquaculture. Moreover in agriculture new candidate species for farming are few, whereas in aquaculture there are probably hundreds. For aquaculture therefore, with its limited history of documentation and development of genetic resources, there is a strong case for

assuming that all distinct wild, feral and farmed populations of farmed and potentially farmable aquatic species are potential sources of unique and useful genetic material for aquaculture. However, choices also have to be made among this vast array of genetic resources. Those choices will again be largely influenced by the current choices of consumers as well as the opinions and foresight of researchers and breeders and other actors in the chain.

6. INFORMATION AND NOMENCLATURE

6.1 Crossing communication barriers

Broadly speaking, aquaculture researchers and most fish breeders talk the language of science and understand genetic terminology, whereas many seed producers and farmers and almost all of the general public do not. Inevitably, there is a mismatch between how scientists document genetic diversity in aquaculture and how most seed producers, farmers and consumers perceive, categorize and name farmed fish. The same applies to the conservation of wild populations, for some of which there is a rich folk taxonomy in local languages (e.g. see May, 2005) as well as a rapidly increasing reliance on molecular genetic data (e.g. see Hedrik, 2004).

Common names are the most obvious way through this barrier. FAO uses common names extensively in its provision of fisheries information, including aquaculture statistics. FishBase (www.fishbase.org) provides authoritative and correct nomenclature at species level for finfish, with user entry possible through the scientific names of fish and through their common names in over 200 languages. However, many of the common names listed by FAO, FishBase and others are highly contrived, for the simple purpose of just assigning a name other than a scientific name, which can be daunting to lay users. Therefore many so-called common names are not actually in common use. For example, the tilapia *Sarotherodon galilaeus* is listed by FAO and FishBase as the "mango tilapia", with FishBase suggesting the USA as the source of this common name. This is a beautiful name, but this author has never heard it used anywhere.

More serious problems with nomenclature can occur when the collectors and compilers of aquaculture statistics fail to keep abreast of changes in the scientific nomenclature of farmed aquatic organisms. Taxonomists are constantly revising nomenclature and often disagree about the status of species, which means that at any given time some diversity in nomenclature is inevitable. Recognizing this, the world's taxonomic databases and information systems increasingly allow not only for entry through common and scientific names but also provide coverage of synonyms and common misspellings of the latter to assist users to find the information that they seek, and also to consider correcting their nomenclature thereafter. FishBase has long provided such coverage for finfish and it is also available in global databases such as the Catalogue of Life (www.sp2000.org) and Namebank (www.ubio.org). The phylogenetics database Deepfin (www.deepfin.org) links finfish systematicists as a research coordination network and is a useful source for nomenclatural changes.

Overall, the goal for all concerned with management of information about genetic resources for aquaculture must be to call all farmed aquatic species, as far as is possible, by their correct scientific names. For some widely farmed fish this is not yet done rapidly. For example, the mrigal, an important farmed carp species, is not yet widely listed under its correct name *Cirrhinus cirrhosus.* Where taxonomic revision has involved splitting or lumping species, some statisticians persist in using old and incorrect names which fail to indicate the importance of what have come to be recognized as the same species or as separate individual species. A good example of the former is the widely farmed silver barb, an Asian carp, now properly called *Barbonymus gonionotus*. It was formerly called *Puntius gonionotus* or *Barbodes gonionotus*, names which are still found in some statistics and research papers. However, the main problem here is that

some aquaculture statistics still refer erroneously to and list separate data for another species, the Java barb or *Puntius javanicus*, all populations of which are now known to be *Barbonymus gonionotus*.

As a further example of the need to check nomenclature, even in international centres of excellence for research and development, in 1999, a FishBase team checked the correctness of all of the scientific names of plants and animals used by the 16 centres of the Consultative Group on International Agricultural Research (CGIAR), including those entered in its System-wide Information Network for Genetic Resources (SINGER) (ICLARM, 2000). The names used by the CGIAR centres and SINGER were compared with the most authoritative sources available; e.g. the Germplasm Resources Information Network (GRIN) and Species 2000. The results were revealing; for example, 3 183 SINGER names did not match valid names or synonyms in GRIN; 400 names used in the SINGER matched synonyms or known misspellings in Species 2000; and 960 SINGER names had no matches in GRIN or Species 2000. It is vital to check all names entered into statistical and other databases that will be used for making policy and decisions about use and conservation of FiGR. Only then will all synonymies and common missspellings be revealed and understood and databases that use scientific names as entry points be fully linkable. Standardized and correct nomenclature at species and interspecific hybrid levels is the first step, before venturing into intraspecific taxa and molecular genetic terminology, which must also be correct and, as far as is possible, standardized.

6.2 Information sources, gaps and future needs

Substantial information about FiGR for aquaculture has been and will continue to be generated by local studies in the developing world, where over 90 percent of aquaculture is practiced and where most wild and captive genetic resources for aquaculture are located. This is part of the global high importance of local studies as contributions to global inferences with respect to fish biodiversity (Palomares *et al.,* 2003). The International Symposia on Genetics in Aquaculture, begun in 1983, contain a wealth of information on aquaculture genetic research and the most important farmed fish species and commodity groups have their associated substantial and ever-increasing bodies of literature on basic research, production, trade etc., including information on breeding programmes and related genetic research results. Good examples are the International Symposia on Tilapia in Aquaculture (ISTAs) (e.g. Fishelson and Yaron, 1983; Bolivar *et al.,* 2004). However, information on FiGR *per se* in such sources is usually limited and much more is scattered among scientific journals, project reports and other grey literature.

Some of the major contributions to FiGR literature have therefore come from workshops and review papers initiated specifically to collect that scattered information (e.g. Pullin, 1988; Agnèse, 1998; Reddy, 1999; Penman *et al*., 2005). These mechanisms are useful for compiling information about on-farm, captive FiGR and wild, free-living FiGR. They help to bridge the gap that often exists between mainstream aquaculture literature and mainstream nature conservation literature. For species and commodity groups that are relatively new to aquaculture – often because of very recent advances in technology that allow captive breeding and mass production of seed – information on genetic resources and development of breeding programmes tends to be generated and disseminated more slowly than that for seed production and growout. The current status of sea cucumber fisheries, farming and CBF affords an example (Lovatelli *et al.,* 2004).

FishBase (www.fishbase.org) is the world's largest biological database on exploited fish, though it covers only finfish. FishBase is constituted and governed as an international consortium of museums, universities and other organizations, including

FAO. Beyond its ongoing contributions to standardization of finfish nomenclature, FishBase contains only limited genetic data of relevance for aquaculture but is still probably the world's largest compendium of such data in the fields that it has been able to cover so far, including: detailed karyological data for about 200 farmed species; limited electrophoretic population genetics data for about 90 farmed species; and limited quantitative genetics records for 9 farmed species. FishBase also provides online linkages to many other sources of relevant information about aquatic biodiversity, including those emerging as the most important global systems, including the Global Biodiversity Information Facility (GBIF; www.gbif.org) and Ocean Biogeographical Information System (OBIS; www.iobis.org).

FishBase and FAO have provided some information packages on farmed aquatic species, through efforts called respectively "Aquaculture Profiles" and the "Cultured Species Information Programme". The effort by FAO is ongoing, whereas that by FishBase, begun in the 1990s, has remained stalled for almost 10 years. Table 4 summarizes the results of both, with respect to their choice of species and their coverage of genetic resources, by actual content and/or by pointers to other sources of information. Only 7 of these 32 information packages contain any information on genetic resources *per se* and only 14 have some links of a limited nature to other sources of genetic resources information.

A new database, "SeaLifeBase", was initiated in December 2005 to develop for important exploited species of aquatic invertebrates (including farmed crustaceans and molluscs) similar coverage to that provided for finfish by FishBase. SeaLifeBase is being executed from the Fisheries Centre, University of British Columbia, hosted by the FishBase team at the WorldFish Center's facility in Los Baños, Laguna, Philippines and supported by the Oak Foundation. Under its auspices, representatives of global and regional biological databases, including some that cover farmed or potentially farmable aquatic organisms (e.g. for seaweeds, Algaebase; for some crustaceans, www.crustacea.net; for finfish, FishBase; and for some molluscs, www.data.acnatsci.org/obis/) met from 25 to 27 May 2006 at an Aquaspecies Workshop in Los Baños, Laguna, Philippines, to explore greater collaboration, linkages and interoperability, including establishment of a so-called "SeaLife" portal to provide access to all. It will be important for FAO and others providing or seeking information on genetic resources for aquaculture to monitor all such developments in this dynamic field of work.

The world's major aquaculture organizations and networks are also useful providers of information of genetic resources for aquaculture, but largely in a current awareness mode and not as genetic resources databases. For example, the Network of Aquaculture Centres in Asia-Pacific (NACA; www.enaca.org) provides a good current awareness facility under the heading "Genetics and Biodiversity". Similarly "oneFish" (www.oneFish.org), a web-based information system developed by the Support Unit for International Fisheries and Aquatic Research (SIFAR; www.sifar.org) in partnership with FAO, provides through its aquaculture and aquaculture resources pages a section entitled "seeds and genetic resources", linking users to important publications and information about ongoing research and donor programmes. The International Network on Genetics in Aquaculture (INGA; www.worldfishcenter.org/inga) is a useful source of information on the application of genetics in aquaculture and on exchanges of germplasm, especially for some farmed carps and tilapias.

There are many other databases and information systems that provide information on aquatic biodiversity, including those accessible via the World Conservation Union (IUCN; www.iucn.org) and the United Nations Environment Programme/World Conservation Monitoring Centre (www.unep-wcmc.org), but none yet addresses adequately the needs of those seeking substantially aggregated and up to date information on genetic resources for aquaculture. In particular, information about

TABLE 4
Farmed aquatic species for which information packages are currently available through A. FishBase Aquaculture Profiles and B. the FAO Cultured Species Information Programme, with indications of current importance in aquaculture and whether these sources contain and provide links to genetic resources (GR) information. "NR" = no reliable production statistics available

A. FishBase Aquaculture Profiles	Production (t)/ year(s)	No. of countries	+ or- GR info	+ or -GR links
Tilapias: *Tilapia rendalli*	843 (1995)	8	-	-
Sarotherodon melanotheron	NR	5	-	+
Oreochromis shiranus	ca.10 to 20	1	-	-
Carps: *Labeo rohita*	NR	13	+	+
Cirrhinus cirrhosus	NR	11	+	+
Catla catla	NR	11	+	+
Others: *Chanos chanos*	371,075 (1995)			
B. The FAO Cultured Species Information Programme				
Seaweeds: *Laminaria japonica*	4 917 788 (1999)	4	-	+
Molluscs: *Mytilus edulis*	NR	12	-	+
Mytilus galloprovincialis	NR	18	-	-
Perna canaliculata	> 70 000 (2002)	1	-	-
Ostrea edulis	6-7 000 (2002)	12	-	+
Mercenaria mercenaria	> 40 000 (2002)	3	-	-
Crassostrea virginica	NR	3	-	-
Ruditapes philippinarum	236 000 (2002)	9	-	-
Crustaceans: *Macrobrachium rosenbergii*	> 200 000 (2002)	12	-	+
Penaeus monodon	676 000 (2001)	21	-	+
Carps: *Hypophthalmichthys molitrix*	4 100 000 (2003)	6	-	-
Aristichthys nobilis	1 722 832 (2002)	24	-	-
Ctenopharyngodon idella	3 572 825 (2002)	>44	+	+
Cyprinus carpio	4 639 460 (2002)	Many	+	+
Carassius auratus	1 702 778 (2002)	14	+	+
Other finfish:				
Acipenser baerii	NR	12	-	+
Anguilla anguilla	ca. 9 000 (2002)	20	-	+
Argyrosomus regius	231	2	-	-
Dicentrarchus labrax	57 000 (2002)	16	-	-
Ictalurus punctatus	270 000 (1996 for USA only)	6	-	-
Oncorhynchus mykiss	ca. 500 000 (2002)	64	-	-
Psetta maxima	ca. 5 000 (2002)	10	-	-
Salmo salar	>1 000 000 (2002)	17	+	-
Sparus aurata	ca. 90 000 (2002)	18	-	-
Amphibians: *Rana catesbiana*	NR	13	-	-

fish breeding programmes, the status and performance of fish strains, hybrids and other genetically altered forms, and fish gene banks is scattered and of highly variable quality; ranging from unverified claims by private breeders to thoroughly documented national collections (e.g. for common carp in Hungary; Bakos and Gorda, 2001). The CABI Compendium on Aquaculture (www.cabi.org/compendium/ac/index.asp) contains useful summaries on major topics concerning genetics in aquaculture and for some species (e.g. *Crassostrea gigas* and *Cyprinus carpio*) its coverage extends to and well referenced summaries that include genetic resources information. However, this coverage does not yet extend to all important farmed fish species; e.g. Nile tilapia. As with the abovementioned attempts by FAO and FishBase to provide aquaculture species profiles, all such efforts face the problem that different authors choose to give

different emphases to aquaculture genetics in general and to genetic resources for aquaculture in particular. Moreover, such summaries require frequent updating in order to provide current information in the fast moving field of aquaculture genetics.

For farmed fish, there is not yet any authoritative publication, comparable to the World Watch List for Domestic Animal Diversity (Scherf 1995) from which reliable world totals of breeds and information on their status can be obtained; neither are there any databases for FiGR comparable to those available online for FAnGR: the FAO — maintained Domestic Animal Diversity Information System (DAD-IS; http://dad.fao.org/home.htm) and the International Livestock Research Institute - maintained Domestic Animal Genetic Resources Information System (DAGRIS; http://dagris.ilri.cgiar.org/dagris/). *In vitro* technologies, especially cryopreservation of fish sperm, are likely to become more widely used for FiGR conservation, as long-term and working gene banks. This will increase the need for online databases through which information about these FiGR can be accessed (e.g. see Kincaid, 2000). The System-wide Information Network on Genetic Resources (SINGER; http://singer.grinfo.net/) of the Consultative Group on International Agricultural Research currently performs this role for PGR, but not for other genetic resources.

Because of these large gaps for information on FiGR, and because remedying them would assist progressive coverage of genetic resources for aquaculture by the FAO and others, proposals were made, meetings held and initial studies done towards a new information network – initially given the working title "Aquatic Animal Diversity Information and Communication System (AADIS)" and later called a "Fisheries Information Network for Genetic Resources (FINGER)" (FAO, 1999; Pettman, 2002; Pullin *et al.,* 2000, 2002). This initiative has not been taken further, and a fresh approach would now seem more desirable in view of the increased capabilities and interoperability of existing global and regional databases and information systems.

The main growth area in information on genetic resources for aquaculture is that of molecular genetics. More and more information about genetic resources will be in the realm of bioinformatics and not at the species level. This already applies to some farmed populations (e.g. Siraj *et al.,* 1998) and to the huge literature on the genetics of wild populations, especially for salmonids where it is greatly assisting conservation efforts as well as leading to better standardization of criteria and indicators (e.g. Waples *et al.,* 2001; Graziano *et al.,* 2005; Verspoor *et al.,* 2005; Utter, 2004). An "SeaLifeBasees Initiative; FISH-BOL" (http://barcoding.si.edu/AllFish.htm) is contributing to the global efforts towards 'barcoding life' for all animal species, based on DNA comparisons for cytochrome c oxidase 1 (www.barcodinglife.com). The main challenge with respect to all bioinformatics is to keep as much information as possible in the public domain and accessible to those in the developing world who need it most. This requires further closing of the digital divide between rich and poor nations.

7. THREATS

7.1 To free-living populations

The world's free-living populations of aquatic species are among its most threatened. Freshwater and diadromous finfish are the world's most threatened species of high importance to humans. Froese and Torres not cited (1999) found that fishes that depend upon freshwater at any stage within their life cycles are 10 times more likely to be threatened than marine or brackishwater species. In 1998, the increasing global threats to finfish, including many species of importance in aquaculture, were the rationale for a major conference convened by the World Fisheries Trust (Harvey *et al.,* 1998). Cowx (2002) ranked recent threats to freshwater fish as follows: alien species introductions; dams and weirs; water quality problems; habitat degradation; overfishing; flow regulation; overabstraction; tourism; mineral extraction; land use change; climate

change; predators; poor legislation; and "naïve economic criteria". Freshwater finfish account for at least 65 percent of the world's production of farmed finfish and some of the world's free-living populations of freshwater finfish also comprise its most threatened FiGR for aquaculture, not only in terms of the wild relatives of currently farmed species but also for other species that are potential new candidates for aquaculture or contributors to breeding programmes and related research. Tilapia in Africa (e.g. Piers, 2002) and Chinese carps in the PRC (e.g. Wu, 2003) are examples of major groups of threatened genetic resources for farmed freshwater fish.

The world water crisis poses some constraints for expansion of inland aquaculture and for management of some of its free-living genetic resources, but also offers some opportunities for multipurpose use of scarce water resources, adding value to them and benefits from them. Aquaculture can often be an occupier of water rather than a consumer of water. These potentials remain largely unexplored. Most reviews of the world water crisis emphasize domestic water supply and restrict consideration of the importance of water for food production to its use for growing crops. Where fish are mentioned at all in water resources policymaking, this is usually in respect of allowing for some water to remain available for maintaining aquatic ecosystems and biodiversity, rather than recognizing the huge current contributions and scope for future growth of freshwater food fish aquaculture. Where water scarcity is great, however, threats to free-living FiGR are often unavoidable, as illustrated by the following communication to a tilapia genetics list server (L. Kaufman; February 25, 2006; tilapia@lists.unh.edu):

"*…the current drought could be threatening the critical refugium populations of* Oreochromis esculentus *and* Oreochromis variabilis *in the Lake Kyoga Basin north of Lake Victoria……Many are assuming that* O. esculentus *is secure because of the introduced population in Nyumba ya Mungo reservoir, but there is substantial genetic differentiation among the various relict and introduced populations that should not be squandered".*

7.2 To captive populations

Crop and livestock farmers typically discontinue their use of many lower yielding, traditional and minor varieties breeds, for obvious commercial reasons. Their future availability for use in future research and breeding programs is therefore often threatened. For example, 22.5 percent to 32 percent of the world's livestock breeds are thought to be at risk of extinction (Drucker *et al*., 2001; FAO data). The same will apply increasingly in aquaculture, as genetic improvement proceeds. Fish seed producers and farmers will choose to keep mainly or exclusively the latest available strains, hybrids etc. The present extent of this has not been documented, but recent indications of wide adoption of GIFT- and GIFT-derived Nile tilapia strains (ADB, 2005b) suggest that it can be rapid.

7.3 Biosafety and biosecurity

For the near future, selective breeding will probably continue to be the main route to genetic improvement in aquaculture. However, increasing use of biotechnology in aquaculture will increase and will involve both use of and impacts upon FiGR and other biodiversity. It must therefore be approached with high precaution and thorough appraisal prior to commercial use. This is biosafety, in the broad sense and it applies to all farmed aquatic organisms, not only to transgenes. As was agreed at a landmark international meeting (ICLARM-FAO, 1999) the characteristics of any genetically altered farmed aquatic organism and its possible impacts on any recipient environments and biota, on-farm and off-farm, are the important biosafety considerations, not the technique(s) by which it was produced.

Despite the high and increasing importance of aquaculture, no farmed aquatic organism has yet been accorded sufficient priority for genome sequencing. There is a strong case for the Nile tilapia genome to be the first farmed fish genome to be sequenced, as this species has global importance in aquaculture and also serves as a model perciform fish (www.hcgs.uhn.edu/cichlid). Development of transgenic fish is well underway (e.g. see http://www.pewagbiotech.ord/research/fish/). Other genetically altered fish, developed from alien and indigenous species, are widely farmed already; for example, highly selected strains, hybrids, artificial polyploids, and monosex populations.

Pullin *et al*. (in press) found that the proportions of world aquaculture production derived from alien species decreased from about 25 percent in the 1950s to about 15 percent in the 1990s, but pointed out that these data are highly influenced by the huge quantities of indigenous carps farmed in the PRC. On a per country basis, they found that contributions of alien species increased from about 40 percent in the 1950s to 45 percent in the 1990s and that the numbers of alien species used in aquaculture totaled about 40 and were increasing. De Silva *et al*., (2005), in assessing the roles of alien species in Asian freshwater aquaculture to 2002, found that they accounted for over 40 percent of total production based upon data that excluded indigenous carps farmed in the PRC. With PRC data included, their contribution dropped to almost 12 percent. Casal (2006), from FAO and FishBase data for 2000, found that alien species accounted for only 5 percent of the PRC's farmed freshwater fish production of 13 269 693 tonnes, but accounted for 72 percent of the 338 861tonnes of farmed fish produced in Indonesia and 87 percent of the 94 844 tonnes produced in Brazil. It is certain that the use in aquaculture of alien species and of genetically altered forms of both alien and indigenous species will increase. The rapid growth of the farming of Nile tilapia and tilapia hybrids in Asia and Latin America, all developed through original introductions from Africa, and the use of alien Asian species within Asia itself are clear evidence. Consequently, there will be increased movements of farmed aquatic organisms, for production, processing and marketing, as well as for research. This will increase the need for assurance of biosafety, with more effective quarantine and other biosecurity measures. For example, their absence or ineffectiveness and the consequent spread of viral diseases have cost shrimp farming dearly – e.g. white spot syndrome virus, one of four viruses responsible for losses of the order of billions of dollars, cost shrimp farming in Asia (US$4-6 billion) from 1992 to 2001 – and made biosecurity in shrimp farming a growth industry (Lightner, 2005). Specific pathogen-free populations of the Pacific white shrimp (*L. vannamei*) are becoming genetic resources of importance for shrimp farming.

When aquatic plants and animals escape, or are released for CBF, from research or production facilities, they can have serious adverse impacts (interbreeding, competition for food and for spawning sites, spreading disease etc.) on other aquatic organisms, wild and farmed, and can cause permanent changes to the recipient ecosystems. This applies not only to farmed alien aquatic species but also to farmed genetically altered forms of indigenous species. International introductions, transfers within States, and releases for CBF can bring about permanent changes in the status and integrity of other biodiversity and indeed of other genetic resources for aquaculture. The inevitability of increased use of alien species and of a wide range of genetically altered forms in aquaculture therefore increases the urgency for action to undertake long-term conservation measures for important free-living populations of the wild relatives of farmed aquatic organisms and other species of current or potential importance for aquaculture and related research (see 8.c. below).

Recent meetings and declarations indicate that international and national awareness of the need for biosafety and biosecurity is increasing (e.g. NACA/FAO, 2000; WorldFish Center, 2002, 2003; Gupta *et al.,* 2004). However, moving from such declarations to effective countermeasures against current threats and to ensuring

more responsible future behaviour among actors involved in aquaculture research and development and the entire aquarium trade is not easy, in developed and developing countries alike. Economic growth is the main basis of development and is almost always antagonistic to fish conservation, as shown recently for the USA in a series of papers and a debate led and published by the American Fisheries Society (Czech *et al*., 2005). Economic growth almost invariably results in widespread losses and degradations of aquatic habitats and reduced aquatic biodiversity.

8. MANAGEMENT

8.1 Concepts and definitions

Management of aquatic genetic resources is full integration of their use and conservation (Pullin, 2000). Conservation of FiGR of actual or future potential use is itself a form of use. Genetic resources can be conserved by one or more of the following options: *in situ/in vivo*, as captive or free-living populations; *ex situ/in vitro,* as gametes, embryos, other tissues and DNA; and *ex situ/in vivo*, as captive populations in research establishments, aquaria, etc.

The Convention on Biological Diversity (CBD 1994) definitions for genetic resources and related terms are followed here, as they are in the mainstream PGR and FAnGR literature. In most FiGR literature, however, use of the terms *in situ* and *ex situ* to describe FiGR is not yet consistent with CBD definitions. According to the CBD (1994), *in situ* conditions are those "*... where genetic resources exist within ecosystems and natural habitats, and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties*"; and *ex situ* conservation is "*conservation of components of biological diversity outside their natural habitats*".

This means that the genetic resources of farmed aquatic organisms that have distinctive properties, and that are held *in vivo* (i.e. as live populations) in their typical farm environments should properly be called *in situ*, as should all wild and feral genetic resources for aquaculture in their typical habitats. The term *ex situ* should be used only for FiGR and aquatic PGR held *in vitro* (e.g. collections of cryopreserved fish spermatozoa, embryos and other tissues) and for FiGR and aquatic PGR held *in vivo* in artificial, off-farm environments (e.g. botanical gardens, aquaria, research establishments and zoos). However, for captive fish populations, the distinction between typical farm environments and these atypical off-farm environments cannot yet be applied as strictly as it can for crop varieties and livestock breeds.

The CBD does not define or elaborate on "distinctive properties". However, for broad categorization of wild and captive genetic resources for aquaculture, it can be assumed that all captive-bred populations of farmed aquatic species have undergone some genetic alteration so as to differ genetically from free-living populations of the same species. The degrees of genetic alteration vary greatly according to with the different histories of farmed aquatic populations with respect to artificial selection, interstrain, interspecifics and intergeneric hybridization, as well as genetic manipulations, including control of sex determination, artificial polyploidy, androgenesis, gynogenesis and transgenesis. Irrespective of all of these purposeful interventions, all captive populations undergo natural selection to hatchery and farm environments.

8.2 *In situ/in vivo*; captive populations on-farm

In situ/in vivo conservation of FiGR on farms is accomplished mostly by seed producers, as broodstock populations. However, there are narrow limits to the diversity of FiGR that can be conserved and used by commercial seed producers and farmers. They must use the bulk of their facilities for holding and selling fish of highly proven

viability and profitability, unless compensated specifically to keep other species and strains for conservation purposes. The same applies to FAnGR, for the conservation of traditional and rare breeds of livestock on-farm.

The main requirements for most conservation of FiGR as broodstock on farms, and indeed as *ex situ/in vivo* populations in other facilities (see 7.e. below), are acquisition of founder stocks with high genetic variance and thereafter maintenance of adequate breeding numbers, so as to avoid inbreeding. Broodstock are often not managed well, especially in developing countries. The temptation is to keep only small effective breeding numbers of highly fecund species, such as farmed carps, and to practice *ad hoc* replacement of far less fecund tilapia broodstock from whatever sources are available. Broodstock replacement is expensive. For example, tilapia broodstock used for seed production should normally be replaced within two years of the start of their productive life.

Excellent guides are available for broodstock management and for the selective breeding that it facilitates (e.g. Tave, 1986, 1989; WorldFish Center, 2004a; Gjedrem, 2005). Where farmed fish breeding programmes are well developed, government ministries and research organizations, fish producers associations, certified private sector breeders, and farmers can all work in concert to conserve valuable breeds and to maintain seed quality; for example, in Hungary, 13 breeding farms of the Carp Breeding Section of the Hungarian Fish Producers Association keep 24 certified common carp strains (Váradi *et al.,* 2002).

8.3 *In situ/in vivo*; free-living populations

Free-living, wild and feral, populations of farmed and potentially farmable aquatic species, in inland, coastal and marine waters and wetlands, comprise genetic resources of immense importance for aquaculture. For example, Pullin *et al.,* (2001), from FishBase data, found among the fish fauna of Africa 2 608 unique freshwater species and 842 unique marine species, with over 100 fish species being used in aquaculture and over 1 000 in the aquarium trade. Information about the genetic diversity of some of their populations is increasing together with efforts for their conservation (e.g. Agnèse, 1994, 1998; Ryman *et al.,* 1995; Lévêque, 1997; Miller and Craig, 2001; Collares-Pereira *et al.,* 2002; Abban *et al.,* 2004), but the genetic diversity of many is still very imperfectly known. For example, local populations of marine organisms, particularly invertebrates, can exhibit high levels of cryptic speciation (Thorpe *et al.,* 2000).

Conservation of important free-living FiGR is essentially nature conservation. It depends upon the maintenance of their habitats and prevention of human influences that could cause genetic change, including isolation from aquaculture development, alien species and genetically altered farmed aquatic organisms. Aquatic protected areas can provide this to some extent, though conservation of FiGR for aquaculture is still seldom mentioned as a major reason for their establishment, relative to other reasons given: e.g. increased recruitment of neighbouring capture fisheries (e.g. not cited Shiple, 2004). Moreover, far greater emphasis has been given so far to marine protected areas than to freshwater protected areas for the more important and threatened FiGR for freshwater aquaculture. As Rice (2005) has pointed out, managing fish habitats for conservation purposes must keep pace with the rapid scientific developments and new thinking about ecosystem management. Habitat science *per se* has so far lagged behind ecosystem science.

Pullin (1990) recommended increased emphasis on conservation of fish genetic diversity among the goals of nature reserves and safari parks but, as with protected areas in general, this would not often guarantee the high degree of isolation needed to prevent disruption and genetic change. Important PGR are conserved in relatively small areas of habitats that are kept pristine or near-pristine as sacred groves etc.

(e.g. Okafor and Ladipo, 1992) and the extents to which FiGR are also conserved at such locations should be documented. For a more widely applicable and essentially new strategy, Pullin (2006b) suggested co-financing the establishment and upkeep of FiGR reserves, permanently isolated from all contact with aquaculture and other disturbances, together with the responsible development of other areas of aquatic ecosystems, including aquaculture development.

8.4 *Ex situ/in vitro*; cryopreserved sperm, embryos and tissue/DNA banking

In vitro cryopreservation of fish sperm has been accomplished for many species (Tiersch and Mazik, 2000) and is probably achievable for all farmed fish, though frozen sperm viability varies greatly with species. Cryopreservation of the early embryos of bivalve molluscs and sea urchins is also technically possible. However, the large size and fragility of most finfish eggs and embryos have so far defeated all attempts at their cryopreservation. Despite widespread successes with cryopreservation of farmed fish sperm at aquaculture research institutes and fish breeding centres around the world (for examples, see papers in Harvey *et al.,* 1998), this technology remains little used by fish breeders and seed producers, especially in developing countries. It is the obvious future mainstay for long-term, *in vitro* gene banking of FiGR for aquaculture, including farmed and potentially farmable fish, their wild relatives, and all other to in situ/in useful and potentially useful fish genetic material. Savolainen *et al.* (2006) have reviewed prospects and practices for banking DNA and tissues. This has been conceived mainly for plants, but could be explored for farmed aquatic animals.

Ex situ/in vitro conservation of FiGR is best viewed as complementary to their *in situ/vivo* conservation, as has been the strategy for most of the world's PGR. The World Fisheries Trust (www.worldfish.org) has long pioneered complementary conservation of FiGR as free-living populations and as cryopreserved fish sperm, and undertakes extensive training for this approach in developing countries.

8.5 *Ex situ/in vivo*; captive populations in aquaria and research establishments

Public and private aquaria have great scope for conserving FiGR, but this has not yet been realized to the extent of the role played by zoos in conservation of FAnGR. Wild relatives and rare breeds of livestock in zoos are often managed not only as public exhibits but also as *in vivo* gene banks. The population genetics of farmed fish held in aquarium collections have been little studied. Public and private aquaculture research establishments already play large roles in conservation of farmed fish, as captive populations. The problem here is that maintaining and replacing in vivo fish populations is expensive in terms of facilities, staffing and feeds, fish health care etc. The fish research collections of many universities that undertake aquaculture research and teaching are indeed *in vivo* gene banks, provided that their existence does not end along with the short-term projects for which many accessions are acquired.

The Research Institute for Fisheries, Aquaculture and Irrigation (HAKI) leads Hungary's National Carp Breeding Programme (CBP), in collaboration with the Common Carp Breeding Section of the Hungarian Fish Producers Association, using standard methodology (OMMI). HAKI keeps an *in vivo* gene bank of over 30 strains of farmed and wild common carp (e.g. Bakos and Gorda, 2001; Bakos *et al.,* 2002) Since 2002, however, the government ceased to provide support for HAKI's *in vivo* carp gene banking, which HAKI must now fund from its own budgets. Some 25 private farmers maintain populations of their own strains under the CBP. Farmers receive subsidies if they produce OMMI-approved common carp strains (L. Váradi, J. Bakos and Z. Jeney; personal communications).

A further constraint in many developing countries is that tradition or economic necessity requires some government research institutions to produce large quantities

of seed for distribution to farmers. This function can severely limit the availability of facilities for *in vivo* gene banking.

9. SHARING BENEFITS AND COSTS: OWNERSHIP AND USE

9.1 Free-living populations

The CBD gives its Parties national sovereignty over their biodiversity, including FiGR for aquaculture. The CBD also provides for recognition of new countries of origin for populations of farmed aquatic organisms that have acquired distinctive properties outside their native ranges; for example, the distinctive farmed strains of common carp developed in Indonesia. The CBD, together with other international conventions that concern aquatic ecosystems (notably the Ramsar Convention on Wetlands, 1971 and the United Nations Convention on Law of the Sea, 1982) also imposes national obligations on Parties to conserve their living aquatic resources.

Poor countries cannot easily take on the burden of conserving their extensive free-living FiGR for use in world aquaculture without external financial and technical support. Many of the world's important free-living FiGR for aquaculture are owned, and often used, by poor indigenous peoples and local communities, who cannot afford to be their long-term stewards for use by the rest of the world unless adequately compensated. The CBD's Article 8j provides for this in common with other international provisions on human rights (e.g. Posey, 1999). Greer and Harvey (2004) have reviewed some of the limited progress made in implementation of these provisions. There have not yet been any well documented examples of the stewards of free-living FiGR for aquaculture and other users of those FiGR for commercial purposes sharing the costs of conservation and the benefits of use.

9.2 Public and private research

Since the 1980s, developed countries seem to have shifted their public-sector research priorities away from increasing the production of food staples (that, coincidentally, provided useful spillovers to developing countries), putting more emphasis on research on environmental, food safety and various other non-food production aspects of agriculture. This trend may require developing countries to invest more in food production research, becoming more self-reliant (Pardey *et al.,* 2006). At the same time, private research and development of biotechnology for staple food commodities has increased, with a growth in intellectual property rights (IPR) and growing concerns as to how these trends will affect developing countries (Wekundah, 2005; Wright and Pardey, 2006a, 2006b).

Private sector research in biotechnology for aquaculture has also increased, especially in developed countries, and the developing countries where most of the world's fish are farmed will need to increase their own public and private research capacities in this area if they are not to be left behind. However, private ownership of FiGR for aquaculture, through assumption of intellectual property rights (IPR) or other restrictions on use, is still rare. There are no well documented examples of substantial financial returns to researchers who have developed and assumed ownership of specific FiGR for aquaculture and related biotechnology. Ownership rights and restrictions on use of FiGR are usually very difficult to enforce. Farmed fish from different breeding programmes and genetic manipulations often look alike and therefore the provenance of a given farmed fish population *in situ* or in a market place is difficult to determine without costly forensic examinations.

For example, GIFT and GIFT-derived and other improved strains of Nile tilapia all look very similar. Without recourse to laboratory tests, a casual observer of their farmed populations and harvests could say only that they must be genetically improved

rather than unimproved fish. Simpler and cheaper genetic marking of superficially similar farmed fish strains, hybrids and other genetically altered forms will likely become available to help their developers to differentiate between legitimate use by those who have signed restrictive use agreements and others who are enjoying pirate use. However, acquiring and enforcing IPR on FiGR for aquaculture as strains, hybrids and other genetically altered forms will remain difficult. Their complexities are increased by the prevalence of public-private partnerships in fish breeding, seed supply and farming. It is common in some developed and in most developing countries for government research establishments, breeding centres and hatcheries to supply genetic material to the private sector and also to act as substantial producers of fish seed, even though this latter function could take significant market share away from private seed producers. This issue has emerged in the public-private relationships associated with tilapia breeding and seed supply in the Philippines (WorldFish Center, 2004b).

It is worth noting, at this early stage of domestication for most farmed fish, that the main traditional and commercial breeds of livestock and pet animals (e.g. the Holstein cow and the Labrador dog) are not privately or even nationally owned. Rather, there is private ownership of and restricted, purchasable access to the progeny of multiple pedigreed strains and to individual sires and dams. Hamilton (1999) found no instances of attempts to claim even national or regional sovereignty over or controlling interests in any livestock breed. Pedigreed fish populations in a single hatchery or farm, and pedigreed fish sires and dams are still very little developed compared to their prevalence in livestock and pet animal breeding, but their development would probably afford a better basis for the acquisition of private rights to and returns from FiGR than attempts to seek patents or other officially recognized IPR on farmed fish strains and other genetically altered forms.

The main requirement for equitable use of FiGR is better organization and oversight of germplasm acquisition and transfers, through Germplasm Acquisition Agreements and Material Transfer Agreements similar to those developed for PGR. Public, private and public-private transfers of FiGR for aquaculture are increasing. Responsible protocols and practices for these are not yet well developed or enforced. The INGA has contributed to improving this situation.

10. STRATEGIC DIRECTIONS

10.1 Increased investment

The growth of aquaculture has outpaced that of all other food production sectors and its high importance and scope for further growth, especially for the benefit of poor consumers and farmers, are clear. Past and present investment in the management of genetic resources for aquaculture fails to reflect this. If this situation continues, it will jeopardize achievement of the potential of aquaculture. Many genetic resources for aquaculture are seriously threatened. Countermeasures require increased investment in their management, to match their economic and social importance.

Effective management of genetic resources for aquaculture almost always has higher costs than are normally encountered with PGR and FAnGR. Setting aside areas of natural ecosystems as off-limits to all forms of disturbance has operational and opportunity costs. Establishing and maintaining *ex situ*, *in vivo* and/or *in vitro* fish gene banks is very expensive compared the costs involved in plant gene banks, and gene banks for FiGR cannot be centralized to the same extents as those for PGR. National, regional and international networks and partnerships, including public-private partnerships, can help in the sharing of costs for and benefits from management of FiGR for aquaculture. For example, in Central and Eastern Europe, the Network of Aquaculture Centres (NACEE; http://agrowebcee.net/subnetwork/nacee/) links 31 institutes from 13 countries, all having strong interests in carp genetic resources (Bakos *et al*., 2002).

10.2 Management as agrobiodiversity

The whole of agriculture and fisheries and their supportive ecosystems function as a global trophic web. However, aquaculture is farming and has much more in common with agriculture than with capture fisheries. In particular, on-farm *in situ* and all *ex situ* genetic resources for aquaculture merit recognition as part of agrobiodiversity and management, along with PGR and FAnGR, through common policies, institutions and mechanisms.

10.3 Improved information systems

Thorough documentation and accessible information on all categories of genetic resources for aquaculture is an urgent requirement. This means gathering, processing and linking information on free-living genetic resources for aquaculture with that for breeding programmes and related research, with the types of seed supplied to farmers, and with production and value statistics for farmed aquatic species, strains and other genetically altered forms. This can be approached progressively. The genetic resources of the more important farmed aquatic plants could be covered under existing arrangements between the International Plant Genetic Resources Institute (IPGRI) and FAO. It would also be relatively easy to prioritize coverage of the most important genetic resources for farmed food fish. The genetic resources for farmed ornamental aquatic species are a lower priority and will continue to be documented to some extents by the aquarium trade and by databases such as FishBase.

10.4 Conservation in changing ecosystems

The future availability and integrity of free-living and captive genetic resources for aquaculture depends upon the status of their environments; i.e., natural aquatic ecosystems and agroecosystems. Brown *et al*., (1997) made this point thus, with reference to pressures such as fragmentation, and pollution: "*….the goal of conserving appropriate genetic diversity is best achieved not by focusing on maintenance of the genes and genotypes that currently exist within a species, but by trying to prevent drastic alteration in the pace and direction of these evolutionary processes*."

This amounts to a call for ecosystem-based management at the genetic level, on-farm as well as for natural ecosystems. The increasing needs to confront climate change and climatic uncertainties are also highly relevant here. However, much of the literature on ecosystem-based management for fisheries emphasizes the species level, higher taxa and their functions, and pays little attention to genetic resources. An ecosystems perspective that includes the genetic level will show that some losses of genetic resources for aquaculture are inevitable as development proceeds. It is important to recognize this and, by monitoring and understanding the processes involved, to improve prospects for keeping important genetic diversity. What actually can be kept and what will be lost are parts of a bigger picture than genetic resources inventories alone can suggest, and the costs of *in situ/in vivo* conservation and complementary *ex situ/in vitro* conservation are always serious constraints. The conservation of free-living populations and traditional breeds of farmed species is like a battlefield where, distasteful though it is, triage is sometimes inevitable. Complementary *ex situ*, *in vitro* and *in vivo*, conservation is vital for important genetic resources that are seriously threatened *in situ*.

10.5 Reconciliation of aquaculture and nature conservation

Conservation of *in situ/in vivo*, free-living genetic resources for aquaculture have yet to be adequately recognized as part of the rationale for greater investment in conservation of natural aquatic biodiversity and habitats. Many nature conservationists can conceive alliances between agriculture or forestry and conservation but most perceive aquaculture principally or solely as a threat. As more responsible aquaculture becomes the norm, the CBD, IUCN and the Ramsar Convention, together with many

nature conservation organizations, especially NGOs, at international, national and local levels, will hopefully find partners within the aquaculture sector itself so as to reconcile and, where possible, to twin their respective goals. FAO and the CGIAR can help this process, but are likely to be more involved with conservation of captive and *in vitro* genetic resources for aquaculture production and related research.

10.6 Progressive linkages with management of FAnGR

Recent meetings and publications (Pullin 2006b; Science Council 2005) have recognized the many lessons to be learned from management of FAnZGR for management of FiGR for aquaculture. For example, there could be much closer linkages with respect *ex situ/in vitro* conservation of FiGR and FAnGR, especially in terms of shared facilities. The main strategy for FiGR here would probably be decentralization, with establishment of and support to relatively small and affordable national and local gene banks, kept within or as close as possible to production areas. Most responsibilities would probably rest with national public sector research establishments, private sector breeders and seed suppliers. The CGIAR would probably not be involved to any extent comparable with its involvement in gene banks for PGR. The WorldFish Center has so far taken only a minor role in this area to date, for GIFT strains of Nile tilapia and for its own collaborative and in-house research. The International Livestock Research Institute is not involved in gene banking for FAnGR, but has collections of PGR for fodder species.

10.7 Exploration of interactive governance and governability

Management of genetic resources for aquaculture is part of the global management of all natural resources. A new approach to this, called interactive governance, is being developed, using capture fisheries as its main model, with some preliminary explorations for aquaculture (Kooiman *et al.,* 2005; Bavinck *et al.,* 2005; Pullin and Sumaila, 2005). Interactive governance recognizes the diversity, complexity, dynamics and scales that are represented in all natural resources that are "systems to be governed". Genetic resources for aquaculture fit this description very well and are therefore subjects for further explorations of the utility of the interactive governance governance approach for their management and for assessments of their governabilities. Research in this general area is being carried out by an international network (www.fishgovnet.org) with a current emphasis on operationalizing interactive governance in capture fisheries, aquaculture and coastal zones, mainly through developing the concept of and methodologies for determining governability (e.g. Chuenpagdee *et al.,* 2005).

11. ACKNOWLEDGEMENTS

The author thanks the following for helpful responses during the preparation of this review: János Bakos, Christine Casal, Jean Collins, Peter Edwards, Rainer Froese, Gideon Hulata, Zsigmond Jeney, Alan Lowther, Graham Mair, Phil Pardey and László Váradi.

12. REFERENCES

Abban, E.K., Casal, C.M.V., Dugan, P. & Falk, T.M. (eds). 2004. Biodiversity, management and utilization of West African fishes. WorldFish Center Conference Proceedings 69. 63p.

ADB. 2005a. An evaluation of small-scale freshwater rural aquaculture development for poverty reduction. Asian Development Bank, Manila, Philippines. 164p.

ADB. 2005b. An impact evaluation of the development of genetically improved farmed tilapia and their dissemination in selected countries. Asian Development Bank, Manila, Philippines. 124p.

Agnèse, J-F. (ed.). 1994. Atelier. Biodiversité et aquaculture en Afrique. Abidjan, 21-25, Novembre 1994. Orstom, Paris. 115p.

Agnèse, J-F. (ed.). 1998. Genetics and aquaculture in Africa. Editions de l'Orstom, Paris. 326p.

Anon. 2006. Diet and the unborn child. The omega point. *The Economist* 378, No. 8461: 76-77.

Bakos, J. & Gorda, S. 2001. Genetic Resources at the Fish Culture Research Institute, Szarvas, Hungary. *FAO Fisheries Technical Paper* 417. Food and Agriculture Organization of the United Nations, Rome. 106p.

Bakos, J., Gorda, S., Váradi, L. & Jeney, Z. 2002. National common carp breeding and control programme in Hungary. In Pond aquaculture in Central and Eastern Europe in the 21st century. *European Aquaculture Society Special Publication* 31: 56-59.

Balon, E.K. 2004. About the oldest domesticates among fishes. *Journal of Fish Biology* 65 (Supplement A): 1-27.

Bardach, J.E., Ryther, J.H. & McLarney, W.O. 1972. Aquaculture. The farming and husbandry of freshwater and marine organisms. Wiley-Interscience, New York. 868p.

Bartley, D.M. & Leber, K. (eds). 2004. Marine ranching. *FAO Fisheries Technical Paper* 429. Food and Agriculture Organization of the United Nations, Rome.

Bartley, D.M., Rana, K. & Immink, A.J. 2001. Interspecific hybrids in aquaculture and fisheries. *Rev. Fisheries and Fish Biol*., 10: 325-337.

Bavinck, M., Chuenpagdee, R., Diallo, M., van der Heijden, P., Kooiman, J., Mahon, R. & Williams, S. 2005. Interactive governance: a guide to better practice. Eburon Academic Publishers, Delft, the Netherlands. 72p.

Bolivar, R. B., Mair, G.C. & Fitzsimmons, K. (eds). 2004 New dimensions in farmed tilapia. Proceedings of the Sixth International Symposium on Tilapia in Aquaculture, 12-16 September, 2004, Manila, Philippines. Volumes I and II. Bureau of Fisheries and Aquatic Resources, Quezon City, Philippines. 804p.

Brown, A., Young, A., Burdon, J., Christidis, L., Clarke, G., Coates, D. & Sherwin, W. 1997. Genetic indicators for state of the environment reporting. Australia: State of the Environment Technical Paper Series (Environmental Indicators). Department of the Environment, Sport and Territories, Canberra, Australia. 29p.

Brugère, C. & Ridler, N. 2004. Global aquaculture outlook in the next decades: an analysis of national aquaculture production forecasts to 2030. *FAO Fisheries Circular* 1001. Food and Agriculture Organization of the United Nations, Rome. 47p.

Caddy, J.F. & Defeo, O., 2003. Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources. *FAO Fisheries Technical Paper* 448. Food and Agriculture Organization of the United Nations, Rome. 159p.

Casal, C.M.V. 2006. Global documentation of fish introductions: the growing crisis and recommendations for action. *Biological Invasions* 8: 3-11.

CBD. 1994. Convention on Biological Diversity. Text and Annexes. Interim Secretariat for the Convention on Biological Diversity, Châtelaine, Switzerland. 34p.

Cheney, D.P. 1999. Strain improvement of seaweeds through genetic manipulation: current status. *World Aquaculture* 30 (2): 55-56, 66-67.

Chuenpagdee, R., Kooiman, J. & Pullin, R.S.V. 2005. Exploring governability in capture fisheries, aquaculture and coastal zones. Paper presented at the MARE Conference, People and the Sea III, 7-9 July 2005, University of Amsterdam, Amsterdam, the Netherlands.

Collares-Pereira, M.J., Cowx, I.G. & Coelho, M.M. (eds). 2002. Conservation of freshwater fishes: options for the future. Fishing News Books Ltd., Oxford, U.K.

Costa-Pierce, B.A. 2003: Rapid evolution of an established feral tilapia (*Oreochromis* spp.): the need to incorporate invasion science into regulatory structures. *Biological Invasions* 5:71-84.

Cowx, I.G. 2002. Analysis of threats to freshwater fish conservation: past and present challenges, p. 201-220. In Collares-Pereira, M.J., Cowx, I.G., and Coelho, M.M. (eds.)

Conservation of freshwater fishes: options for the future. Fishing News Books Ltd., Oxford, U.K.

Czech, B. and 12 co-authors. 2005. Economic growth, fish conservation, and the AFS: conclusion to a forum, beginning of a movement? *Fisheries* 31 (1): 40-43.

De Silva, S.S., Nguyen, T.T.T., Abery, N.W. & Amarasinghe, U.S. 2005. An evaluation of the role and impact of alien fish in Asian inland aquaculture. *Aquaculture Research* 2005: 1-17.

Drucker, A. 2001. The economic valuation of farm animal genetic resources: a survey of available methods. *Ecological Economics* 36: 1-18.

Edwards, P. 1980. Food potential of aquatic macrophytes. *ICLARM Studies and Reviews* 5. International Center for Living Aquatic Resources Management: Manila, Philippines.51p.

Eknath, A.E. and 13 co-authors. 1993. Genetic improvement of farmed tilapias: the growth performance of eight strains of *Oreochromis niloticus* tested in eleven farm environments. *Aquaculture* 111: 171-188.

Elvevoll, E.O. & James, D.G. 2000 Potential benefits of fish for maternal, foetal and neonatal nutrition: a review of the literature. *Food, Nutrition and Agriculture* 27: 28-39.

FAO. 1995. *Code of Conduct for Responsible Fisheries.* Rome, FAO. 41p.

FAO. 1997. Aquaculture development. *FAO Technical Guidelines for Responsible Fisheries.* 5. Rome, FAO. 40p.

FAO. 1999. Towards a strategy for the sustainable use and conservation of aquatic animal diversity. Information Note, prepared on the occasion of the twenty-third session of the Committee on Fisheries, 15-19 February 1999. Rome, FAO. 6p.

FAO. 2002. Aquaculture development and management: status, issues, and prospects. Sub-Committee on Aquaculture, Committee on Fisheries. COFI:/AQ/I/2002/2. Rome, FAO. 13p.

FAO. 2005. FAO Fisheries Department, Fishery Information Data and Statistics Unit. Fishstat Plus: Universal software for fishery statistical time series. Vers. 2.30 (available at www.fao.org/fi/statist/FISOFT/FISHPLUS.asp

FAO/NACA-STREAM. 2005. Workshop on aquatic resources and livelihoods: connecting policy and people, 17-19 March 2005, Los Baños, Laguna, Philippines. Available: http://www.streaminitiative.org/pdf-news/StatementsSTREAMFAOTCP.pdf

Fishelson, L. & Yaron, Z. Compilers. 1983. International Symposium on Tilapia in Aquaculture. Tel Aviv University, Tel Aviv, Israel. 624p.

Froese, R. & Torres, A. 1999. Fishes under threat: and analysis of the fishes in the 1996 IUCN Red List, p. 133-144. In Pullin, R. S. V., Bartley, D. M. and Kooiman, J. (eds.) Towards Policies for Conservation and Sustainable Use of Aquatic Genetic Resources. ICLARM Conference Proceedings 59. 277p

Gillespie, S. & Haddad, L. 2001. Attacking the double burden of malnutrition in Asia and the Pacific. Asian Development Bank, Manila, Philippines. 180p.

Gjedrem, T. Editor .2005. Selection and breeding programs in aquaculture. Springer, Dordrecht, the Netherlands. 364p.

Graziano, S.L., Brown, K.H. & Nielsen, J.L. 2005. Nomenclature of mitochondrial DNA haplotypes for *Oncorhynchus mykiss. Transactions of the American Fisheries Society* 134: 1271-1273.

Greer, D. & Harvey, B. 2004. Blue genes: sharing and conserving the world's aquatic biodiversity. Earthscan and the International Development Research Centre, London and Ottawa. 231p.

Gupta, M.V., Bartley, D.M. & Acosta, B.O. (eds). 2004. Use of genetically improved and alien species for aquaculture and conservation of aquatic biodiversity in Africa. *WorldFish Center Conference Proceedings* 68. 113p.

Hamilton, N.D. 1999. Intellectual Property Rights and Livestock. Comments to the Consultative Group of International Agricultural Resource (sic) (CGIAR) Centers Meeting of Genetic Resource Specialists. Consultative Group on International Agricultural Research, Washington DC.12p.

Harvey, B., Ross, C., Greer, D. & Carolsfeld, J. (eds). 1998. Action before extinction: an international conference on conservation of fish genetic diversity. World Fisheries Trust, Vancouver B.C., Canada. 259p.

Hedrik, P.W. 2004. Recent developments in conservation genetics. *Forest Ecology and Management* 197: 3-19.

Huntingford, F.A., Adams, C., Braithwaite, V.A., Kadri, S., Pottinger, T.G., Sandøe, P.& Turnbull, J.F. 2006. Current issues in fish welfare. *Journal of Fish Biology* 8: 332-372.

ICLARM. 2000. Authoritative nomenclature for species used in SINGER and the CGIAR. Report to the Intercenter Working Group on Genetic Resources, System-wide Genetic Resources Programme of the Consultative Group on International Agricultural Research. International Plant Genetic Resources Institute, Rome. 3p. (unpublished)

ICLARM-FAO. 1999. Consensus statement, p. 253. In Pullin, R.S.V., Bartley, D.M. and Kooiman, J. (eds.) Towards policies for conservation and sustainable use of aquatic genetic resources. *ICLARM Conference Proceedings* 59. 277p.

Kaiser, M. 2002. Social perceptions and ethics in aquaculture: aquaculture as a responsible supplier for the new millennium, p. 166-182. In Creswell, R.L., and Flos, R. (eds) Perspectives on responsible aquaculture for the new millennium. World Aquaculture Society, Baton Rouge LA.

Kanungo, U.K., Sinha, S. & Naik, M.L. 2001. Net primary productivity of some aquatic macrophytes in sewage-sullage mixture. *Journal of Environmental Biology* 22 (3): 219-223.

Kincaid, H. 2000. Development of databases for germplasm repositories, p. 323-331. InTiersch, T.R., and Mazik, P.M. (eds.) Cryopreservation in aquatic species. World Aquaculture Society, Baton Rouge LA.

Kooiman, J., Bavinck, M., Jentoft, S. & Pullin, R.S.V. (eds). 2005. Fish for life: interactive governance for fisheries. Amsterdam University Press, Amsterdam, the Netherlands. 427p.

Leber, K.M., Kitada, S., Blankenship, H. L. & Svåsand, T. (eds). 2004. Stock enhancement and sea ranching: developments, pitfalls and opportunities. Blackwell Publishing Ltd, Oxford, U.K. 584p.

Lévêque, C. 1997. Biodiversity dynamics and conservation. The freshwater fish of tropical Africa. Cambridge University Press, Cambridge, U.K. 438p.

Lightner, D. 2005. Biosecurity in shrimp farming: pathogen exclusion through use of SPF stock and routine surveillance. *Journal of the World Aquaculture Society* 36 (3): 229-248.

Lorenzen, K. and 12 co-authors. 2001. Strategic review of enhancements and culture-based fisheries, p.221-237. In R. P. Subasinghe, P. Bueno, M.J. Phillips, C. Hough, S.E. McGladdery and Arthur, J.R. (eds.) Aquaculture in the Third Millenium. Technical Proceedings of the Conference on Aquaculture in the Third Millenium, Bangkok, Thailand, 20-25 February 2000. Network of Aquaculture Centres in Asia-Pacific, Bangkok, Thailand and the Food and Agriculture Organization of the United Nations, Rome.

Lovatelli, A., Conand, C., Purcell, S., Uthicke, Sven., Hamel, J-F. & Mercier, A. 2004. Advances in sea cucumber aquaculture and management. *FAO Fisheries Technical Paper* 463. Food and Agriculture Organization of the United Nations, Rome. 425p.

May, D. 2005. Folk taxonomy of reef fish and the value of participatory monitoring in akatobi national Park, southeast Sulawesi, Indonesia. Traditional Marine Resource Management and Knowledge 18: 18-35.

McHugh, D.J. 2003. A guide to the seaweed industry. *FAO Fisheries Technical Paper* 441. Food and Agriculture Organization of the United Nations, Rome.105p.

Miller, P. & Craig, J.F. (eds). 2001. Fish biodiversity and conservation. Proceedings of the Fisheries Society of the British Isles Annual Symposium, 9-13 July, 2001, University of Leicester, U.K. *Journal of Fish Biology* 59 (Supplement A). 387p.

NACA/FAO. 2000. Aquaculture development beyond 2000: the Bangkok Declaration and Strategy. Conference on Aquaculture in the Third Millenium, 20-25 February, 2000,

Bangkok, Thailand. Network of Aquaculture Centres in Asia-Pacific, Bangkok, Thailand and the Food and Agriculture Organization of the United Nations, Rome. 23p.

Nandeesha, M.C. 2001. Farmers as scientists. Andra Pradesh fish farmers go into revolutionary carp research. *Aquaculture Asia* VI (4): 29-32.

Nash, C.E. (ed.). 1993. Production of aquatic animals (crustaceans, molluscs, amphibians and reptiles). Elsevier Science B.V., Amsterdam, the Netherlands. 244p.

Nash, C.E. & Novotny, A.J. (eds). 1995. Production of aquatic animals (fishes). Elsevier Science B.V., Amsterdam, the Nehterlands. 405p.

New, M.B. 2003. An overview of the status of global; aquaculture, excluding China. In Phillips, B., Megrey, B. and Yingqi Zhou (eds.) Proceedings of the Third World Fisheries Congress. Feeding the world with fish in the next millennium – the balance between production and environment. *American Fisheries Society Symposium* 38: 59-101. American Fisheries Society, Bethesda, MA.

Okafor, J.C. & Ladipo, D.O. 1992. Fetish groves in the conservation of threatened flora in southern Nigeria, p. 167-179. In Bennun, L.A., Aman, R.A. and Crafter, S.A. (eds.) Conservation of biodiversity in Africa. Local initiatives and institutional roles. Centre for Biodiversity, National Museums of Kenya, Nairobi, Kenya.

Ottolenghi, F., Silvestri, C., Giordano, P. Lovatelli, A. & New, M.B. 2004. Capture-based aquaculture. The fattening of eels, groupers, tunas and yellowtails. Food and Agriculture Organization of the United Nations, Rome. 308p.

Palomares, M.L.D., Samb, B., Diouf, T., Vakily, J.M. & Pauly, D. (eds). 2003. Fisheries Biodiversity: Local Studies as Basis for Global References. *ACP-EU Fisheries Research Report* No. 14. 281p.

Pardey, P., Alston, J. & Beintema, N. 2006. Agricultural R & D spending at a critical crossroads. *Farm Policy Journal* 3(1): 1-9.

Penman, D.J., Gupta, M.V. & Dey M.M. (eds). 2005. Carp genetic resources for aquaculture in Asia. *WorldFish Center Technical Report* 65. The WorldFish Center: Penang, Malaysia. 152p.

Pettman, I. 2002. Development of an Aquatic Animal Diversity Information System (AADIS): the establishment of standard search procedures and protocols. Consultant's report to the Food and Agriculture Organization of the United Nations, Rome. 209p.

Piers, A. 2002. A threatened genus of tilapiine fish - *Oreochromis*. *The Fisheries Society of the British Isles Newsletter*, Spring 2002: 1-2.

Pillay, T.V.R. 1990. Aquaculture. Principles and practices. Fishing News Books, Blackwell Scientific Publications, Oxford, U.K. 575p.

Popkin, B.M., Horton, S.H. & Kim, S. 2001. The nutrition transition and prevention of diet-related diseases in Asia and the Pacific. Asian Development Bank, Manila, Philippines. 59p.

Posey, D.A. 1999. Developing *sui generis* options for the protection of living aquatic resources on indigenous and local communities, p. 187-126. In Pullin, R.S.V., Bartley, D.M. and Kooiman, J. (eds.) Towards policies for conservation and sustainable use of aquatic genetic resources. *ICLARM Conference Proceedings* 59. 277p.

Pullin, R.S.V. Editor. 1988. Tilapia genetic resources for aquaculture. *ICLARM Conference Proceedings* 16. 108p. (Also available in French)

Pullin, R.S.V. 1990. Down-to earth thoughts on conserving aquatic genetic diversity. *Naga. The ICLARM Quarterly* 13 (1): 5-8.

Pullin, R.S.V. 2000. Management of aquatic biodiversity and genetic resources. *Reviews in Fisheries Science* 8 (4): 379-393.

Pullin, R.S.V. 2002. Draft glossary of standard terms for a proposed Fisheries Information Network for Genetic Resources (FINGER). Consultant's report to the Food and Agriculture Organization of the United Nations, Rome. 71p.

Pullin, R.S.V. 2006a. Aquaculture up and down the food web. Paper presented at Thinking Big: a Global Look at Fisheries Science, a Symposium to honour Professor Daniel Pauly

for the 13th International Cosmos Prize and his 60th Birthday, May 2-3, 2006, Fisheries Centre, Aquatic Ecosystem Research Laboratory, University of British Columbia, Vancouver B.C., Canada. 34p.

Pullin, R.S.V. 2006b. Conservation of farmed fish genetic resources: broad options, strategies; availability of methods, and comparisons with those for conservation of the genetic resources of other farmed animals. In Options and Strategies for the Conservation of Farm Animal Genetic Resources: Report of an International Workshop and Presented Papers (7-10 November 2005, Montpellier, France) [CD-ROM]. CGIAR System-wide Genetic Resources Programme (SGRP)/International Plant Genetic Resources Institute, Rome, Italy.

Pullin, R.S.V., Bartley, D.M. & Kooiman, J. (eds).1999. Towards policies for conservation and sustainable use of aquatic genetic resources. *ICLARM Conference Proceedings* 59. 277p.

Pullin, R.S.V., Bartley, D.M. & Harvey, B. 2000. Aquatic animal diversity: sailing new seas of information. Paper presented at the FAO Expert Consultation on the Development of an Aquatic Animal Diversity Information and Communication System, 16-17 November, 2000, Food and Agriculture Organization of the United Nations, Rome. 2p.

Pullin, R.S.V., Casal, C.M.V. & Brummett, R.E. 2001. Fish genetic resources of Africa, p.60-74. In P.H. Skelton and G. G. Teugels (eds.) African Fish and Fisheries – Diversity and Utilisation. Annales Sciences Zoologiques 288. Musée Royale de l'Afrique Centrale, Tervuren, Belgium. 105p.

Pullin, R.S.V. & Sumaila, U.R. 2005. Aquaculture, p. 93-107. In Kooiman, J., Bavinck, M., Jentoft, S., and Pullin, R.S.V. (eds.) Fish for life: interactive governance for fisheries. Amsterdam University Press, Amsterdam, the Netherlands.

Pullin, R.S.V., Froese, R. & Pauly, D. (in press). Indicators for the sustainability of aquaculture, Chapter 3, p. 00-00. In Bert, T.M. (ed.) Ecological and genetic implications of aquaculture. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Reddy, P.V.G.K. 1999. Genetic resources of Indian major carps. *FAO Fisheries Technical Paper* 387. Food and Agriculture Organization of the United Nations, Rome. 76p.

Rice, J.C. 2005. Understanding fish habitat ecology to achieve conservation. *Journal of Fish Biology* 67 (Supplement B): 1-22.

Rutten, M.J.M., Komen, H., Deerenberg, R.M., Siwek, M. & Bovenhuis, H. 2004 a. Genetic characterization of four strains of Nile Tilapia (*Oreochromis niloticus* L.) using microsatellite markers. *Animal Genetics* 35: 93-97.

Rutten, M.J.M., Bovenhuis, H. & Komen, H. 2004 b. Modelling fillet traits based on body measurements in three Nile tilapia strains (*Oreochromis niloticus* L.). *Aquaculture* 231 (1-4): 113-122.

Ryman, N., Utter, F. & Laikre, L. 1995. Protection of the intraspecific biodiversity of exploited fishes. *Reviews in Fish Biology and Fisheries* 5: 417-446.

Savolainen, V., Powell, M.P., Davis, K., Reeves, G. & Corthuis, A. (eds). 2006. DNA and tissue banking for biodiversity and conservation: theory, practice and uses. Kew Publishing, Richmond, U.K. 168p.

Scherf, B. (ed.). 1995. World Watch List for domestic animal diversity. 2nd Edition. Food and Agriculture Organization of the United Nations, Rome. 769p.

Science Council Secretariat. 2005. Conservation of livestock and fish genetic resources. Joint report of two studies commissioned by the CGIAR Science Council Secretariat, Consultative Group on International Agricultural Research, Rome, Italy. 89p.

Shipley, J.B. (ed.). 2004. Aquatic protected areas as fisheries management tools. American Fisheries Society Symposium 42. American Fisheries Society, Bethesda, Maryland. 301p.

Siraj, S.S., Seki, S. & Taniguchi, N. 1998. DNA fingerprinting in a Malaysian strain of Javanese carp, *Puntius gonionotus* (Bleeker), detected by YNZ22 DNA probe. *Aquaculture Research* 29 (6): 453-455.

Stickney, R.R. Editor. 2000. Encyclopedia of aquaculture. John Wiley and Sons Inc., New York. 1063p.

Tacon, A.G.J., Hasan, M.R. & Subasinghe, R.P. 2006. Use of fishery resources as feed inputs for aquaculture development: trends and policy implications. *FAO Fisheries Circular* 1018. 105p.

Tave, D. 1986. Genetics for fish hatchery managers. AVI Publishing Corporation Inc., Westport, Connecticut, USA. 299p.

Tave, D. 1999. Inbreeding and broodstock management. *FAO Fisheries Technical Paper*. 392. Food and Agriculture Organization of the United Nations, Rome.122p.

Thorpe, J.P., Solé-Cava, A.M. & Watts, P.C. 2000. Exploited marine invertebrates: genetics and fisheries. *Hydrobiologia* 420: 165-184.

Tiersch, T.R. & Mazik, P.M. (eds). 2000. Cryopreservation in aquatic species. World Aquaculture Society, Baton Rouge LA.

Unson, J. 2006. ARMM moves to protect seaweed growers. *The Philippine Star*. Nation section, January 26, 2006: p. A-2.

Utter, F. 2004. Population genetics, conservation and evolution in salmonids and other widely cultured fishes; some perspectives over six decades. *Reviews in Fish Biology and Fisheries* 14: 125-144.

Van Hove, C. 1989. Azolla and its multiple uses with emphasis on Africa. Translation from the French by J.E. Ruelle. Food and Agriculture Organization of the United Nations: Rome, Italy. 53p.

Váradi, L., Gorda, S., Bakos, J. & Jeney, Z. 2002. Management of broodstock and quality control of fish seed in Hungary. *Naga. WorldFish Center Quarterly* 25 (3/4): 45-47.

Verspoor, E. and 12 co-authors. 2005. Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. *Journal of Fish Biology* 67 (Supplement A): 3-54.

Waples, R.S. and 15 co-authors. 2001. Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology* 59 (Supplement A): 1-41.

Wekundah, J.M. 2005. Genomics for the poor: an analysis of the constraints and possibilities for social choices in genomics for developing countries. Tailoring Biotechnologies 1 (1): 119-138.

WorldFish Center. 2002. Nairobi Declaration. Conservation of aquatic biodiversity and use of genetically improved and alien species for aquaculture in Africa. Published from an Expert Consultation on Biosafety and Environmental Impact of Genetic Enhancement and Introduction of Improved Tilapia Strains/Alien Species in Africa, 20-23 February, 2002, Nairobi, Kenya. WorldFish Center, Penang, Malaysia. 13p. http://www.cta.int/pubs/nairobi/declaration.pdf

WorldFish Center. 2003. Dhaka Declaration on ecological risk assessment of genetically improved fish. WorldFish Center, Penang, Malaysia. 18p. http://www.worldfishcenter.org/Pubs/Dhaka%20booklet/Dhaka_booklet.pdf

WorldFish Center. 2004a. Proceedings of the Final Workshop on Public-Private Partnerships in Tilapia Genetics and Dissemination of Research Outputs: Philippine Experience. WorldFish Center, Penang, Malaysia. CD-ROM.

WorldFish Center. 2004b. GIFT technology manual. An aid to tilapia selective breeding. The WorldFish Center, Penang, Malaysia. 46p.

Wright, B. & Pardey, P. 2006a. The evolving rights to intellectual property in the agricultural biosciences. *International Journal of Technology and Globalization* 2 (1/2): 12-29.

Wright, B. & Pardey, P. 2006b. Changing intellectual property regimes: implications for developing country agriculture. *International Journal of Technology and Globalization* 2 (1/2): 93-114.

Wu, Q.J. 2003. Viewpoints on the conservation of genetic resources of farmed fishes in China. In Phillips, B., Megrey, B. and Yingqi Zhou (eds.) Proceedings of the Third World Fisheries Congress. Feeding the world with fish in the next millennium – the balance between production and environment. *American Fisheries Society Symposium* 38: 637-641. American Fisheries Society, Bethesda, MA.

Young, J.A. & Muir, J.F. 2002. Tilapia: both fish and fowl? *Marine Resource Economics* 17: 163-173.

Zhen, Li. 1988. Chinese goldfish. Foreign Languages Press, Beijing, Peoples' Republic of China. 100p.

Fish genomics and analytical genetic technologies, with examples of their potential applications in management of fish genetic resources

Zhanjiang (John) Liu
The Fish Molecular Genetics and Biotechnology Laboratory
Department of Fisheries and Allied Aquacultures and Program of Cell and Molecular Biosciences, Aquatic Genomics Unit, Auburn University, United States of America

1. SUMMARY

The successful completion of the human genome project marked the start of a genomics revolution, which has the potential to impact aquaculture and fisheries production and has implications for the future management of fish genetic resources (FiGR). Aquaculture has the potential to compensate for dwindling capture fisheries, but biological and production hurdles must be overcome in order to develop cost-effective and sustainable aquaculture. Diseases are major threats to sustainability, and therefore the disease problems should be given high priority. In addition, important production and performance traits (such as growth rate, feed conversion efficiency, body conformation and fillet yield) must be improved in order to make aquaculture more productive and profitable. Genetic enhancement of farmed fish is needed not only to meet the demands of fish production, but also to ensure profitability.

The analytical genetic technologies most relevant to aquaculture and capture fisheries include: DNA markers, genome mapping, microarrays, and sequencing. DNA marker technologies are not only the basis for genetic linkage mapping, but also for the analysis of genetic resources, strain differentiation, species differentiation, parentage identification, and preservation of genetic diversity and conservation of genetic integrity.

The application of genomics in aquaculture is still at the early stages. For many important species of farmed fish, molecular markers have been developed allowing genetic analysis for FiGR conservation and genetic enhancement of farmed fish. Linkage and physical maps have been developed allowing elucidation of genes responsible for important performance and production traits; genome reagents such as expressed sequence tags have been produced providing material basis for the development of microarray technology.

Studies of the genomes of farmed and fished aquatic species have shown both common and unique characteristics that provide both advantages and challenges. In most cases, the genomes of farmed aquatic species are smaller than or comparable to the human genome. Many farmed aquatic species have high fecundity that provides large full-sib and half-sib families, and this greatly facilitates quantitative trait loci (QTL) mapping. However, the large number of farmed aquatic species tends to dilute genomic research efforts.

The genomics revolution and its impacts on aquaculture are expected to contribute to resolving problems such as diseases, environmental impacts, and low profit margins. The major potential applications of genome technologies, primarily in aquaculture but also to some extents in capture fisheries include: marker-assisted selection (MAS) for genetic enhancement; environmetal improvements through enhanced productivity as well as the development of novel technologies for environment monitoring, development of effective vaccines and their delivery technologies; monitoring antibiotic resistance; diagnosis for fish diseases and for the safety of aquatic produce; accurate identification of fish stocks for capture fisheries management and for their use as FiGR in aquaculture; conservation of FiGR, including protection of endangered species, in response to fish production strategies and consumer interests; and the development and application of transgenic fish technology including, for example, sterilization technology to address concerns about their possible environmental impacts .

A great challenge for aquaculture and capture fisheries is the long-term conservation of FiGR**.** Genome technologies provide new tools for genetic analysis. Innovative DNA marker technologies have opened a broad avenue for the analysis of genetic diversity based on genotypes. Some aquaculture operations still use wild fish seed. For these and for future fish breeding programs, conservation of wild FiGR is important.

The applications of genomics in aquaculture and capture fisheries raise ethical, economic, environmental, legal, and social concerns. The most prominent of these at present relate to the development and use of genetically modified organisms. More research is needed not only to resolve issues related to safety of using transgenic fish, but also to produce novel technologies allowing safe use of transgenic technology.

Public education about genomics and its applications is a key issue. **The public is relatively naïve and ill-informed about genomics. Conversely, genomics researchers may not understand the practical needs of aquaculture and capture fisheries or of fish consumers. While information dissemination about genomics to the public is very important, better exchanges of information between genome researchers and aquaculture and fisheries professionals are also essential.**

Fish genomics and analytical genetic technologies are reviewed here, with some examples of their implications for FiGR management. Genomics is a highly dynamic research field, currently dominated by human genomics but rapid developments in genomics can afford new opportunities for applications in aquaculture and capture fisheries, particularly in the areas of FiGR conservation and genetic enhancement.

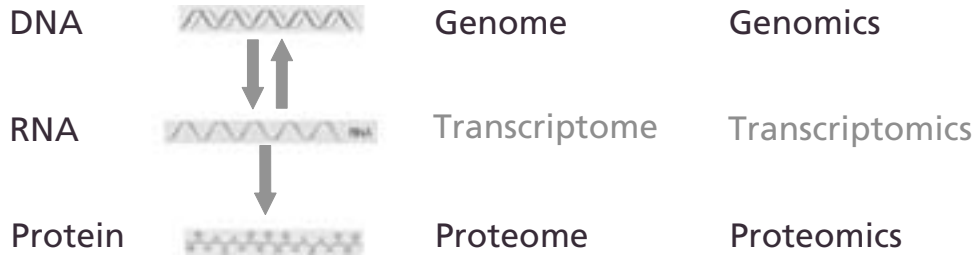
2. BACKGROUND

Genomics began to receive substantial attention as a result of the Human Genome Project. The Human Genome Project faced the tasks of decoding the three billion base pairs of the human genome. Genomics always generates large data sets and these demand new ways of data management. Genomics draws data from cytogenetics, molecular genetics, quantitative genetics, and population genetics, and has led to the development of bioinformatics, through which raw genome information links to meaningful biological information. Genomics comprises the study of genome structure, organization, expression, evolution, and functions. Many sub-branches of genomics are emerging, including aquaculture genomics (http://www.genomicglossaries.com).

Genomes and genomics

The term genome refers to the complete genetic material of an organism. This includes the nuclear and mitochondrial genomes for plant and animals, and also chloroplast genomes for plants. Mitochondrial and chloroplast genomes are small and contain only a limited number of genes. The focus of most genome research is on the nuclear genome,

FIGURE 1
The genome and genomics in relation to central genetics dogma



though mitochondrial genomes have been extremely useful for the identification of fish species and populations. Genomics is the science that studies the genome.

The genetic information stored in DNA cannot be used without being transcribed into RNA which then, with very few exceptions, must be translated into proteins in order to have biological functions. The term genomics often is used to cover not only this narrow sense genomics, but also transcriptomics, and in many cases proteomics as well. As Figure 1 shows, the entire DNA content of an organism (the genome) is transcribed into RNA (the entire RNA content of the organism is called the transcriptome), and the RNA is translated into proteins (the proteome). Genomics, transcriptomics, and proteomics are sciences that study the genome, transcriptome, and proteome, respectively. Genomics can be divided into structural genomics, which studies the structures, organization, and evolution of genomes, and functional genomics, which studies expression and functions of the genomes.

Genetic diversity at the genome level

Through the long process of evolution, many mutations and other genetic changes have accumulated. Accumulation of different mutations in reproductive isolated populations and individuals, as a result of their environment, is the fundamental basis of fish genetic diversity. The basic idea behind fish population genetic analysis is to unravel such differences and their inheritance among populations.

Whereas the genome is relatively stable in an organism, the transcriptome is highly dynamic. The types of transcripts and their relative levels of expression are highly regulated by tissue specificity, developmental stage, physiological state, and the environment. For instance, an organism might have 25 000 genes, but not all are expressed in every type of cell. Those genes required for the basic cell structure and functions are probably expressed in all tissues, organs, and cell types; whereas each cell type expresses a subset of the genes specific for those cell types. Many genes are expressed throughout the life history of an organism, but certain genes are expressed only at a specific developmental stage. The environment can insert its effect on gene expression in multiple dimensions. Temperature, pH, water quality, stress, dissolved oxygen, and many other environmental factors can induce or suppress expression of a large number of genes. Environmental pollution can lead to activation and suppression of expression of many genes in both the types of genes being expressed, and the levels of gene expression. Consequently, genome technologies have much to do with the environment, as well as the genome. It is now widely believed that the complexity of the transcriptome is much larger than the genome, because of alternatively processed transcripts. The information stored in the genome is amplified and diversified once at the RNA level, and is further amplified and diversified at the protein level by post-translational glycosylation, acetylation, phosphorylation, and other modifications leading to drastically different biological functions.

3. THE GENOMICS REVOLUTION AND ITS EMERGING TRENDS

Francis Collins, the Director of the National Human Genome Research Institute (NHGRI), with inputs from 600 scientists, described the "three-floor house" for the future of genomics (Box 1).

From this three-floor house plan of genomics, the following trends can be deduced:

- Genomics goes functional
- Genomics goes global
- Genomics will continue to be dominated by human genomes and human health concerns
- Genomics goes environmental
- Genomics moves towards systems biology, metagenomics, and predictive biology
- Advances in genomics will accelerate; some significant discoveries and their impacts will probably be unintentional

Genomics goes functional

The first and the overwhelming trend of genomics is that it is going functional. Although having the human genome sequenced still seems new, genomics research is rushing ahead to the next step, functional genomics. What functional genomics covers depends largely on who is being asked, but many scientists agree that the scope of functional

BOX 1

The three floor house of future genomics

First floor: genomics to biology

- Define the structure of genetic variations with tools like the HapMap.
- Decode many additional genomes.
- Reduce the cost of decoding an individual genome from $30 million today to $1,000.
- Identify the functional elements of the human genome.
- Identify all proteins of the cell and their interactions.
- Build a computational model of a human cell and extend it to many types of human cells.

Second floor: genomics to health

- Identify genetic and environmental risk factors for common diseases.
- Build "sentinel" systems to detect diseases before they become advanced.
- Get academic researchers to embrace modern drug discovery techniques to create promising compounds.
- Gather and study genotypes from a 500,000-person segment of the U.S. population for 7 to 10 years.
- Figure out modern-day health disparities such as why some groups are afflicted with specific diseases more than others.
- Use genomics outside our borders to combat malaria, tuberculosis, and other diseases.

Third floor: genomics to society

- Enhance genetic privacy and protection via legislation.
- Understand genomics with respect to race and ethnicity. Be wary of demagogues who would exploit genomics for political purposes.
- Understand genomics' impact on human characteristics such as intelligence and sexual orientation.
- Define areas that should not be exploited, such as designing characteristics of future generations.

Source: Francis Collins: http://www.bio-itworld.com/archive/041503/collins-sidebar/

genomics ranges from expression profiling, the relationship between genome expression and functions, discovery of gene functions and their interrelationships, understanding networking among genes in relation to carrying out their functions, to proteomics and protein-protein interactions. Potential application areas include clinical diagnostics, agro biotechnology, environmental biotechnology, and pharmacogenomics. Although functional genomics remains young enough that people argue over their definition, few squabble over the value of this field. Advances in areas from gene expression to proteomics promise to push ahead basic research, biotechnology, and medicine. In fact, some experts predict an annual compound growth rate of 28% for the next six years in commercial sectors of functional genomics. As functional genomics moves forward, it will provide many options for applications in aquaculture and capture fisheries.

Genomics goes global

Genomics is going yet more global as many countries have an interest in participation, and no one wants to fall behind. Genome science is so big that no single individual or single laboratory can do it alone. It requires collaborations, team work, and international cooperation. Not only is international cooperation important for genome research because many of the genetic resources are shared by the international communities, collaboration among the private sector is another trend. The complexity concomitant with genomics and proteomics has had two key organizational impacts for large pharmaceutical companies (Arlington and Peakman, 2001). First, it has created a situation wherein the industry no longer has the resources to cover every technology, disease and therapeutic area. The second impact of the genomics revolution is to lower the entry barriers to new competitors who might be much more nimble in finding and validating targets and leads using virtual networks. These changes are per se healthy from the perspective that more opportunities are created for new players, while existing giant players have to ask the hard question about how to maintain a competitive edge in the genomics era with explosive growth with the amount of available information. Companies and national programs need to consider making adequate investments in education and capacity building to provide the human resources needed to take genomics forward.

More consortia are likely to be established to address the big questions that genomics can answer, but such questions are too big and too risky for companies to tackle on an individual competitive basis (Arlington and Peakman, 2001). Aquaculture research communities are already working collaboratively by forming various genome consortia including Salmonids Genome Consortium, Oyster Genome Consortium, and Catfish Genome Consortium etc. (e.g., http://web.uvic.ca/cbr/grasp/). The Animal Genome Project in the United States of America is organized under a National Project of NRSP-8, in which aquaculture genome is a component. Under NRSP-8, each species has a coordinator (http://www.animalgenome.org/).

Genomics will continue to be dominated by human genomes and human health concerns

Human genomics and human health concerns will continue to dominate genomics, even though many other areas, such as agricultural genomics and environmental genomics may be equally important because they affect human health. All of the genomics information and genetic technologies developed to date will be exploited to the maximal extent in human health and pharmaceutical developments. Genome technologies and genomic information allow genetic testing to be performed with a much greater precision for the prediction of predisposition to disease and ailments, carrier status, and prenatal testing. Such capabilities likely will lead to a trend of using genome technologies for pre-symptom predictions of diseases. Genome information,

genome resource, and genetic technologies also assist development of pharmaceutical products, including genes and gene products.

Genomics goes environmental

Public concern about environment changes and environmental quality is high and there are driving forces to address this in government, NGOs, and the public at large, with modern technologies available for the benefit of the environment (Gracey and Cossins, 2003; Cossins and Crawford, 2005; Almeida *et al.* 2005). Such technologies can be grouped into two general categories: those that enhance agricultural production with the same or less input, and those that can provide novel sentinels for environmental monitoring. For instance, broodstocks can be selected for better feed conversion efficiencies using gene-assisted technologies allowing greater yields with less feed, reducing environmental problems from agricultural production including aquaculture; microarrays can provide precise information on environmental pollution and its impact on the organisms involved in the system. Functional genomics is expected to contribute information for defining environmental issues, as well as technology for environmental monitoring and environment-friendly technologies for agriculture, aquaculture, and natural resource utilization.

Genomics moves towards metagenomics, systems biology, and predictive biology

Genomics is moving toward systems biology, metagenomics, and predictive biology. Genomics, once wholly described by single-organism sequencing efforts, is poised to fulfill its scientific promise in a number of different ways as sequence information is transformed into biological meaning by evolving technologies, theoretical frameworks and practical goals. Systems biology and metagenomics are two of the most ambitious of these emerging genomic sciences, concerned with 'total' understanding of cellular and ecological systems. Metagenomics is also referred to as environmental genomics or community genomics. It is the culture-independent genomic analysis of microbial communities (Eyers *et al.*, 2004; Galperin, 2004; Riesenfeld *et al.*, 2004; Rodriguez-Valera, 2004; Schloss and Handelsman, 2003). Systems biology aims to reconcile the exponentially growing amount of data about macromolecules, cells, tissues, organisms, populations, and ecosystems into coherent and systemic views of organization (Ge *et al.*, 2003; Kitano *et al.*, 2002). The genomics era has led to a much greater understanding of physiology and pathology at the molecular level and is enabling scientists to begin to unravel cellular processes as the result of the interplay of networks of genes. The publication of the human genome sequence and the use of expression databases and sophisticated bioinformatics software to find and characterize new genes and gene families have identified a huge number of potential and actual targets in a wide range of diseases. Further, the understanding of genome variation and the impact this has on health and disease will significantly improve the development and delivery of new medicines. On top of systems biology, modern genome sciences should generate information concerning expression of genomes as to "when this happens, then that happens". Predictive biology will provide insights as to whether and when certain conditions, such as disease epidemics, may or may not happen.

Advances in genomics will accelerate: some significant discoveries and their impacts will probably be unintentional

With the great expectations from the human genome project and the potentially revolutionary advances of sequencing technology, it is likely that genomics will make new rapid leaps forward. While sequencing a single genome was regarded as utopia 20 years ago, sequencing thousands of human genomes is now possible. Such sequencing

capacities and efficiency, when coupled to the ability to analyse the genomics data and to disseminate them through bioinformatics, suggest that there will be great advances in genomics. However, some discoveries and their impacts will probably be unintentional. Computerized analysis of complex genomics data can bring discoveries that are not related to the main purposes for which they were collected.

4. EXAMPLES OF FISH GENOMICS AND ANALYTICAL GENETIC TECHNOLOGIES

Since the completion of the Human Genome Project, major progress has been made in genome research, including the genomics of some farmed fish. The first Workshop on Aquaculture Species Genome Mapping was held in May 1997 in Dartmouth, Massachusetts, United States of America. Thus it was decided to focus on five species groups in the United States of America: catfish, tilapia, salmon/trout, shrimps, and oysters. In 2003, an Aquaculture Genome Project joined USDA project NRSP-8, as a part of the National Animal Genome Project, with the addition of striped bass (*Morone saxatilis*) as the sixth aquaculture species of focus in the United States of America.

The most potentially useful genomic and analytical genetic technologies for application in aquaculture and capture fisheries are: DNA markers, genome mapping, and microarrays (see Annex 1). DNA marker technologies include various techniques and methods for the analysis of genetic variation at the individual, population, or species levels. They are not only the basis for genetic linkage mapping, but also for the analysis of genetic resources, strain differentiation, species differentiation, parentage identification, and preservation of genetic diversity and conservation of genetic integrity.

Examples of major aquaculture genome projects

The US NRSP-8 project was initiated in 1998 and it is now in its second five-year phase (2003-2008). The major objective in the first phase was to develop molecular markers, and construction of genetic linkage, physical, and radiation hybrid maps. The project has three objectives in its current phase: 1) enhance and integrate genetic and physical maps of agriculturally important animals for cross species comparisons and sequence annotation; 2) facilitate integration of genomic, transcriptional, proteomic and metabolomic approaches toward better understanding of biological mechanisms underlying economically important traits; and 3) facilitate and implement bioinformatic tools to extract, analyze, store and disseminate information (http://www.animalgenome.org/).

The Genome Research on Atlantic Salmon Project (GRASP) has been conducted in Canada, where Atlantic salmon (*Salmo salar*) is an important farmed fish. In this project, genetic linkage maps and physical maps have been constructed for the Atlantic salmon genome. Genome reagents and tools have been prepared, including large numbers of expressed sequence tags (ESTs), bacterial artificial chromosome (BAC) end sequences (BES), and microarray platforms. This project has been renewed and re-termed as the cGRASP project (Consortium for Genomic Research on All Salmonids Project; http://web.uvic.ca/cbr/grasp/).

Several major genome projects have been conducted and initiated in Europe, including the SalMap project for mapping the Atlantic salmon genome, the BASSMAP project for mapping the genome of the European sea bass (*Dicentrarchus labrax*), the BRIDGEMAP project for genome of sea bream (*Sparus aurata*), and a metagenomics project focused on evolution of genome components coping with environmental stresses. The BRIDGEMAP project is a collaborative project funded by the EU initiated in 2001 with three major objectives: 1) construction of a framework genetic linkage map of sea bream for aquaculture as well as for population monitoring for fisheries; 2) To develop basic genome tools and reagents from sea bream for use in comparative genomics across species; and 3) Construction of physical maps using

bacterial artificial chromosome (BAC) libraries and radiation hybrid mapping panels (http://www.bridgemap.tuc.gr/).

In China, the Grass Carp Genome Project was initiated in 2005 and officially announced in the 13th International Congress On Genes, Gene Families And Isozymes (http://www.cafs.ac.cn/page/cafs/guanggao/jiyin/show1eng.htm). This project involves multiple institutions in China and is aimed at producing genome reagents like ESTs, BAC libraries, BAC end sequences, physical maps, linkage maps, before eventually sequencing the entire genome of the grass carp *(Ctenopharyngodon idella)*. Genome studies of shrimps have been conducted for several years in China and Thailand and ESTs and microarrays have been produced; linkage maps have also been constructed (http://pmonodon.biotec.or.th/; Wang *et al*., 2006). In Japan, genome projects have been conducted with Japanese flounder, yellow tail, shrimps, and oysters. Fish genome studies are in progress in many parts of world, but the major efforts are located in the United States of America, Canada, Europe, China, and Japan. Genome projects are expensive and many developing countries cannot afford them.

Major achievements of aquaculture genomics

Framework genetic linkage maps have been established in salmon, trout, tilapia, catfish, shrimp, oysters, and many other species (Table 1). Large numbers of molecular markers have been developed and efforts for mapping more markers are increasing. Basic genome reagents have been or are now being established for farmed finfish, crustaceans and molluscs. Large-insert DNA libraries, such as BAC libraries, are available for Atlantic salmon, rainbow trout (*Oncorhynchus mykiss*), tilapia (*Oreochromis* spp.), channel catfish (*Ictalurus punctatus*), and several other finfish species. Two BAC libraries have been constructed for oysters and those for shrimps are being constructed. Physical maps have been constructed in Atlantic salmon (Ng *et al*., 2005), Nile tilapia (*Oreochromis niloticus*) (Katagiri *et al.*, 2005), and channel catfish (Xu *et al.*, 2007). Gene discovery efforts through sequencing ESTs are increasing. A total of almost one million ESTs are now available from farmed aquatic species, of which a large percentage is from Atlantic salmon, rainbow trout, and channel catfish. The Joint Genome Institute (JGI) of the US Department of Energy (DOE) has initiated large EST projects for channel catfish (to produce 600 000 ESTs, John Liu of Auburn University serves as the principal investigator), oysters (to produce 600 000 ESTs, Dennis Hedgecock of the University of Southern California serves as the principal investigator), and genome survey project in tilapia-related species (to sequence a total of 10% genome coverage from five tilapia-related species, Thomas Kocher of the University of New Hampshire serves as the principal investigator). Descriptions of these JGI sequencing projects can be found at http://www.jgi.doe.gov/News/news_5_12_05.html. cDNA microarray technologies have been developed and used in Atlantic salmon, shrimps, oysters, and channel catfish. Although farmed fish genome research had a late start, this allowed researchers to learn lessons from scientists working with other species, and more advanced genome technology also provided greater efficiency.

Research on the genomes of farmed fish has focused on performance and production traits such as growth rate, feed conversion efficiency, disease resistance, tolerance to environmental stresses such as high ammonia, low dissolved oxygen, tolerance to cold temperature and to various salinities**.** In most cases, the genomes of farmed aquatic species are smaller than, or comparable to the human genome. Many farmed fish species have high fecundity, which provides opportunities to create large resource and reference families that allow great selection pressure to be applied at the phenotypic level for the analysis of quantitative trait loci (QTL). Experiments can be repeated many times as the related expense is relatively small. The large size of resource families allows accurate mapping of important genes responsible for traits. However,

TABLE 1
Genetic linkage maps, constructed using various marker systems, for various fish, shrimp, and molluscs species

Species	Common name	Marker system used	References
Salmonids			
Oncorhynchus mykiss	Rainbow trout	AFLP; RAPD Microsatellites	Young *et al.*, 1998; Nichols *et al.*, 2003b; Felip *et al.*, 2005; Sakamoto *et al.*, 2000; Rogers *et al.*, 2003; Danzmann *et al.*, 2005
Salmo salar	Atlantic salmon	AFLP, Microsatellites	Moen *et al.*, 2004c; Gilbey *et al.*, 2004
Salmo trutta	Brown trout	Microsatellites	Gharbi *et al.*, 2006
Salvelinus alpinus	Arctic char	Microsatellites	Woram *et al.*, 2004
Tilapia			
Oreochromis spp.	Tilapia	AFLP, Microsatellites	Kocher *et al.*, 1998; Agresti *et al.*, 2000; McConnell *et al.*, 2000; Lee *et al.*, 2005
Catfish			
Ictalurus punctatus	Channel catfish	AFLP; Microsatellites	Liu *et al.*, 2003; Waldbieser *et al.*, 2001
Clarias macrocephalus	Walking catfish	AFLP	Poompuang and Na-Nakorn, 2004
Carp			
Cyprinus carpio	Common carp	RAPD, Microsatellites	Sun and Liang, 2004
Other fish species			
Dicentrarchus labrax	European sea bass	Microsatellites	Chistiakov *et al.*, 2005
Seriola quinqueradiata and Seriola lalandi	Yellowtails	Microsatellites	Ohara et al., 2005
Paralichthys olivaceus	Japanese flounder	AFLP, Microsatellites	Coimbra *et al.*, 2003
Plecoglossus altivelis	Ayu	AFLP, Microsatellites	Watanabe *et al.*, 2004
Astyanax mexicanus	Cave fish	RAPD	Borowsky *et al.*, 2002
Oryzias latipes	Medaka	RAPD, Microsatellites	Ohtsuka *et al.*, 1999; Naruse *et al.*, 2004
Poecilia reticulata [	Guppy	RAPD	Khoo *et al.*, 2003
Danio rerio	Zebrafish	RAPD, Microsatellites	Postlethwait *et al.*, 1994; Mohideen *et al.*, 2000; Knapik *et al.*, 1998; Shimoda *et al.*, 1999; Woods *et al.*, 2000, 2005
Xiphophorus sp.		RAPD, Microsatellites	Kazianis *et al.*, 1996; Walter *et al.*, 2004
Shrimp			
Penaeus monodon	Black tiger shrimp	AFLP	Wilson *et al.*, 2002
Penaeus vannamei	White shrimp	AFLP	Pérez *et al.*, 2004
Penaeus japonicus	Kuruma prawn	AFLP	Li *et al.*, 2003
Penaeus chinensis	Chinese shrimp	AFLP	Li *et al.*, 2006
Molluscs			
Crassostrea virginica	Eastern oyster	Microsatellites	Yu and Guo, 2003
Crassostrea gigas	Pacific oyster	AFLP, Microsatellites	Li and Guo, 2004; Hubert and Hedgecock, 2004
Chlamys farreri	Zhikong scallop	AFLP	Li *et al.*, 2005
Haliotis discus hannae	Pacific abalone	AFLP, RAPD, microsatellites	Liu *et al.*, 2006; Sekino and Hara, 2007
Other			
Stongylocentrotus nudus	Sea urchin	AFLP	Zhou *et al.*, 2006

farmed fish genomics faces great challenges because there are many farmed fish species and funding levels for aquaculture genomics have been low. Technically, labeling of individual fish in research is often a daunting task, unless intrusive procedures are used; the aquatic environment also makes real time observations extremely difficult; genome duplication is widespread in teleost fishes, which poses challenges related to complexities for the analysis of gene arrangement, expression and function.

Sequencing farmed fish genomes

In spite of the large effort in genome sequencing of the zebrafish (*Danio rerio*) (http://www.sanger.ac.uk/Projects/D_rerio/), green spotted pufferfish (*Tetraodon nigroviridis*) (http://www.genoscope.cns.fr/externe/English/Projets/Projet_C/), Japanese pufferfish (*Fugu rubripes)* (http://www.genomenewsnetwork.org/articles/11_01/Pufferfish_sequenced.shtml) and medaka (*Oryzias latipes*) (http://dolphin.lab.nig.ac.jp/medaka/), no genomes of aquaculture species have been sequenced. White papers have been generated advocating sequencing a few genomes of important aquaculture species including those for rainbow trout (http://www.animalgenome.org/aquaculture/salmonids/RainbowProposal.pdf) and oysters (http://findarticles.com/p/articles/mi_m0QPU/is_2_24/ai_n15390229). The major constraints for sequencing the fish genomes are financial. In the overall genomics revolution, there has been little attention so far to the genomics of farmed fish, even for the most important species. Plant and livestock genomes have been given priority. Of the major agricultural animals, bovine, swine, and chicken genomes are being sequenced. The entire genome sequences would provide research and application advantages for the involved species. Taking USDA funding priorities as an example, only species whose genome is sequenced with a draft sequence over five fold of the genome coverage (i.e., the total base pairs sequenced should be greater than five times of the genome size of the species) is eligible for funding from the Functional Genomics Program. Obviously, no species used in aquaculture meets the criteria. All aquaculture species are thus currently excluded from its funding. However, emerging sequencing technologies might enable genomes to be sequenced more cheaply and efficiently and then it should be possible to sequence important farmed fish genomes. With or without this, fish genomics should focus on FIGR management (use and conservation), genetic enhancement, and the environmental aspects of fish genomes. Among these, genetic enhancement often takes the priority, but it is very important to note that FiGR management, and environmental genetic issues are often directly related to genetic enhancement, and should be given much greater attention.

5. ACTUAL AND POTENTIAL APPLICATIONS OF GENOMICS AND ANALYTICAL GENETIC TECHNOLOGIES IN FISH GENETIC RESOURCES MANAGEMENT

Aquaculture production is growing rapidly to provide food fish for the world's rapidly growing population and now provides approximately 40% of food fish consumed by humans (FAO, 2006). Many capture fisheries are currently harvested at or above maximum sustainable levels, and are in global decline because of over-harvesting and habitat degradation. Wild fish genetic resources (FiGR) are being depleted and some are facing extinction. Some aquaculture operations still depend on wild FiGR for seed and broodstock and wild fish populations are important resources for fish genetics research, including breeding programs and genomics.

The genomics revolution and genetic analytical technologies have many actual and potential applications for capture fisheries and aquaculture, including FiGR management. Their practical applications in aquaculture include, *inter alia*, marker-assisted selection (MAS), environment protection, genetic management of broodstocks, and genetic improvement of framed fish. Analytical genetic technologies will contribute

to lessening the adverse environmental impacts of aquaculture as well as to resolution of the disease problems through genetic enhancement, development of effective vaccines and their delivery systems, and development of rapid and accurate diagnostic tools. Future applications also include the safe use of transgenic technologies. Annex 1 summarizes major genomics and other methods of genetic analysis for application to natural and farmed aquatic species.

Diseases are major threats to sustainable aquaculture, in crustacean farming, especially shrimp farming, and in the farming of some mollucs, especially oysters. Diseases also affect the farming of many types of finfish, including carps, catfish and salmonids. Countermeasures to ensure the health and survival of farmed fish, including genetic technologies, are much needed. Superior broodstocks resistant to major diseases are needed. Although rich genetic resources must exist among aquaculture species for resistance to major fish diseases, for fast growth and for efficient feed conversion, genomic research is required to identify and then utilize these. Resistance-linked markers are especially needed for marker-assisted selection. Direct selection of disease resistance has proven to be very difficult in aquaculture. Genome based-technologies could provide solutions to meet some of the challenges presented by economically important pathogens. Genetic technologies for increasing and identifying disease resistance have proven safe, reliable, and environmentally sound for livestock. Mapping of large numbers of markers will pave the way for seeking QTLs for disease resistance in fish. This will add a new dimension to the new generation of technology for genetic improvement of disease resistance through marker-assisted selection in aquaculture. Genome research should facilitate marker-assisted selection for genetic improvement in many production traits of farmed fish. Some recent QTL studies are listed in Table 2.

Genetic improvement through marker-assisted selection

Marker-assisted selection is a major potential application that is used as an argument for expanding research on the genomics of farmed fish. DNA marker technologies are already used routinely for stock identification is routine in some farmed fish species (Beacham *et al*., 2000; 2005, Duchesne and Bernatchez, 2007). A few markers linked with performance and production traits have been identified (Moen *et al*., 2004a; 2004b; Martyniuk *et al*., 2003; O'Malley *et al*., 2003; Reid *et al*., 2005; Nichols *et al.,* 2003a; Palti *et al.,* 2001; Cnaani *et al.,* 2003). However, despite a great deal of promise, only a handful of cases demonstrating practical usefulness of MAS in reducing frequencies of recessive alleles causing genetic diseases, determining simple Mendelian traits and improvement in a few species have been reported so far (Dentine, 1999; Dekkers, 2004). In livestock, commercial implementation of MAS related to improvement of quantitative traits has been employed for removal of deleterious major genes, growth rate, meat quality, disease resistance and reproductive traits in pigs and in other species such as cattle where markers are used routinely for improvement of protein percentage in milk and marbling and tenderness in beef cattle. Dekkers (2004) has summarized the progress and use of markers as "the current attitude toward MAS is … cautious optimism". Fine QTL mapping will allow traits-linked markers to be identified and used for MAS, which should not replace traditional selective breeding, but should complement to ensure accurate and effective selection and to contirbute indicators at the molecular level that phenotypically selected fish truly contain the genes that breeders believe they do. Specific studies related to performance and production traits for aquaculture species must be accomplished before applying MAS in aquaculture. With low levels of funding, it is anticipated that such research may still requires years of effort, and actual MAS in aquaculture may still need at least five years.

TABLE 2
Recent QTL studies conducted in various farmed fish species

Common name	Speciesname	Traits	References
Salmonids			
Atlantic salmon	*Salmo salar*	Body weight, condition factor, Disease resistance, sex	Reid *et al.*, 2005; Moen *et al.*, 2004; 2004c; Grimholt *et al.,* 2003 ; Artieri *et al.*, 2006
Rainbow trout	*Oncorhynchus mykiss*	Albinism, condition factor, disease resistance, growth rate, killer cell-like activity, meristic traits, pyloric caecae number, precocious maturation, spawning date, upper thermal tolerance	Danzmann *et al.*, 1999; Palti *et al.*, 1999; 2001; Sakamoto *et al.*, 1999; Nakamura *et al.*, 2001; Ozaki *et al.*, 2001; Perry *et al.*, 2001; 2005; Robison *et al.*, 2001; Martyniuk *et al.*, 2003; Nichols *et al.*, 2003a; O'Malley *et al.*, 2003; Somorjai *et al.*, 2003; Khoo *et al.*, 2004; Nichols *et al.*, 2004; Zimmerman *et al.*, 2004; 2005; Moen *et al.*, 2004b; Reid *et al.*, 2005; Rodriguez *et al.*, 2005
Coho salmon	*Oncorhynchus kisutch*	Flesh color	Arenada *et al*., 2005
Arctic char	*Salvelinus alpinus*	Temperature tolerance, growth rate, condition factor	Somorjai *et al.*, 2003; Tao and Boulding, 2003; Reid *et al.*, 2005
Tilapia			
Tilapias	*Oreochromis* spp.	Body and peritoneum coloration, cold tolerance, disease resistance, growth rate, immune response prolactin expression level, survival sex determination, sex ratio, stress response	Shirak *et al.,* 2000; 2002; 2006 ; Streelman and Kocher 2002; Palti , 2002; Cnaani *et al.*, 2003; 2004 a; 2004b; 2004c; Lee *et al.,* 2003; 2004; 2005; Moen *et al.*, 2004a;
Carp			
Common carp	*Cyprinus carpio*	Cold tolerance	Sun and Liang, 2004
Molluscs			
Eastern oyster	*Crassostrea virginica*	Disease resistance	Yu *et al.*, 2006
Shrimp			
Kuruma prawn	*Penaeus japonicus*	Body weight, total length, and carapace length	Li *et al.*, 2006
Other			
Zebrafish	*Danio rerio*	Behavioral and morphological differentiation	Wright *et al.*, 2006

Protection of the environment, with increasing aquaculture production and profitability

Aquaculture has a great challenge ahead to address potential environmental impacts and genomics can make significant contributions. Genome research should focus on how to benefit aquaculture and at the same time on how to protect the environment. Through research on the gemones of farmed fish, new technologies can be developed for monitoring the aquatic environment using bioindicators, biomarkers and genome expression signatures (e.g. Almeida *et al.*, 2005; Gracey and Cossins, 2003; Cossins and Crawford, 2005). Environmental genomics is therefore an important focus for farmed fish genomics. Metagenomics and ecogenomics include the goal of using genome technologies to improve environmental quality. Environmental genomics is now a major driving force (e.g. Travis *et al.*, 2003; MacGregor, 2003; Frazier *et al.*, 2003; Almeida *et al.*, 2005).

Disease diagnosis, food safety, disease resistance, fish vaccines, drug-resistant pathogens

Genomics can contribute much to the accurate diagnosis of fish diseases and to ensuring the safety of aquatic produce. Existing technologies are practical and capable of delivering results immediately (Kerr and Cunningham, 2006; Adams and Thompson, 2006).

Genome research, through QTL mapping, MAS and transgenesis, provides potential avenues for addressing some of the disease problems that threaten aquaculture. Through QTL mapping, it is possible to locate major genes responsible for disease resistance. Through MAS, brood stocks can be developed containing disease resistance genes (e.g. Palti *et al*., 1999; Moen *et al*., 2004b; Nichols *et al*., 2003a) and conceptually, traditional hybridization can be used to allow their introgression (Liu *et al*., 2003; Senanan *et al*., 2004).

Vaccines should be developed for fish as for livestock, though their applications in aquaculture have some limitations (Lorenzen *et al*., 2002; Evensen *et al*., 2005). One major difference is the large number of individuals in populations of farmed fish species and their relatively low individual value. The aquatic environment also poses technical difficulties. Genome research may allow development of more effective vaccines, including DNA vaccines (Kurath, 2005). Effective vaccine delivery systems must also be developed. Genome technologies should also provide means for monitoring drug resistance in fish pathogens. This is a significant problem because countries that produce fish but have relaxed laws with respect to drug use in aquacutlure could contribute to increases in drug resistance in many pathogens, including some that affect humans (Graslund and Bengtsson, 2001; Cabello, 2006).

Genetic characterization

Genetic marking and identification of fish species, strains, lines, populations, and individuals is very important not only for aquaculture and hatchery operations, but also for capture fisheries management. Genome technologies have the capacity to provide "diagnostic kits" to identify many important species and populations, using DNA marker technologies (for reviews, see Liu and Cordes, 2004; Grant, 2007; Pullin, 2007; Smith, 2007).

DNA marker technologies should be adapted for wider use in the characterization of wild FiGR. This is particularly important for fish species and stocks that are captured by humans, because some fisheries might be depleting FiGR. For endangered species and stocks, genome technologies can characterize fish produce even after it has been cooked. This should provide greater levels of law enforcement. Consumers should also be protected to ensure that fish produce is labeled accurately at the point of sale (Maldini *et al*., 2006).

Transgenic fish

Early attempts to develop transgenic fish were hindered by a lack of fish promoters and much of the early research was conducted with viral promoters (Dunham and Liu, 2006). Gene-based genetic improvements have now been well demonstrated in fish species using transgenic technologies. In spite of low public acceptance, transgenic work in salmon has demonstrated that growth rate can be enhanced over 10 times by transferring only a growth hormone gene (Du *et al*., 1992; Roberts *et al.*, 2004; Devlin *et al.*, 2004), illustrating the plasticity of some fish genomes and their functions. Other transgenic fish have been developed with improved growth rate, color, disease resistance, survival in cold and body composition, and the ability to produce pharmaceutical proteins. Transgenic zebrafish with altered coloration have been commercialized and

applications are pending for commercialization of transgenic salmon, carp and tilapia transgenes with tranfered growth hormone genes (for examples of reviews, see Devlin *et al*., 2006; Kapuscinski, 2005; Domergue *et al.*, 2005; Fu *et al.*, 2005; Napier *et al.*, 2004; Zbikowska, 2003; ; FAO, 2000; Maclean, 2000; Zhu and Sun, 2000; Iyengar *et al.*, 1996; Chen *et al.*, 1996; Gong and Hew, 1995; Hew *et al.,* 1992; Houdebine and Chourrout, 1991; Chen and Powers, 1990).

To minimize environmental risks, additional technologies such as transgenic sterilization need to be developed (Dunham and Liu, 2006). Genomic research has produced an abundance of molecular genetic information including many genes for consideration for gene transfer, highly regulated gene promoters, and knowledge about their expression and function. Functional genomics analysis should be applied in the future to enhance the capacity and versatility of transgenic technology, and to facilitate assessment of the biosaftey aspects of development and use of transgenic fish.

Increased research will be needed for determining environmental risk, measuring the fitness of transgenic fish and for determining the safety of aquatic produce derived from them. The future success and application of transgenic fish will be dictated by successful demonstration of acceptable environmental risk, assurance of food safety, appropriate government regulation and labeling, public education and opinion, and development of genetic sterilization for transgenic fish. Where commercial production of transgenic food fish is the objective, fish promoters should be used. Advances in genomics will provide these as well as important genes for gene transfer that could have greater public acceptance.

Some important commercial traits of farmed fish - such as resistance to diseases, feed conversion efficiency, tolerance to poor water quality, harvestability, carcass yield, increased reproduction and improved utilization of plant resources have yet to be addressed by transgenic technology. Basic information from genomic research may be the starting point to address effetively genetic enhancement of these traits. One of the greatest future potential benefits of gene transfer in fish could be enhancement of disease resistance in fish. Transgenic fish with enhanced disease resistance would increase profitability, production, efficiency and the welfare of the cultured fish. Preliminary research (Dunham *et al*., 2002; Chiou *et al*., 2002; Sarmasik *et al*., 2002) indicates great promise for success of this approach for enhancing disease resistance.

The use of transgenic fish in recreational fisheries could involve release of transgenic fish into open waters or into more confined, urban environments. Public opinion will vary in regards to this application and the use of transgenic fish in aquaculture of food fish and ornamental fish will likely occur much earlier than their use in recreational fisheries. In the ornamental fish trade, a transgenic petfish named Glofish has already been marketed (Gong *et al*., 2002, 2003).

Combining genetic technologies

Transgenic technology is no silver bullet; neither are genome technologies or traditional selective breeding. Genomics and combined genetic technologies are expected to lead to a much larger scope of genetically improved farmed fish. Partly, this is because the history of domestication and selective breeding of many farmed fish species has been short and great potentials for genetic improvement have yet to be realized. Continued selection plus the application of MAS will likely overcome many of the challenges faced by traditional selection alone, and provide faster and more effective results. Markers for complex traits are more difficult to be identified, and usually complex traits are controlled by multiple genes. Nonetheless, MAS has great potential to fulfill the promises made by agricultural genomics.

6. ENVIRONMENTAL AND SOCIAL ISSUES

A number of governmental and non-governmental organizations (NGO) have started discussions on issues of genomics related to ethics, environment, economy, law, and society (GE_3LS). Genome Canada (http://www.genomecanada.ca/) has conducted annual GE_3LS symposium for several years focusing on conflicting worldviews, social cohesion, ownership, and the democratic deficit. These themes were explored in relation to the application of genomics and proteomics to the fields of agriculture, environment, fisheries and forestry. In the United States of America, the Department of Energy (DOE) and the National Institutes of Health (NIH) Genome Programs set aside 3% to 5% of their respective annual Human Genome Project budgets for the study of the project's ethical, legal, and social issues (ELSI) (http://www.ornl.gov/sci/techresources/Human_Genome/elsi/elsi.shtml). Many of the issues and concerns discussed in this section were obtained from this website because published papers are scarce in this area. As the GE_3LS issues started to emerge with human genome related issues, many of the similar concerns related to genomics will emerge in aquaculture and fisheries related areas.

GMOs in aquaculture

An important issue in aquaculture and fisheries is the application of GMOs, the genetically modified organisms produced through the use of genetic engineering. Other issues include genetic impact of farmed and ornamental fish on wild populations, the ownership of and access to FiGR, and imbalances of genome technologies and capacities in various parts of the world.

The linkage of genomics to biotechnology and transgenic technology is its ability to rapidly discover, identify and characterize genes of economic importance. Such genes can be used for biotechnology, pharmaceutical purposes, or transgenics. A number of controversies exist concerning the use of genetically engineered organisms. The supporting forces come from the benefits GMO's can bring to the society. The fundamental argument for the development of GMOs is the increased food production efficiency for growing human populations.

Researchers at the University of Guelph have developed a new breed of Yorkshire pigs trademarked Enviropig™ that use plant phosphorus more efficiency (Golovan *et al.*, 2001a, 2001b). Non-transgenic pigs are unable to use an indigestible form of phosphorus called phytate present in the cereal grain diet. Therefore producers add supplemental phosphate or phytase enzyme to the diet in order to meet the phosphorus requirement for optimal growth and development. The novel trait of the Enviropig™ enables it to degrade the indigestible phytate and absorb the phosphate eliminating the need to supplement the diet with readily available phosphate, and as a consequence the phosphorus content of the manure is reduced by as much as 60%. Digestion of the phytate also leads to improvements in digestion of minerals in the diet. Clearly, potential use of such transgenic animals would have positive impact to the environment, and such research may inspire similar research in fish.

Consumer choice

Informing consumers of fish products about their identity and origin, by accurate labeling, facilitates consumer choice and product development and marketing. However, economic interests and international trade politics may seriously constrain product labeling. Labeling is not yet mandatory in some countries (e.g. United States of America). Another consideration is consumer awareness or public education. A survey conducted in New Jersey (http://www.nal.usda.gov/bic/Pubpercep/) found that most residents (91%) felt they had an "adequate" or "very good" understanding of how food is grown and produced. However, much of the public was unfamiliar

TABLE 3
Existing genomic reagents and tools for important aquaculture and fisheries species. All information was obtained from the National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov/) by using Entrez, the Life Sciences Search Engine as of 6 December 2006. Expressed sequence tags represent sequence reads from single pass sequencing of transcribed sequences, while total DNA sequences are number of sequence reads obtained from both expressed sequences and genomic sequences

Common name	Scientific name	Importance in aquaculture, capture Fisheries, or both	Number of expressed sequence tags (ESTs)	Total DNA sequences	Characterized proteins
Atlantic salmon	*Salmo salar*	Both	430 340	434 380	1 380
Rainbow trout	*Oncorhynchus mykiss*	Aquaculture	262 256	265 613	2 727
Catfish	*Ictalurus spp.*	Aquaculture	57 084	79 108	1 641
Common carp	*Cyprinus carpio*	Aquaculture	19 344	20 555	1 099
Eastern oyster	*Crassostrea virginica*	Aquaculture	9 018	9 125	73
Tilapia	*Oreochromis spp.*	Both	676	6 688	519
Pacific oyster	*Crassostrea gigas*	Both	4 201	5 259	284
Scallop	*Chlamys farreri*	Both	3 466	3598	208
Striped bass	*Morone saxatilis*	Aquaculture	1 055	1055	201
Grass carp	*Ctenopharyngodon idella*	Aquaculture	534	809	227
Skipjack tuna	*Katsuwonus pelamis*	Fisheries	0	323	77
Japanese anchovy	*Engraulis japonicus*	Fisheries	0	238	127
Alaska Pollock	*Theragra chalcogramma*	Fisheries	0	161	252
Silver carp	*Hypophthalmichthys molitrix*	Aquaculture	0	84	19
Bighead carp	*Aristichthys Nobilis*	Aquaculture	0	70	21
Indian carp	*Labeo rohita*	Aquaculture	0	48	10
Atlantic herring	*Clupea harengus*	Fisheries	0	45	35
Capelin	*Mallotus villosus*	Fisheries	0	39	8
Crucian carp	*Carassius auratus*	Aquaculture	0	29	10
Blue whiting	*Micromesistius poutassou*	Fisheries	0	24	9
Chilean jack mackerel	*Trachurus symmetricus*	Fisheries	0	11	1
Constricted tagelus	*Tagelus dombeii*	Aquaculture	0	9	0
Anchoveta	*Engraulis ringens*	Fisheries	0	8	7
Largehead hairtail	*Trichiurus lepturus*	Fisheries	0	4	0

with traditional methods for producing hybrid plants and animals. While over half the population (54%) acknowledged that they had heard of cross-fertilization or cross-breeding, only 28 percent said they had eaten a fruit or vegetable produced by this method. This is surprising because most commercially available fruit and vegetables are now hybrids. Even more surprising, 17% of the population interviewed believed that they have eaten a fruit or vegetable produced by genetic engineering, though no such product is yet available. This demonstrates the great need for improving public education and awareness about applications of genetics in food production.

Geographical distribution of fish production and fish genomics research

Developed countries will likely play leading roles in the development of farmed fish genomics and genetic technologies that in turn will enhance aquaculture production. However, most of the world's farmed fish production, comes from developing countries

(Pullin, 2007 in this volume; FAO, 2006). How the farmed fish genome technologies will be disseminated is a major concern. Efforts should be made to promote international cooperation and collaboration in genome research and utilization of results and products.

Genetic maps have yet to be developed for many important farmed fish and for many important species that are targeted by capture fisheries. Some of the available genome reagents and resources of fish genomic research so far are summarized in Table 3, from which it is clear that the major genome research activities have been focused on farmed fish species. Much more international collaboration is needed in order to enhance genomics research efforts on major farmed fish and capture fisheries species of the world. Microsatellites are needed for genetic linkage mapping and mapping of QTL, as well as for population genetic studies. ESTs are needed for analysis of gene expression, and also ESTs serve as rich sources for polymorphic markers, and serve as material basis for the development of microarrays unless otherwise the genome sequence is available. Genome sequence surveys (GSS) allow sampling of the genome for the assessment of the genome composition, repeat structure, as well as for polymorphic marker identification.

Need for globally accessible information

There are currently no comprehensive globally accessible databases on FiGR. It will be important to gather information on intraspecific genetic diversity for major capture fisheries species and major farmed fish species (Pullin, 2007). Databases of DNA fingerprints will help in species identification and also in the interest of protection of endangered species and the consumer's interest (Smith, 2007). Law enforcement agencies have trouble in identification of fish in markets and served in restaurants. In many cases, endangered species are involved, but unless more effective genome technologies are developed to provide rapid and accurate identification using fingerprinting techniques, it is difficult to provide effective means for the protection of endangered species. In some cases, inferior fish products are mislabeled as having come from more expensive species. Genome research on major farmed fish species has generated molecular markers allowing population studies and genetic resource analysis. In contrast, little genome information exists for most capture fisheries species and this is limiting the application of genome technologies in assessment of the status and conservation of wild FiGR.

Public education

The public is generally ill-informed and naïve about biotechnology in food production, including the pros and cons of transgenics, genomics and genetic technologies. Public education should be considered an important issue. Many professionals in capture fisheries and aquaculture also do not understand well the potentials and implications of genomics and genetic technologies. While information dissemination from genomics to the public is very important, better exchanges of information between genome researchers and aquaculture and fisheries professionals are also essential. As noted by Dr. Alex Mackenzie, Vice President of Research at Genome Canada, "in order for us to conduct ourselves optimally as a society, I think an informed populace is our most potent weapon" (http://www.iog.ca/about_us.asp?pageid=28).

7. REFERENCES

Adams, A. & Thompson, K.D. 2006. Biotechnology offers revolution to fish health management. *Trends in Biotechnology,* **24**: 201-205.

Agnèse, J.F., Adépo-Gourène, B., Abbans, E.K. & Fermon, Y. 1997. Genetic differentiation among natural populations of the Nile tilapia *Oreochromis niloticus* (Teleostei, Cichlidae). *Heredity,* 79: 88–96.

Agresti, J.J., Seki, S., Cnaani, A., Poompuang, S., Hallerman, E.M., Umiel, N., Hulata, G., Gall, G.A.E. & May, B. 2000. Breeding new strains of tilapia: development of an artificial center of origin and linkage map based on AFLP and microsatellite loci. *Aquaculture,* **185**(1-2): 43-56.

Ahmadian, A., Gharizadeh, B., Gustafsson, A.C., Sterky, F., Nyren, P., Uhlen, M. & Lundeberg, J. 2000. Single-nucleotide polymorphism analysis by pyrosequencing. *Analytical Biochemistry,* **280:** 103-110.

Alderborn, A., Kristofferson, A. & Hammerling, U. 2000. Determination of single-nucleotide polymorphisms by real-time pyrophosphate DNA sequencing. *Genome Research,* **10**: 1249-258.

Almeida, J.S., McKillen, D.J., Chen, Y.A., Gross, P.S., Chapman, R.W. & Warr, G. 2005. Design and calibration of microarrays as universal transcriptomic environmental biosensors. *Comparative and Functional Genomics,* **6**: 132–137.

Anonymous. 1997. Fisheries science review. *Nature*, **386**:105-110.

Araneda, C., Neira, R. & Iturra, P. 2005. Identification of a dominant SCAR marker associated with colour traits in coho salmon (*Oncorhyncus kisutch*). *Aquaculture*, **247**: 67-73.

Arlington, S. & Peakman, T. 2001. Assessing the impact of current trends in genomics on the future of pharmaceutical R&D. *Drug Discovery Today*, **6**: 161-162.

Artieri, C.G., Mitchell, L.A., Ng, S.H., Parisotto, S.E., Danzmann, R.G., Hoyheim, B., Phillips, R.B., Morasch, M., Koop, B.F. & Davidson, W.S. 2006. Identification of the sex-determining locus of Atlantic salmon (*Salmo salar*) on chromosome 2. *Cytogenetics and Genome Research,* **112**: 152-159.

Bagley, M.J., Anderson, S.L. & May, B. 2001. Choice of methodology for assessing genetic impacts of environmental stressors: polymorphism and reproducibility of RAPD and AFLP fingerprints. *Ecotoxicology*, **10**: 239-244.

Beacham, T.D., Hay, D.E. & Le, K.D. 2005. Population structure and stock identification of Eulachon (Thaleichthys pacificus), an anadromous smelt, in the pacific northwest. *Marine Biotechnology,* **7**: 363-72.

Beacham, T.D., Pollard, S. & Le, K.D. 2000. Microsatellite DNA population structure and stock identification of steelhead trout (Oncorhynchus mykiss) in the Nass and Skeena rivers in northern British Columbia. *Marine Biotechnology*, **2**: 587-600.

Billington, N. 2003. Mitochondrial DNA. Hallerman E M (ed.) Population genetics: principles and applications for fisheries scientists. *American Fisheries Society, Bethesda, Maryland*: 59-100.

Birky, C.W., Fuerst, P. & Maruyama, T. 1989. Organelle gene diversity under migration, mutation, and drift: equilibrium expectations, approach to equilibrium, effect of heteroplasmic cells, and comparison to nuclear genes. *Genetics*, **121**: 613– 627.

Borowsky, R. & Wilkens, H. 2002. Mapping a cave fish genome: polygenic systems and regressive evolution. *Journal of Heredity,* **93**(1): 19-21.

Burris J, Cook-Deegan, R. & Alberts, B. 1998. The Human Genome Project after a decade: policy issues. *Nature Genetics,* 20: 333-5.

Cabello, F.C. 2006. Heavy use of prophylactic antibiotics in aquaculture: a growing problem for human and animal health and for the environment. Environ Microbiol. 8:1137-44.

Campbell, D. & Bernatchez, L. 2004. Generic scan using AFLP markers as a means to assess the role of directional selection in the divergence of sympatric whitefish ecotypes. *Molecular Biology and Evolution,* **21**: 945-956.

Cariello, N.F., Scott, J.K., Kat, A.G., Thilly, W.G. & Keohavong, P. 1988. Resolution of a missense mutant in human genomic DNA by denaturing gradient gel electrophoresis and direct sequencing using in vitro DNA amplification. *American Journal of Human Genetics,* **42**: 726-734.

Chapman, R.W. 1989. Mitochondrial and nuclear gene dynamics of introduced populations of *Lepomis macrochirus*. *Genetics*, **123**: 399-404.

Chen, T.T. & Powers, D.A. 1990. Transgenic fish. *Trends in Biotechnology*, **8**(8): 209-215.

Chen, T.T., Vrolijk, N.H., Lu, J.K., Lin, C.M., Reimschuessel, R. & Dunham, R.A.1996. Transgenic fish and its application in basic and applied research. *Biotechnology Annual Review*, **2**: 205-236.

Chiou, P.P., Lin, C.M., Perez, L. & Chen ,T.T. 2002. Effect of cecropin B and a synthetic analogue on propagation of fish viruses in vitro. *Marine Biotechnology*, **4**: 294-302.

Chistiakov, D.A., Hellemans, B. & Volckaert, F.A.M. 2006. Microsatellites and their genomic distribution, evolution, function and applications**.** A review with special reference to fish genetics. *Aquaculture,* 255: 1-29.

Chistiakov, D.A., Hellemans, B., Haley, C.S., Law, A.S., Tsigenopoulos, C.S., Kotoulas, G., Bertotto, D., Libertini, A. & Volckaert, F.A. 2005. A microsatellite linkage map of the European sea bass *Dicentrarchus labrax* L. *Genetics,* **170** (4): 1821–1826.

Chong, L.K., Tan, S.G., Yusoff, K. & Siraj, S.S. 2000. Identification and characterization of Malaysian river catfish, *Mystus nemurus* (C&V): RAPD and AFLP analysis. *Biochemical Genetics,* **38**: 63-76.

Cnaani, A., Tinman, S., Avidar, Y., Ron, M. & Hulata, G. 2004a. Comparative study of biochemical parameters in response to stress in *Oreochromis aureus*, *O. mossambicus* and two strains of *O. niloticus*. *Aquaculture Research*, **35**: 1434-1440.

Cnaani, A., Zilberman, N., Tinman, S., Hulata, G. & Ron, M. 2004b. Genome-scan analysis for quantitative trait loci in an F_2 tilapia hybrid. *Molecular Genetics and Genomics,* **272**: 162-172.

Cnaani, A., Hallerman, E.M., Ron, M., Weller, J., Indelman, M., Kashi, Y., Gall, G. A. E. & Hulata, G. 2003. Detection of a chromosomal region with two quantitative trait loci, affecting cold tolerance and fish size, in an F_2 tilapia hybrid. *Aquaculture,* **223**(1-4): 117-128.

Cnaani, A., Zilberman, N., Tinman, S., Hulata, G. & Ron, M. 2004. Genome-scan analysis for quantitative trait loci in an F2 tilapia hybrid. *Molecular Genetics and Genomics,* **272**(2): 162-72.

Coimbra, M.R.M., Kobayashi, K., Koretsugu, S., Hasegawa, O., Ohara, E., Ozaki, A., Sakamoto, T., Naruse, K. & Okamoto, N. 2003. A genetic linkage map of the Japanese flounder, *Paralichthys olivaceus*. *Aquaculture,* **220**(1-4): 203-218.

Cossins, A.R. & Crawford, D.L. 2005. Fish as models for environmental genomics. *Nature Reviews in Genetics*, **6**: 324-33.

Cotton, R.G. 1993. Current methods of mutation detection. *Mutation Research,* **285:** 125-144.

Crespi, B.J. & Fulton, M.J. 2004. Molecular systematics of Salmonidae: combined nuclear data yields a robust phylogeny. *Molecular Phylogenetics and Evolution,* **31**: 658–679.

Crollius, H.R., Jaillon, O., Dasilva, C., Ozouf-Costaz, C., Fizames, C., Fischer, C., Bouneau, L., Billault, A., Quetier, F., Saurin, W., Bernot, A. & Weissenbach, J. 2000. Characterization and repeat analysis of the compact genome of the freshwater pufferfish *Tetraodon nigroviridis. Genome Research,* **10**(7): 939-49.

Crossland, S., Coates, D., Grahame, J. & Mill, P.J. 1993. Use of random amplified polymorphic DNAs (RAPDs) in separating two sibling species of *Littorina*. *Marine Ecology Progress Series*, **96**: 301-305.

Danzmann, R.G., Jackson, T.R. & Ferguson, M.M. 1999. Epistasis in allelic expression at upper temperature tolerance QTL in rainbow trout. *Aquaculture,* **173**: 45-58.

Danzmann, R.G. & Gharbi, K. 2007. Linkage mapping in aquaculture species. *In*: Aquaculture Genome Technologies, (Z. Liu ed.), Blackwell Publishing, Ames, IA., in press.

Danzmann, R.G., Cairney, M., Davidson, W.S., Ferguson, M.M., Gharbi, K., Guyomard, R., Holm, L.-E., Leder, E., Okamoto, N., Ozaki, A., Rexroad, III C.E., Sakamoto, T., Taggart, J.B. & Woram, R.A. 2005. A comparative analysis of the rainbow trout genome

with 2 other species of fish (Arctic charr and Atlantic salmon) within the tetraploid derivative Salmonidae family (subfamily: *Salmoninae*). *Genome*, **48**: 1037-1051.

Dekkers, J.C.M. 2004. Commercial application of marker- and gene-assisted selection in livestock: strategies and lessons. *Journal of Animal Science,* 82(E Suppl): E313–E328.

Dentine, M.R. 1999. Chapter 17: Marker-assisted selection. In: The genetics of cattle (ed. by R Fries, A Ruvinsky) pp.497–510. CAB International, Cambridge MA.

Devlin, R.H., D'Andrade, M., Uh, M. & Biagi, C.A. 2004. Population effects of growth hormone transgenic coho salmon depend on food availability and genotype by environment interactions. *Proceedings of the National Academy of Sciences United States of America,* 101: 9303-9308.

Devlin, R.H., Sundstrom, L.F. & Muir, W.M. 2006. Interface of biotechnology and ecology for environmental risk assessments of transgenic fish. *Trends in Biotechnology*, **24**(2): 89-97.

Diamond, I. & Woodgate, D. 2005. Genomics research in the UK--the social science agenda. *New Genetics and Society*, 24: 239-52.

Domergue, F., Abbadi, A.& Heinz, E. 2005. Relief for fish stocks: oceanic fatty acids in transgenic oilseeds. *Trends in Plant Science,* **10**(3): 112-116.

Du, S.J., Gong, Z.Y., Fletcher, G.L., Shears, M.A., King, M.J., Idler, D.R. & Hew, C.L. 1992. Growth enhancement in transgenic Atlantic salmon by the use of an "all fish" chimeric growth hormone gene construct. *Biotechnology*, 10: 176-81.

Duchesne, P. & Bernatchez, L. 2007. Individual-based genotype methods in aquaculture, In: Aquaculture Genome Technologies, (J. Liu ed.), Blackwell Publishing, Ames, IA, in press.

Dunham, R. & Liu, Z.J. 2006. Transgenic fish-where we are and where do we go? *Israel Journal of Aquaculture-Bamidgeh,* 58(4): 297-319.

Dunham, R.A. 2004. Aquaculture and fisheries biotechnology. Genetic approaches. CABI Publishing, Cambridge MA, pp. 1-367.

Dunham, R.A., Warr, G.W., Nichols, A., Duncan, P.L., Argue, B., Middleton, D.& Kucuktas, H. 2002. Enhanced bacterial disease resistance of transgenic channel catfish *Ictalurus punctatus* possessing cecropin genes. *Marine Biotechnology,* **4**: 338-344.

Evensen, O., Brudeseth, B. & Mutoloki, S. 2005. The vaccine formulation and its role in inflammatory processes in fish—effects and adverse effects. *Developmental Biology*, 121: 117-125.

Ewart, K.V., Belanger, J.C., Williams, J., Karakach, T., Penny, S., Tsoi, S.C., Richards, R.C. & Douglas, S.E. 2005. Identification of genes differentially expressed in Atlantic salmon (*Salmo salar*) in response to infection by *Aeromonas salmonicida* using cDNA microarray technology. *Developmental and Comparative Immunology*, **29**(4): 333-347.

Eyers, L., George, I., Schuler, L., Stenuit, B., Agathos, S. N. & El Fantroussi, S. 2004. Environmental genomics: exploring the unmined richness of microbes to degrade xenobiotics. *Appllied Microbiology and Biotechnology,* **66**: 123-130.

FAO. 2000. Genetically modified organisms and fisheries. *State of World Fisheries and Aquaculture.* FAO, Rome. http://www.fao.org/DOCREP/003/X8002E/x8002e05.htm#P30

FAO. 2006. *State of World Aquaculture.* FAO Fishery Technical Paper No 886. FAO, Rome.

Felip, A., Young W.P., Wheeler, P.A. & Thorgaard, G.H. 2005. An AFLP-based approach for the identification of sex-linked markers in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture,* **247**(1-4): 35-43

Frazier, M.E., Johnson, G.M., Thomassen, D.G., Oliver, C.E. & Patrinos, A.2003. Realizing the potential of the genome revolution: the genomes to life program. *Science,* 300: 290-293.

Fu, C., Hu, W., Wang, Y. & Zhu, Z. 2005. Developments in transgenic fish in the People's Republic of China. *Reviews in Science and Technology*, **24**(1): 299-307.

Galperin, M.Y. 2004. Metagenomics: from acid mine to shining sea. *Environmental Microbiology,* **6**: 543-545.

Garber, A.F. & Sullivan, C.V. 2006. Selective breeding for the hybrid striped bass (*Morone chrysops, Rafinesque M. saxatilis, Walbaum*) industry: status and perspectives. *Aquaculture Research,* **37**: 319-338.

Ge, H., Walhout, A.J. & Vidal, M. 2003. Integrating 'omic' information: a bridge between genomics and systems biology. *Trends in Genetics,* **19**: 551-560.

Gharbi, K., Gautier, A., Danzmann, R.G., Gharbi, S., Sakamoto, T., Hoyheim, B., Taggart, J.B., Cairney, M., Powell, R., Krieg, F., Okamoto, N., Ferguson, M.M., Holm, L.E. & Guyomard, R. 2006. A linkage map for brown trout (*Salmo trutta*): chromosome homeologies and comparative genome organization with other salmonid fish. *Genetics*, **172**(4): 2405-2419.

Gilbey, J., Verspoor, E., McLay, A. & Houlihan, D. 2004. A microsatellite linkage map for Atlantic salmon (*Salmo salar*). *Animal Genetics*, **35**(2): 98-105.

Golovan, S.P., Hayes. M.A., Phillips, J.P. & Forsberg, C.W. 2001b. Transgenic mice expressing bacterial phytase as a model for phosphorus pollution control. *Nature Biotechnology*, **19**(5): 429-433.

Golovan, S.P., Meidinger, R.G., Ajakaiye, A., Cottrill, M., Wiederkehr, M.Z., Barney, D.J., Plante, C., Pollard, J.W., Fan, M.Z., Hayes, M.A., Laursen, J., Hjorth, J.P., Hacker, R.R., Phillips, J.P. & Forsberg, C.W. 2001a. Pigs expressing salivary phytase produce low-phosphorus manure. *Nature Biotechnology*, **19**(8): 741-745.

Gong, Z. & Hew, C.L. 1995. Transgenic fish in aquaculture and developmental biology. *Current Topics in Developmental Biology,* **30**: 177-214.

Gong, Z., Ju, B., Wang, X., He, J., Wan, H., Sudha, P.M. & Yan, T. 2002. Green fluorescent protein expression in germ-line transmitted transgenic zebrafish under a stratified epithelial promoter from keratin 8. *Developmental Dynamics*, 223: 204-215.

Gong, Z., Wan, H., Tay, T.L., Wang, H., Chen, M. & Yan, T. 2003. Development of transgenic fish for ornamental and bioreactor by strong expression of fluorescent proteins in the skeletal muscle. *Biochemical Biophysical Research Communications*, **308**: 58-63.

Gracey, A.Y. & Cossins, A.R. 2003. Application of microarray technology in environmental and comparative physiology. *Annual Review Physiology*, **65**: 231-59.

Graslund, S. & Bengtsson, B.E. 2001. Chemicals and biological products used in south-east Asian shrimp farming, and their potential impact on the environment--a review. *Science of the Total Environment*, **280**: 93-131.

Grimholt, U., Larsen, S., Nordmo, R., Midtlyng, P., Kjoeglum, S., Storset, A., Saebo, S., & Stet, R.J. 2003. MHC polymorphism and disease resistance in Atlantic salmon (*Salmo salar*): facing pathogens with single expressed major histocompatibility class I and class II loci. *Immunogenetics*, **55**: 210-219.

Hacia, J.G., Fan, J.B., Ryder, O., Jin, L., Edgemon, K., Ghandour, G., Mayer, R.A., Sun, B., Hsie, L., Robbins, C.M., Brody, L.C., Wang, D., Lander, E.S., Lipshutz, R., Fodor, S.P. & Collins, F.S. 1999. Determination of ancestral alleles for human single-nucleotide polymorphisms using high-density oligonucleotide arrays. *Nature Genetics,* **22:** 164-167.

Hallerman, E.M., Dunham, R. & Smitherman, R.O. 1986. Selection or drift-isozyme allele frequency changes among channel catfish selected for rapid growth. *Transactions of the American Fisheries Society*, **115**: 60–68.

He, C., Chen, L., Simmons, M., Li, P., Kim, S. & Liu, Z.J. 2003. Putative SNP discovery in interspecific hybrids of catfish by comparative EST analysis. *Animal Genetics,* **34**: 445-448.

Hecker, K.H., Taylor, P.D. & Gjerde, D.T. 1999. Mutation detection by denaturing DNA chromatography using fluorescently labeled polymerase chain reaction products. *Analytical Biochemistry,* **272:** 156-164.

Hew, C.L., Davies, P.L. & Fletcher, G. 1992. Antifreeze protein gene transfer in Atlantic salmon. *Molecular Marine Biology and Biotechnology*, **1**(4-5): 309-317.

Hirschfeld, D., Dhar, A.K., Rask, K. & Alcivar-Warren, A. 1999. Genetic diversity in the eastern oyster (*Crassostrea virginica*) from Massachusetts using RAPD technique. *Journal of Shellfish Research*, **18**: 121-125.

Houdebine, L.M. & Chourrout, D. 1991. Transgenesis in fish. *Experientia,* **47**(9): 891-897.

Hubert, S., and Hedgecock, D. 2004. Linkage maps of microsatellite DNA markers for the Pacific oyster *Crassostrea gigas*, *Genetics,* **168**(1): 351–362.

Iyengar, A., Muller, F. & Maclean, N. 1996. Regulation and expression of transgenes in fish -- a review. *Transgenic Research,* **5**(3): 147-166.

Jorde, P.E., Palm, S. & Ryman, N. 1999. Estimating genetic drift and effective population size from temporal shifts in dominant gene marker frequencies. Molecular Ecology, 8: 1171-1178.

Ju, Z., Dunham, R.A. & Liu, Z. 2002. Differential gene expression in the brain of channel catfish (*Ictalurus punctatus*) in response to cold acclimation. *Molecular Genetics and Genomics,* **268**: 87-95.

Kai, Y., Nakayama, K. & Nakabo, T. 2002. Genetic differences among three colour morphotypes of the black rockfish, *Sebastes inermis*, inferred from mtDNA and AFLP analyses. *Molecular Ecology,* **11**: 2591-2598.

Kalin, I., Shephard, S. & Candrian, U. 1992. Evaluation of the ligase chain reaction (LCR) for the detection of point mutations. *Mutatation Research,* **283**: 119-123.

Kapuscinski, A.R. 2005. Current scientific understanding of the environmental biosafety of transgenic fish and shellfish. *Reviews in Science Technology,* **24**: 309-22.

Katagiri, T., Kidd, C., Tomasino, E., Davis, J.T., Wishon, C., Stern, J.E., Carleton, K.L., Howe, A.E. & Kocher, T.D. 2005. A BAC-based physical map of the Nile tilapia genome. *BMC Genomics*, **6**(1): 89.

Kazianis, S., Morizot, D.C., McEntire, B.B., Nairn, R.S. & Borowsky, R.L. 1996. Genetic mapping in *Xiphophorus* hybrid fish: assignment of 43 AP-PCR/RAPD and isozyme markers to multipoint linkage groups. *Genome Research*, **6**(4): 280-289.

Kerr, C.R. & Cunningham, C.O. 2006. Moving molecular diagnostics from laboratory to clinical application: a case study using infectious pancreatic necrosis virus serotype A. *Letters in Applied Microbiology* **43**: 98-104.

Khoo, G., Lim, M.H., Suresh, H., Gan, D.K., Lim, K.F., Chen, F., Chan, W.K., Lim, T.M. & Phang, V.P. 2003. Genetic linkage maps of the guppy (*Poecilia reticulata*): assignment of RAPD markers to multipoint linkage groups. *Marine Biotechnology*, **5**(3): 279-293.

Kitano, H. 2002. Systems biology: a brief overview. *Science,* **295**: 1662-4.

Klinbunga, S., Ampayup, P., Tassanakajon, A., Jarayabhand, P. & Yoosukh, W. 2000. Development of species-specific markers of the tropical oyster (*Crassostrea belcheri*) in Thailand. *Marine Biotechnology,* **2**: 476-484.

Knapik, E.W., Goodman, A., Ekker, M., Chevrette, M., Delgado, J., Neuhauss, S., Shimoda, N., Driever, W, Fishman, M.C. & Jacob, H.J. 1998. A microsatellite genetic linkage map for zebrafish (*Danio rerio*), *Nature Genetics,* **18(4)**: 338–343.

Kocabas, A., Dunham, R. & Liu, Z.J. 2004. Alterations in gene expression in the brain of white catfish (*Ameirus catus*) in response to cold acclimation. *Marine Biotechnology,* **6**: S431-S438.

Kocher, T.D., Lee, W.J., Sobolewska, H., Penman, D. & McAndrew, B. 1998. A genetic linkage map of a cichlid fish, the tilapia (*Oreochromis niloticus*), *Genetics,* **148**(3): 1225–1232.

Kurath, G. 2005. Overview of recent DNA vaccine development for fish. *Developmental Biology*, **121**: 201-213.

Lee, B.-Y., Hulata, G. & Kocher, T.D. 2004. Two unlinked loci control the sex of blue tilapia (*Oreochromis aureus*). *Heredity,* **92**:543-549

Lee B.-Y., Penman, D.J. & Kocher, T.D. 2003. Identification of the sex-determining region in tilapia (*Oreochromis niloticus*) using bulked segregant analysis. *Animal Genetics,* **34**: 379-383.

Lee, B., Lee, W.J., Streelman, J.T., Carleton, K.L., Howe, A.E., Hulata, G., Steffan, A., Stern, J.E., Terai, Y. & Kocher, T.D. 2005. A second generation linkage map of tilapia (*Oreochromis spp.*), *Genetics,* **170**(1): 237–244.

Li, B., Kadura, I., Fu, D.J. & Watson, D.E. 2004. Genotyping with TaqMAMA. *Genomics,* **83**: 311-320.

Li, L. & Guo, X. 2004. AFLP-based genetic linkage maps of the pacific oyster *Crassostrea gigas* Thunberg. *Marine Biotechnology*, **6**(1): 26-36.

Li, L., Xiang, J., Liu, X., Zhang, Y., Dong, B. & Zhang, X. 2005. Construction of AFLP-based genetic linkage map for Zhikong scallop, *Chlamys farreri* Jones et Preston and mapping of sex-linked markers. *Aquaculture,* **245**(1-4): 63-73.

Li, Y., Byrne, K., Miggiano, E., Whan, V., Moore, S., Keys, S., Crocos, P., Preston, N. & Lehnert, S. 2003. Genetic mapping of the kuruma prawn *Penaeus japonicus* using AFLP markers. *Aquaculture,* **219**(1-4): 143-156.

Li, Y., Dierens, L., Byrne, K., Miggiano, E., Lehnert, S., Preston, N. & Lyons, R. 2006. QTL detection of production traits for the Kuruma prawn *Penaeus japonicus* (Bate) using AFLP markers. *Aquaculture,* **258**: 198-210.

Li, Z., Li, J., Wang, Q., He, Y. & Liu, P. 2006. AFLP-based genetic linkage map of marine shrimp *Penaeus (Fenneropenaeus) chinensis*. *Aquaculture,* **261**: 463-472

Liu, X, Guo, X., Gao, Q., Zhao, H. & Zhang, G. 2006. A preliminary genetic linkage map of the Pacific abalone *Haliotis discus hannae* Ino. *Marine Biotechnology,* **8**: 386-397.

Liu, Z., Karsi, A., Li, P., Cao, D. & Dunham, R. 2003. An AFLP-based genetic linkage map of channel catfish (*Ictalurus punctatus*) constructed by using an interspecific hybrid resource family. *Genetics*, **165**(2): 687-694.

Liu, Z., Li, P., Kucuktas, H., Nichols, A., Tan, G., Zheng, X., Argue, B.J. & Dunham, R.A. 1999. Development of Amplified Fragment Length Polymorphism (AFLP) Markers Suitable for Genetic Linkage Mapping of Catfish. *Transactions of the American Fisheries Society,* **128**: 317-327.

Liu, Z., Nichols, A., Li, P. & Dunham, R.A. 1998. Inheritance and usefulness of AFLP markers in channel catfish (*Ictalurus punctatus*) blue catfish (*I. furcatus*) and their F1 F2 and backcross hybrids. *Molecular Genetics and Genetics*, **258**: 260-268.

Liu, Z.J. & Cordes, J. 2004. DNA marker technologies and their applications in aquaculture genetics. *Aquaculture*, **238**: 1-37.

Lorenzen, N., Lorenzen, E., Einer-Jensen, K. & LaPatra, S.E. 2002. DNA vaccines as a tool for analysing the protective immune response against rhabdoviruses in rainbow trout. *Fish and Shellfish Immunology*, **12**: 439-53.

MacGregor, J.T. 2003. The future of regulatory toxicology: impact of the biotechnology revolution. *Toxicological Sciences*, **75**: 236-248.

Maclean, N. & Laight, R.J. 2000. Transgenic fish: an evaluation of benefits and risks. *Fish and Fisheries,* **1**(2): 146-172.

Maldini, M., Marzano, F.N., Fortes, G.G., Papa, R. & Gandolfi, G. 2006. Fish and seafood traceability based on AFLP markers: Elaboration of a species database. *Aquaculture,* **261**: 487-494.

Malmgren, H., Gustavsson, J., Tuvemo, T. & Dahl, N. 1996. Rapid detection of a mutation hot-spot in the human androgen receptor. *Clinical Genetics,* **50**: 202-205.

Martyniuk, C.J., Perry, G.M.L., Mogahadam, H.K., Ferguson, M.M.& Danzmann, R.G. 2003. The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout. *Journal of Fish Biology* **63**: 746-764.

May, B. 2003. Allozyme variation. Pp.23-36 in Hallerman EM (ed), Population genetics: principles and applications for fisheries scientists. *American Fisheries Society, Bethesda, Maryland.*

McConnell, S.K., Beynon, C., Leamon, J. & Skibinski, D.O. 2000. Microsatellite marker based genetic linkage maps of *Oreochromis aureus* and *O. niloticus* (Cichlidae): extensive linkage group segment homologies revealed. *Animal Genetics*, **31**(3): 214-218.

Merker, R.J. & Woodruff, R.C. 1996. Molecular evidence for divergent breeding groups of walleye (*Stizostedion vitreum*) in tributaries to western Lake Erie. *Journal Great Lakes Research,* **22**: 280-288.

Mickett, K., Morton, C., Feng, J., Li, P., Simmons, M., Cao, D., Dunham, R. & Liu, Z.J. 2003. Assessing genetic diversity of domestic populations of channel catfish (*Ictalurus punctatus*) in Alabama using AFLP markers. *Aquaculture,* **228**: 91-105.

Mock, K.E., Brim-Box, J.C., Miller, M.P., Downing, M.E. & Hoeh, W.R. 2004. Genetic diversity and divergence among freshwater mussel (*Anodonta*) populations in the Bonneville Basin of Utah. *Molecular Ecology,* **13**: 1085-1098.

Moen, T., Agresti, J.J., Cnaani, A., Moses, H., Famula, T.R., Hulata, G., Gall, G.A.E. & May, B. 2004a. A genome scan of a four-way tilapia cross supports the existence of a quantitative trait locus for cold tolerance on linkage group 23. *Aquaculture Research,* **35**: 893-904.

Moen, T., Fjalestad, K.T., Munck, H. & Gomez-Raya, L. 2004b. A multistage testing strategy for detection of quantitative trait Loci affecting disease resistance in Atlantic salmon. *Genetics,* **167**(2): 851-858.

Moen, T., Hoyheim, B., Munck, H. & Gomez-Raya, L. 2004. A linkage map of Atlantic salmon (*Salmo salar*) reveals an uncommonly large difference in recombination rate between the sexes. *Animal Genetics*, **35**(2): 81-92.

Mohideen, M.A., Moore, J.L. & Cheng, K.C. 2000 Centromere-linked microsatellite markers for linkage groups 3, 4, 6, 7, 13, and 20 of zebrafish (*Danio rerio*). *Genomics*, **67**(1): 102-106.

Nakamura, K., Ozaki, A., Akutsu, T., Iwai, K., Sakamoto, T., Toshizaki, G. & Okamoto, N. 2001. Genetic mapping of the dominant albino locus in rainbow trout (*Oncorhynchus mykiss*). *Molecular Genetics and Genomics*, **265**: 687-693.

Napier, J.A., Sayanova, O., Qi, B. & Lazarus, C.M. 2004. Progress toward the production of long-chain polyunsaturated fatty acids in transgenic plants. *Lipids*, **39**(11): 1067-1075.

Naruse, K., Tanaka, M., Mita, K., Shima, A., Postlethwait, J. & Mitani, H. 2004. A medaka gene map: the trace of ancestral vertebrate proto-chromosomes revealed by comparative gene mapping. *Genome Research*, **14**(5): 820-828.

Ng, S.H., Artieri, C.G., Bosdet, I.E., Chiu, R., Danzmann, R.G., Davidson, W.S., Ferguson, M.M., Fjell, C.D., Hoyheim, B., Jones, S.J., de Jong, P.J., Koop, B.F., Krzywinski, M.I., Lubieniecki,K., Marra, M.A., Mitchell, L.A., Mathewson, C., Osoegawa, K., Parisotto, S.E., Phillips, R.B.,Rise, M.L., von Schalburg, K.R., Schein, J.E., Shin, H., Siddiqui, A., Thorsen, J., Wye, N., Yang,G. & Zhu, B. 2005. A physical map of the genome of Atlantic salmon, Salmo salar. *Genomics*, **86**(4): 396-404.

Nichols, K.M., Bartholomew, J. & Thorgaard, G.H. 2003a. Mapping multiple genetic loci associated with Ceratomyxa shasta resistance in Oncorhynchus mykiss. *Diseases of Aquatic Organisms,* **56**: 145-154.

Nichols, K.M., Young, W.P., Danzmann, R.G., Robison, B.D., Rexroad, C., Noakes, M., Phillips, R.B., Bentzen, P., Spies, I., Knudsen, K., Allendorf, F.W., Cunningham, B.M., Brunelli, J., Zhang, H., Ristow, S., Drew, R., Brown, K.H., Wheeler, P.A. & Thorgaard, G.H. 2003b. A consolidated linkage map for rainbow trout (*Oncorhynchus mykiss*), *Animal Genetics,* **34**(2): 102–115.

Nichols. K.M., Wheeler, P.A. & Thorgaard, G.H. 2004. Quantitative trait loci analyses for meristic traits in Oncorhynchus mykiss. *Environmental Biology of Fishes*, **69**: 317-331.

Nielsen, E.E., Hansen, M.M. & Mensberg, K-L.D. 1998. Improved primer sequences for the mitochondrial ND1, ND3/4 and ND5/6 segments in salmonid fishes. Application to RFLP analysis of Atlantic salmon. *Journal of Fish Biology*, **53**: 216–220.

Nurmi, J., Kiviniemi, M., Kujanpaa, M., Sjoroos, M., Ilonen, J. & Lovgren, T. 2001. High-throughput genetic analysis using time-resolved fluorometry and closed-tube detection. *Analytical Biochemistry*, **299**(2): 211-217.

Ohara, E., Nishimura, T., Nagakura, Y., Sakamoto, T., Mushiake, K. & Okamoto, N. 2005. Genetic linkage maps of two yellowtails (*Seriola quinqueradiata* and *Seriola lalandi*). *Aquaculture,* **244**(1-4): 41-48.

Ohtsuka, M., Makino, S., Yoda, K., Wada, H., Naruse, K., Mitani, H., Shima, A., Ozato, K., Kimura, M. & Inoko, H. 1999. Construction of a linkage map of the medaka (*Oryzias latipes*) and mapping of the Da mutant locus defective in dorsoventral patterning. *Genome Research*, **9**(12): 1277-1287.

Okumuş, I. & Çiftci, Y. 2003. Fish Population Genetics and Molecular Markers: II-Molecular Markers and Their Applications in Fisheries and Aquaculture. *Turkish Journal of Fisheries and Aquatic Sciences*, **3**: 51-79.

O'Malley, K.G., Sakamoto, T., Danzmann, R.G. & Ferguson, M.M. 2003. Quantitative trait loci for spawning date and body weight in rainbow trout: testing for conserved effects across ancestrally duplicated chromosomes. *Journal of Heredity,* **94**(4): 273-284.

Ozaki, A., Sakamoto, T., Khoo, S., Nakamura, K., Coimbra, M.R.M., Akutsu, T. & Okamoto, N. 2001. Quantitative trait loci (QTLs) associated with resistance/susceptibility to infectious pancreatic necrosis virus (IPNV) in rainbow trout (*Oncorhynchus mykiss*). *Molecular Genetics and Genomics,* **265**: 23-31.

Palti, Y., Parsons, J.E. & Thorgaard, G.H. 1999. Identification of candidate DNA markers associated with IHN virus resistance in backcrosses of rainbow (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*). *Aquaculture,* **173**: 81-94.

Palti, Y., Shirak, A., Cnaani, A., Hulata, G., Avtalion, R.R. & Ron, M. 2002. Detection of genes with deleterious alleles in an inbred line of tilapia (*Oreochromis aureus*). *Aquaculture,* **206**: 151-164.

Palti, Y., Nichols, K.M., Waller, K.I., Parsons, J.E. & Thorgaard, G.H. 2001. Association between DNA polymorphisms tightly linked to MHC class II genes and IHN virus resistance in backcrosses of rainbow trout and cutthroat trout. *Aquaculture,* **194**: 283-289.

Parker, P.G., Snow, A.A., Schug, M.D., Booton, G.C. & Fuerst, P.A. 1988. What molecules can tell us about populations: choosing and using a molecular marker. *Ecology,* **79**: 361-382.

Partis, L. & Wells, R.J. 1996. Identification of fish species using random amplified polymorphic DNA (RAPD). *Molecular and Cellular Probes,* **10**: 435-441.

Pérez, F., Erazo, C., Zhinaula, M., Volckaert, F. & Calderón, J. 2004. A sex-specific linkage map of the white shrimp *Penaeus (Litopenaeus) vannamei* based on AFLP markers. *Aquaculture,* **242**(1-4): 105-118.

Perry, G.M., Danzmann, R.G., Ferguson, M.M. & Gibson, J.P. 2001. Quantitative trait loci for upper thermal tolerance in outbred strains of rainbow trout (*Oncorhynchus mykiss*). *Heredity*, **86**(Pt 3): 333-341.

Perry, G.M., Ferguson, M.M., Sakamoto, T. & Danzmann, R.G. 2005. Sex-linked quantitative trait loci for thermotolerance and length in the rainbow trout. *Journal of Heredity*, **96**(2): 97-107.

Poompuang, S. & Na-Nakorn, U. 2004. A preliminary genetic map of walking catfish (*Clarias macrocephalus*). *Aquaculture,* **232**(1-4): 195-203.

Postlethwait, J.H., Johnson, S.L., Midson, C.N., Talbot, W.S., Gates, M., Ballinger, E.W., Africa, D., Andrews, R., Carl, T., Eisen, J.S., *et al.*, 1994. A genetic linkage map for the zebrafish. *Science,* **264** (5159): 699-703.

Pruett, C.L., Saillant, E. & Gold, J.R. 2005. Historical population demography of red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico based on analysis of sequences of mitochondrial DNA. *Marine Biology*, **147**: 593–602.

Purcell, M.K., Nichols, K.M., Winton, J.R., Kurath, G., Thorgaard, G.H., Wheeler, P., Hansen, J.D., Herwig, R.P. & Park, L.K. 2006. Comprehensive gene expression

profiling following DNA vaccination of rainbow trout against infectious hematopoietic necrosis virus. *Molecular Immunology,* **43**(13): 2089-2106.

Reid, D.P., Szanto, A., Glebe, B., Danzmann, R.G. & Ferguson, M.M. 2005. A QTL for body weight and condition factor in Atlantic salmon (*Salmo salar*): comparative analysis with rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*). *Heredity,* **94**(2): 166-172.

Riesenfeld, C. S., Schloss, P.D. & Handelsman, J. 2004. Metagenomics: genomic analysis of microbial communities. *Annual Reviews in Genetics,* **38**: 525-52.

Rise, M.L., Jones, S.R., Brown, G.D., von Schalburg, K.R., Davidson, W.S. & Koop, B.F. 2004b. Microarray analyses identify molecular biomarkers of Atlantic salmon macrophage and hematopoietic kidney response to Piscirickettsia salmonis infection. *Physiological Genomics,* **20**(1): 21-35.

Rise, M.L., von Schalburg, K.R., Brown, G.D., Mawer, M.A., Devlin, R.H., Kuipers, N., Busby, M., Beetz-Sargent, M., Alberto, R., Gibbs, A.R., Hunt, P., Shukin, R., Zeznik, J.A., Nelson, C., Jones, S.R., Smailus, D.E., Jones, S.J., Schein, J.E., Marra, M.A., Butterfield, Y.S., Stott, J.M., Ng, S.H., Davidson, W.S. & Koop, B.F. 2004a. Development and application of a salmonid EST database and cDNA microarray:data mining and interspecific hybridization characteristics. *Genome Research,***14**(3): 478-90.

Roberts, S.B., McCauley, L.A., Devlin, R.H. & Goetz, F.W. 2004. Transgenic salmon overexpressing growth hormone exhibit decreased myostatin transcript and protein expression. *Journal of Experimental Biology*, **207**: 3741-8.

Robison, B.D., Wheeler. P.A., Sundin, K., Sikka, P. & Thorgaard, G.H. 2001. Composite interval mapping reveals a major locus influencing embryonic development rate in rainbow trout (Oncorhynchus mykiss). *Journal of Heredity*, **92**(1): 16-22.

Rodriguez, M.F., LaPatra, S., Williams, S., Famula, T. & May, B. (2005) Genetic markers associated with resistance to infectious hematopoietic necrosis in rainbow and steelhead trout (*Oncorhynchus mykiss*) backcrosses. *Aquaculture,* **241**: 93-115.

Rodriguez-Valera, F. 2004. Environmental genomics, the big picture? *FEMS Microbiology Letters,* **231**: 153-158.

Rogers, S.M., Campbell, D., Baird, S.J., Danzmann, R.G., Bernatchez, L., Nichols, K.M., Young, W.P., Danzmann, R.G., Robison, B.D., Rexroad, C., Noakes, M., Phillips, R.B., Bentzen, P., Spies, I., Knudsen, K., Allendorf, F.W., Cunningham, B.M., Brunelli, J., Zhang, H., Ristow, S., Drew, R., Brown, K.H., Wheeler, P.A. & Thorgaard, G.H. 2003. A consolidated linkage map for rainbow trout (*Oncorhynchus mykiss*). *Animal Genetics*, **34**(2): 102-115.

Ross, P., Hall, L., Smirnov, I. & Haff, L. 1998. High level multiplex genotyping by MALDI-TOF mass spectrometry. *Nature Biotechnology,* **16:** 1347-1351.

Sakamoto, T., Danzmann, R.G., Okamoto, N., Ferguson, M.M. & Ihssen, P.E. 1999. Linkage analysis of quantitative trait loci associated with spawning time in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture,* **173**: 33-43.

Sakamoto, T., Danzmann, R.G., Gharbi, K., Howard, P., Ozaki, A., Khoo, S.K., Woram, R.A., Okamoto, N., Ferguson, M.M., Holm, L.E., Guyomard, R. & Hoyheim, B. 2000. A microsatellite linkage map of rainbow trout (*Oncorhynchus mykiss*) characterized by large sex-specific differences in recombination rates. *Genetics,* **155**(3): 1331-1345.

Sarmasik, A., Warr, G. & Chen, T.T. 2002. Production of transgenic medaka with increased resistance to bacterial pathogens. *Marine Biotechnology*, **4**: 310-322.

Sarropoulou, E., Kotoulas, G., Power, D.M. & Geisler, R. 2005. Gene expression profiling of gilthead sea bream during early development and detection of stress-related genes by the application of cDNA microarray technology. *Physiological Genomics,* **23**(2): 182-191.

Schloss, P.D. & Handelsman, J. 2003. Biotechnological prospects from metagenomics. *Current Opinions in Biotechnology,* **14**: 303-310.

Seki, S., Agresti, J.J., Gall, G.A.E., Taniguchi, N. & May, B. 1999. AFLP analysis of genetic diversity in three populations of ayu *Plecoglossus altivelis. Fish. Sci.,* **65**:888-892.

Sekino, M. & Hara, M. 2007. Linkage maps for the pacific abalone (genus *Haliotis*) based on microsatellite DNA markers. *Genetics*, in press.

Senanan, W., Kapuscinski, A.R., Na-Nakorn U. & Miller, L.M. 2004. Genetic impacts of hybrid catfish farming (*Clarias macrocephalus*×*C. gariepinus*) on native catfish populations in central Thailand. *Aquaculture,* **235**: 167-184.

Senger, F., Priat, C. , Hitte, C., Sarropoulou, E. & Franch R. 2006. The first radiation hybrid map of a perch-like fish: The gilthead seabream (*Sparus aurata* L). *Genomics,* **87**: 793-800.

Shimoda, N., Knapik, E.W., Ziniti, J., Sim, C., Yamada, E., Kaplan, S., Jackson, D., de Sauvage, F., Jacob, H. & Fishman, M.C. 1999. Zebrafish genetic map with 2000 microsatellite markers, *Genomics,* **58**(3): 219–232.

Shirak, A., Bendersky, A., Hulata, G., Ron, M. & Avtalion, R.R. 2006. Altered self-erythrocyte recognition and destruction in an inbred line of tilapia *(Oreochromis aureus*). *Journal of Immunology,* **176**: 390-394.

Shirak, A., Palti, Y., Cnaani, A., Korol, A.B., Hulata, G., Ron, M. & Avtalion, R.R. 2002. Association between loci with deleterious alleles and distorted sex ratios in an inbred line of tilapia (Oreochromus aureus). *Journal of Heredity,* **93**: 270-276.

Shirak, A., Shmarina, A., Kuperman, Y.& Avtalion, R.R. 2000. Inheritance of body and peritoneum color in hybrids of *Oreochromis aureus* and red *O. niloticus*. *Israel Journal of Aquaculture – Bamidgeh,* **52**: 21-29.

Simmons, M., Mickett, K., Kucuktas, H., Li, P., Dunham, R. & Liu, Z.J. 2006. Comparison of domestic and wild catfish populations provide no evidence for genetic impact. *Aquaculture,* **252**: 133-146.

Somorjai, I.M., Danzmann, R.G. & Ferguson, M.M. 2003. Distribution of temperature tolerance quantitative trait loci in Arctic charr (*Salvelinus alpinus*) and inferred homologies in rainbow trout (*Oncorhynchus mykiss*). *Genetics,* **165**(3): 1443-1456.

Sorrentino, R., Potolicchio, I., Ferrara, G.B. & Tosi, R. 1992. A new approach to HLA-DPB1 typing combining DNA heteroduplex analysis with allele-specific amplification and enzyme restriction. *Immunogenetics,* **36:** 248-254.

Storm, N., Darnhofer-Patel, B., van den Boom, D. & Rodi, C.P. 2003. MALDI-TOF mass spectrometry-based SNP genotyping. *Methods in Molecular Biology,* **212**: 241-262.

Streelman, J.T. & Kocher, T.D. 2002. Microsatellite variation associated with prolactin expression and growth of salt-challenged tilapia. *Physiological Genomics*, **9**: 1-4.

Sun, X. & Liang, L. 2004. A genetic linkage map of common carp (*Cyprinus carpio* L.) And mapping of a locus associated with cold tolerance. *Aquaculture,* **238**(1-4): 165-172.

Sun, Y., Song, W., Zhong, Y., Zhang, R., Abatzopoulos, T.J. & Chen, R. 1999. Diversity and genetic differentiation in *Artemia* species and populations detected by AFLP markers. *International Journal of Salt Lake Research*, **8**: 341-350.

Suzuki, Y., Orita, M., Shiraishi, M., Hayashi, K. & Sekiya, T. 1990. Detection of *ras* gene mutations in human lung cancers by single-strand conformation polymorphism analysis of polymerase chain reaction products. *Oncogene,* **5:** 1037-1043.

Tao, W.J. & Boulding, E.G. 2003. Associations between single nucleotide polymorphisms in candidate genes and growth rate in Arctic charr (*Salvelinus alpinus L.*). *Heredity*, **91**: 60-69.

Tassanakajon, A., Pongsomboon, S., Jarayabhand, P., Klinbunga, S. & Boonsaeng, V.V. 1998. Genetic structure in wild populations of black tiger shrimp (*Penaeus monodon*) using randomly amplified polymorphic DNA analysis. *Journal of Marine Biotechnology,* **6**: 249-254.

Tautz, D. 1989. Hypervariability of simple sequences as a general source for polymorphic DNA markers. *Nucleic Acids Research*, **17**: 6563-6571.

Tautz, D. & Renz, M. 1984. Simple sequences are ubiquitous repetitive components of eukaryote genomes, *Nucleic Acids Research,* **17:** 4127–4138.

Travis, C.C., Bishop, W.E. & Clarke, D.P. 2003. The genomic revolution: what does it mean for human and ecological risk assessment? *Ecotoxicology*, **12**: 489-95.

Utter, F., Aebersold, P. & Winans, G. 1987. Interpreting genetic variation detected by electrophoresis. In Ryman N, Utter F (ed) Population Genetics and Fishery Management. Washington Sea Grant Program, University of Washington Press, Seattle, United States of America.

Van Oppen, M.J.H., Klerk, H., Olsen, J.L. & Stam, W.T. 1996. Hidden diversity in marine algae: some examples of genetic variation below the species level. *Journal of Marine Biology Association UK,* **76**: 239-242.

Von Schalburg, K.R., Rise, M.L., Cooper, G.A., Brown, G.D., Gibbs, A.R., Nelson, C.C., Davidson, W.S. & Koop, B.F. 2005. Fish and chips: various methodologies demonstrate utility of a 16,006-gene salmonid microarray. *BMC Genomics,* **6**: 126.

Waldbieser, G.C., Bilodeau, A.L. & Nonneman, D.J. 2003. Complete sequence and characterization of the channel catfish mitochondrial genome. *DNA Sequence,* **14**: 265:277.

Waldbieser, G.C., Bosworth, B.G., Nonneman, D.J. & Wolters, W.R. 2001. A microsatellite-based genetic linkage map for channel catfish, *Ictalurus punctatus*. *Genetics,* **158**(2): 727–734.

Walter, R.B., Rains, J.D., Russell, J.E., Guerra, T.M., Daniels, C., Johnston, D.A., Kumar J., Wheeler, A., Kelnar, K., Khanolkar, V.A., Williams, E.L., Hornecker, J.L., Hollek, L., Mamerow, M.M., Pedroza, A. & Kazianis, S. 2004. A microsatellite genetic linkage map for *Xiphophorus*. *Genetics,* **168**(1): 363–372.

Wang, B., Li, F., Dong, B., Zhang, X., Zhang, C. & Xiang, J. 2006. Discovery of the genes in response to white spot syndrome virus (WSSV) infection in fenneropenaeus chinensis through cdna microarray. *Marine Biotechnology,* 8(5): 491-500.

Watanabe, T., Fujita, H., Yamasaki, K., Seki, S. & Taniguchi, N. 2004. Preliminary study on linkage mapping based on microsatellite DNA and AFLP markers using homozygous clonal fish in ayu (*Plecoglossus altivelis*). *Marine Biotechnology,* **6**(4): 327-334.

Welsh, J. & McClelland, M. 1990. Fingerprinting genomes using PCR with arbitrary primers. *Nucleic Acids Research,* **18**: 7213-7218.

Whitehead, A., Anderson, S.L., Kuivila, K.M., Roach, J.L. & May, B. 2003. Genetic variation among interconnected populations of *Catostomus occidentalis*: implications for distinguishing impacts of contaminants from biogeographical structuring. *Molecular Ecology,* **12**: 2817-2833.

Williams, J.G.K., Kubelik, A.R., Livak, K.J., Rafalski, J.A. & Tingey, S.V. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. *Nucleic Acids Research,* **18**: 6531-6535.

Wilson, K., Li, Y., Whan, V., Lehnert, S., Byrne, K., Moore, S., Pongsomboon, S., Tassanakajon, A., Rosenberg, G., and Ballment, E., *et al.* 2002. Genetic mapping of the black tiger shrimp *Penaeus monodon* with amplified fragment length polymorphism. *Aquaculture,* **204**(3-4): 297-309.

Wirgin, I., Grunwald, C., Garte, S.J. & Mesing, C. 1991. Use of DNA fingerprinting in the identification and management of a striped bass population in the southeastern United States. *Transactions of the American Fisheries Society*, **120**: 273-282.

Wolfus, G.M., Garcia, D.K. & Alcivar-Warren, A. 1997. Application of the microsatellite techniques for analyzing genetic diversity in shrimp breeding programs. *Aquaculture,* **152**: 35-47.

Woods, I.G., Kelly, P.D., Chu, F., Ngo-Hazelett, P., Yan, Y.L., Huang, H., Postlethwait, J.H. & Talbot, W.S. 2000. A comparative map of the zebrafish genome. *Genome Research*, **10**(12): 1903-1914.

Woods, I.G., Wilson, C., Friedlander, B., Chang, P., Reyes, D.K., Nix, R., Kelly, P.D., Chu, F., Postlethwait, J.H. & Talbot, W.S. 2005. The zebrafish gene map defines ancestral vertebrate chromosomes. *Genome Research*, **15**(9): 1307-1314.

Woram, R.A., McGowan, C., Stout, J.A., Gharbi, K., Ferguson, M.M., Hoyheim, B., Davidson, E.A., Davidson, W.S., Rexroad, C. & Danzmann, R.G. 2004. A genetic linkage map for Arctic char (*Salvelinus alpinus*): evidence for higher recombination rates and segregation distortion in hybrid versus pure strain mapping parents, *Genome,* **47**(2): 304–315.

Wright, D., Nakamichi, R., Krause, J. & Butlin, R.K. 2006. QTL Analysis of Behavioral and Morphological Differentiation Between Wild and Laboratory Zebrafish (*Danio rerio*). *Behavior Genetics,* **36**(2): 271-284.

Xu, P., Wang, S., Liu, L., Peatman, E., Somridhivej, B., Thimmapuram, J., Gong, G. & Liu, Z.J. 2006. Channel catfish BAC end sequences for marker development and assessment of syntenic conservation with other fish species. *Animal Genetics* **37**(4): 321-326.

Xu, P., Wang, S., Liu, L., Thorsen, J. & Liu, Z. 2007. A BAC-based physical map of the channel catfish genome. Genetics, in review.

Young, W.P., Wheeler, P.A., Coryell, V.H., Keim, P. & Thorgaard, G.H. 1998. A detailed linkage map of rainbow trout produced using doubled haploids. *Genetics*, **148**: 839-50.

Youngson, A.F., Dosdat, A., Saroglia, M. & Jordan, W.C. 2001. Genetic interactions between marine finfish species in European aquaculture and wild conspecifics." *Journal of Applied Ichthyology,* **17**(4): 153-162.

Yu, Z. & Guo, X. 2006. Identification and mapping of disease-resistance QTLs in the eastern oyster, *Crassostrea virginica* Gmelin. *Aquaculture,* **254**(1-4): 160-170.

Yu, Z. & Guo, X. 2003. Genetic linkage map of the eastern oyster *Crassostrea virginica* Gmelin. *Biological Bulletin,* **204**(3): 327–338.

Yue, G., Li, Y., Chen, F., Cho, S., Lim, L.C. & Orban, L. 2002. Comparison of three DNA marker systems for assessing genetic diversity in Asian arowana (*Scleropages formosus*). *Electrophoresis* **23**: 1025-1032.

Zbikowska, H.M. 2003. Fish can be first--advances in fish transgenesis for commercial applications. *Transgenic Research*, **12**(4): 379-389.

Zhou, Z., Bao, Z., Dong, Y., Wang, S., He, C., Liu, W., Wang, L. & Zhu, F. 2006. AFLP linkage map of sea urchin constructed using an interspecific cross between *Strongylocentrotus nudus* (♀) and *S. intermedius* (♂). *Aquaculture,* **259**: 56-65.

Zhu, Z.Y. & Sun, Y.H. 2000. Embryonic and genetic manipulation in fish. *Cell Research*, **10**(1): 17-27.

Zimmerman, A.M., Evenhuis, J.P., Thorgaard, G.H. & Ristow, S.S. 2004. A single major chromosomal region controls natural killer cell-like activity in rainbow trout. *Immunogenetics,* **55**(12): 825-835.

Zimmerman, A.M., Wheeler, P.A., Ristow S.S. & Thorgaard G.H. 2005. Composite interval mapping reveals three QTL associated with pyloric caeca number in rainbow trout, *Oncorhynchus mykiss*. *Aquaculture,* **247**(1-4): 85-95.

ANNEX 1

Genetic marker, mapping and other technologies

Allozyme markers

Allozymes", or "allelic isozymes", are the different allelic forms of the same enzymes encoded at the same locus (Parker *et al.*, 1998). The most common use of allozyme electrophoresis is to detect genetic variation in natural populations. In the last 30 years, large amounts of allelic frequency data were collected from many fish species for management purposes. Although use of allozyme data in aquaculture appears to be limited compared to its use in capture fisheries population studies, aquaculture has utilized this information for its development because aquaculture and fisheries sometimes cannot be separated from each other (Dunham 2004). Allozyme electrophoresis in aquaculture is used for stock identification, parentage analysis, hybrid identification, inbreeding analysis and limited genetic mapping (Liu and Cordes 2004). Although allozyme studies have not found common application in marker assisted selection, correlations between certain allozyme markers and performance traits has been reported (Hallerman *et al.*, 1986). Similarly, due to the limited number of polymorphic loci available, use of these markers in linkage mapping in fish is limited.

The major drawback of allozyme analysis is the necessity for a large amount of fresh or frozen tissue samples. This often requires lethal sampling, especially if a full array of allozyme markers is to be studied. Furthermore, although allozymes represent actual gene products, they often measure a very small portion of the genomic variation because a limited number of loci are involved (Utter *et al.*, 1987). Although cheap and technically easy, numbers of allozyme loci and polymorphisms are low (Agnèse *et al.*, 1997). These drawbacks seriously limit the applications of allozymes for genome studies.

Mitochondrial DNA markers

The mitochondrial genome evolves more rapidly than the nuclear genome. The rapid evolution of the mtDNA makes it highly polymorphic within a given species. Mitochondrial DNA is maternally inherited for the most part, but there are reports of paternal leakage during fertilization (Birky *et al*., 1989). Mitochondrial DNA analysis is actually a restriction fragment length polymorphism (RFLP) analysis except that the target molecule is mtDNA rather than nuclear genomic DNA (Liu and Cordes 2004). The high levels of polymorphism, the maternal inheritance and the relatively small size of mtDNA make the RFLP analysis using mtDNA one of the easiest methods for many population studies (Okumus and Ciftci, 2003; Liu and Cordes, 2004, May, 2003; Billington, 2003). Mitochondrial DNA markers have been used extensively to analyze genetic variation in several different aquaculture species including striped bass (Wirgin *et al.,* 1991; Garber and Sullivan, 2006), channel catfish (Waldbieser *et al*., 2003), walleye (Merker and Woodroff, 1996), salmonids (Nilesen *et al*., 1998, Crespi and Fulton 2004), red snapper (Pruett *et al.,* 2005), and bluegill (Chapman, 1989). There are two major drawbacks of mtDNA markers. One is the non-Mendelian inheritance of mtDNA; and the second is the proportion of the total genomic variation one can observe with mtDNA alone. These characteristics place limitations to the validity of using mtDNA for genetic studies.

RFLP markers

Restriction fragment length polymorphism (RFLP) was the most popular approach for analysis of genetic variation during the 1980's. As indicated by its name, RFLP is based on DNA fragment length differences after digesting genomic DNA with one or more restriction enzymes. In spite of its earlier popularity, RFLP is able to

detect only large shifts in DNA fragment sizes. It is unable to detect the vast majority of point mutations. As a result, polymorphic rates are low at most loci. The efforts involved in RFLP marker development have been enormous. RFLP attempts to detect genetic variation one locus at a time. The low polymorphic rates, when coupled with expensive and laborious processes, have made application of RFLP limited. It should be particularly noted that RFLP requires previous genetic information, such as the availability of probes or sequence information, information often not available for many fish or other aquaculture species. Future use of RFLP will focus on analysis of Single Nucleotide Polymorphisms (SNP) residing within restriction sites.

RAPD markers

Random amplified polymorphic DNA (RAPD) is a PCR-based multilocus DNA fingerprinting technique (Welsh and McClelland, 1990; Williams *et al.*, 1990). RAPD markers are inherited as Mendelian markers in a dominant fashion. RAPDs have all the advantages of a PCR-based marker, with the added benefit that primers are commercially available and do not require prior knowledge of the target DNA sequence or gene organization. Other advantages of RAPDs are the ease with which a large number of loci and individuals can be screened. The major weakness of RAPD is its low reproducibility due to the use of low annealing temperatures, and its dominant mode of inheritance. RAPD makers have been widely used for species and strain identification in fishes (Partis and Wells, 1996; Liu *et al.*, 1998; 1999) and mollusks (Klinbunga *et al.*, 2000; Crossland *et al.*, 1993), analysis of population structure in black tiger shrimp (Tassanakajon *et al.*, 1998) and marine algae (Van Oppen *et al.*, 1996), analysis of genetic impact of environmental stressors (Bagley *et al.*, 2001), and analysis of genetic diversity (Wolfus *et al.*, 1997; Hirschfeld *et al.*, 1999; Yue *et al.*, 2002). RAPD markers have also been used for linkage mapping in fish species (Table 1). However, as more efficient and reliable marker systems such as AFLP emerged, the use of RAPD markers in genome research declined rapidly. However, it is a very useful marker system for rapid hybrid identification, strain identification, and population studies in fisheries species where other genomic information may be lacking.

AFLP markers

Amplified fragment length polymorphism (AFLP) is a PCR-based DNA fingerprinting technique that provides robust analysis of the genome variations. AFLP markers are inherited in a Mendelian fashion as dominant markers. Several major strengths make AFLP markers of choice in many situations. First AFLP requires no prior molecular information for application to the species of interest. This is particularly useful for aquaculture and fisheries species where molecular information is often not available. Second, AFLP is highly robust allowing generation of a large number of polymorphic markers with limited efforts and resources. Third, it is highly reproducible and reliable. The major weakness of AFLP markers is their dominant nature of inheritance. AFLP is more technically demanding, requiring special equipment such as automated DNA sequencers for optimal operations. AFLP is well adapted for many types of genetic analysis such as analysis of genetic diversity, population structures, migration, hybrid identification, strain identification, parentage identification, genetic resource analysis, reproduction contribution, endangered species protection, marker-assisted selection, and genome mapping. Despite the advantages of AFLP, published literature on its application for the analysis of genetic variation of fish population genetic studies is still limited due to technical difficulties and requirement for special equipment (Seki *et al.*, 1999; Jorde *et al.*, 1999; Sun *et al.*, 1999; Chong *et al.*, 2000; Kai *et al.*, 2002; Mickett *et al.*, 2003; Whitehead *et al.*, 2003; Mock *et al.*, 2004; Campbell and Bernatchez, 2004; Simmons *et al.*, 2006). Many AFLP analyses in fish so far have been limited to genetic linkage analysis (Table 1), and analysis of parental genetic contribution involving

interspecific hybridization (Youngson *et al.*, 2001) and meiogynogenesis (Felip *et al.* 2005). In a recent study of the black rockfish (*Sebastes inermis*), Kai *et al.* (2002) used AFLP to distinguish three color morphotypes, in which diagnostic AFLP loci were identified as well as loci with significant frequency differences. In such reproductive isolated populations, it is likely that "fixed markers" of AFLP can be identified to serve as diagnostic markers. Fixed markers are associated most often with relatively less migratory, reproductive isolated populations. With highly migratory fish species, fixed markers may not be available. However, distinct populations are readily differentiated by difference in allele frequencies. For instance, Chong *et al.* (2000) used AFLP for the analysis of five geographical populations of Malaysian river catfish (*Mystus nemurus*) and found that AFLP was more efficient for the differentiation of sub-populations and for the identification of genotypes within the populations than RAPD although similar clusters of the populations were concluded with either analysis. Genetic resource diversity have been assessed using AFLP (Micketti, 2003), and a comparison of the aquacultured catfish with wild populations suggested that the domestic fish had much narrower genetic diversity (Simmons *et al.*, 2006). The impact of the aquaculture catfish on wild catfish populations was found to be little, if any (Simmons *et al.*, 2006).

Microsatellite markers

Microsatellites are tandemly arranged simple sequence repeats (Tautz and Renz, 1984; 1989). Microsatellites are highly abundant in various eukaryotic genomes including all aquaculture species studied to date. Generally speaking, more compact genomes tend to contain smaller proportion of repeats including simple sequence repeats. For example, the highly compact genome of Japanese pufferfish contains 1.29% microsatellites (Crollius *et al.*, 2000). During a genomic sequencing survey of channel catfish, microsatellites were found to represent 2.58% of the catfish genome (Xu *et al.*, 2006). In most fish species, dinucleotide $(AC)_n$ repeats are the most abundant forms of microsatellites. Microsatellites are highly polymorphic such that they are suitable for differentiation of individuals, as well as populations, and species. Microsatellites are inherited in a Mendelian fashion as co-dominant markers. As microsatellites have the greatest differentiating power, they have been widely used in aquaculture and fisheries in areas including linkage mapping (Table 1, Liu and Cordes, 2004; Chistiakov *et al.*, 2006), analysis of genetic diversity, population genetics and conservation genetic analysis, parentage analysis, molecular epidemiology and pathology, QTL mapping (Chistiakov *et al.*, 2006). Microsatellites are highly adaptable for marker-assisted selection, but have not been applied in aquaculture yet because the linkage maps and QTL analysis for important traits are still lacking.

SNP markers

Single nucleotide polymorphisms (SNPs) are alternative bases at a given nucleotide position. Such sequence differences due to base substitutions have been well characterized since the beginning of DNA sequencing in 1977, but the ability to genotype SNPs rapidly in large numbers of samples was not possible until in the late 1990s. SNPs are becoming a focal point in molecular marker development since they are the most abundant polymorphism in any organism, adaptable to automation, and reveal hidden polymorphism not detected with other markers and methods. Theoretically, a SNP within a locus can produce as many as four alleles, however, most SNPs are usually restricted to one of two alleles and have been regarded as bi-allelic. SNP markers are inherited as co-dominant markers. Several approaches have been used for SNP discovery including SSCP analysis (Hecker *et al.*, 1999), heteroduplex analysis (Sorrentino *et al.*, 1992), and direct DNA sequencing. DNA sequencing has been the most accurate and most-used approach for SNP discovery. Random shotgun

sequencing, amplicon sequencing using PCR, and comparative EST analysis are among the most popular sequencing methods for SNP discovery.

Despite technological advances, SNP genotyping is still a challenging endeavor and requires specialized equipment. Traditional methods available for SNP genotyping include: direct sequencing, single base sequencing (reviewed by Cotton, 1993), allele-specific oligonucleotide (ASO, Malmgren *et al.,* 1996), denaturing gradient gel electrophoresis (DGGE, Cariello *et al.*, 1988), single strand conformational polymorphism assays (SSCP, Suzuki *et al.*, 1990), and ligation chain reaction (LCR, Kalin *et al.*, 1992). Each approach has its advantages and limitations, but all are still useful for SNP genotyping, especially in small laboratories limited by budget and labor constraints. Large-scale analysis of SNP markers, however, depends on the availability of expensive, cutting-edge equipment. Several options are available for efficient genotyping using state of the art equipment. Particularly popular are methods involving MALDI-TOF (Matrix-assisted laser desorption ionization - time of flight) mass spectrometry (Ross *et al.*, 1998; Storm *et al.*, 2003), pyrosequencing (Ahmadian *et a.,,* 2000; Alderborn *et al*., 2000; He *et al.*, 2003), Taqman allelic discrimination (Li *et al.*, 2004), real-time (quantitative) PCR (Nurmi *et al.*, 2001), and the use of microarray or gene chips (Hacia *et al.*, 1999). Mass spectrometry and microarray technologies require a large investment in equipment. The equipment for pyrosequencing and quantitative PCR is generally under $100 000, and should be more affordable to many laboratories working in the area of aquaculture genetics. Another consideration is the expense of genotyping in relation to sample sizes. Microarray (gene chip) technology and quantitative PCR are particularly useful in medical and clinical settings where large numbers of samples (thousands of individuals per locus) are involved and that can justify the cost involved in the development of the gene chips and hybridization probes. Mass spectroscopy and pyrosequencing are relatively cost-effective (after acquisition of the equipment) when working with relatively small sample sizes (e.g., hundreds of individuals per locus), as is most likely the case with aquaculture and fisheries species.

SNPs can be genotyped with a wide range of techniques and instrumentations, from small-scale, low-budget to expensive high-throughput systems. For SNP genotyping, the greatest determinants of the genotyping platform depend on the availability of equipment. Given the availability of the equipment, considerations can be made based on budget, number of markers, number of individuals, and the requirement for robustness. In spite of its low levels of application in aquaculture and fisheries genome research, SNP markers should gain popularity as more and more sequence information becomes available in aquaculture species. Equally important, once the genetic linkage maps are well constructed, genome scans for QTLs are expected to follow to study traits important to aquaculture, which then depends on the use of well-defined association analysis. As SNP markers are great markers for the analysis of trait-genotype associations, their increased application in aquaculture and fisheries is assured.

Microarray technology

In addition to DNA marker technologies and genome mapping technologies, microarray technology is very important for genome scale analysis of gene expression. This is particularly important for environment-related issues. While microarrays utilize several recent technological innovations, they are, at their core, simply a high density dot blot where DNA samples are applied to a solid support in the form of very small dots, and hybridized to specific DNA probes. Microarrays achieve higher gene feature densities and, therefore, greater power for expression analysis by applying new tools to this old process. High-density spotting robots and photolithography allow each feature to be placed accurately within nanometers of the next feature on a glass slide,

clearly an impossible task with the human hand. Furthermore, fluorescence-based probe labeling provides a cleaner and clearer signal than the radiation traditionally used in blotting. Finally, laser scanners facilitate the resolution of such tremendous feature densities and provide accurate fluorescent signal quantification. Microarray technology allows the changes of gene expression with a specific treatment to be determined at the entire genome scale. For instance, Ju *et al.*, (2002) used microarray technology to determine which genes were up or down regulators in the brain of catfish after treating the fish with cold temperature, and found that 61 genes were significant up-regulators and 12 were down-regulators.

Potential applications of microarray technology in aquaculture and fisheries are wide open. As a genome expression analysis technology, it can be used for analysis of gene expression after any treatment. The first microarray experiment was conducted in catfish for the analysis of cold acclimation (Ju *et al.*, 2002; Kocabas *et al.*, 2004). The microarray created by the GRASP project is widely used in the aquaculture community (Rise *et al.*, 2004a; von Schalburg *et al.*, 2005) for gene expression profiling after infection and vaccination, and stress (Rise *et al.*, 2004b; Purcell *et al.*, 2006; Ewart *et al.*, 2005; Sarropoulou *et al.*, 2005). It is expected that microarrays will find great applications in aquaculture and fisheries.

Gene mapping technologies

Although the term gene mapping is widely used in the scientific community, it really refers to several different types of mapping approaches including genetic linkage mapping, physical mapping for the construction of BAC contigs, radiation hybrid mapping, QTL mapping, cytological mapping by FISH (fluorescent in situ hybridization), and comparative mapping. The goal of linkage mapping is to conduct mapping using polymorphic DNA markers in a segregating population (usually F2 population or backcross progenies). Physically linked DNA markers co-segregate. The greater the marker distance, the more likely the recombination during meiosis. Based on co-segregation, markers are placed into the same linkage groups; based on recombinant frequency, marker distances are assigned. Linkage mapping is the basis for genome analysis, and linkage maps have been constructed in many aquaculture and a few fisheries species. The quality of linkage maps are measured by marker density. All aquaculture linkage maps are framework maps or intermediate density maps.

Quantitative trait loci (QTL) mapping technology

The goal of QTL mapping is to locate the positions of quantitative trait loci. Most, if not all, performance and production traits of aquaculture are controlled by multiple genes and therefore are inherited as quantitative traits. These genes segregate along with linked DNA markers. By measuring association of trait segregation patterns with marker segregation patterns, it is possible to place trait (or genes responsible for the trait) on linkage maps. QTL studies have been conducted mainly in farmed fish species; for example, rainbow trout. It is expected that QTL mapping will be the key to genetic improvements using marker-assisted selection.

Physical mapping technology

Although several approaches are available for physical mapping, the most popular is the BAC-based approach (Bacterial Artificial Chromosome). This approach is based on restriction fingerprinting. Adjacent overlapping DNA segments should share fingerprints that allow large insert BAC clones to be lined up in a linear fashion reflective of their position in the genome.

BAC-based physical mapping has been conducted in several fish species, but mostly with model species. BAC-based physical maps have been only conducted in a few farmed fish; for example, Nile tilapia (*Oreochromis niloticus*) (Katagiri *et al.*, 2005),

Atlantic salmon (*Salmo salar*) (Ng *et al*., 2005), and channel catfish (Xu *et al.*, 2007). BAC libraries have been constructed for more farmed species including rainbow trout, Pacific and eastern oysters, and penaeid shrimps. Because physical maps are required for position-based gene cloning, it is expected that physical maps will be constructed soon for many important farmed fish species.

Other mapping technologies

Cytological approaches have been used to map genes to chromosomes of some farmed fish species, but because of its relatively low resolution, this mapping strategy is used only as a complementary strategy for the purpose of chromosome marking and related purposes. Radiation hybrid mapping panels have been only established in zebrafish (*Danio rerio*) and European sea bass (*Dicentrarchus labrax*) (Senger *et al*. 2006). Although this approach has been extremely popular in mammalian species, its application in fish is limited. The major reason is that BAC-based physical mapping provides greater levels of resolution and is also more cost effective. The goal of comparative mapping is to use known information from a map-rich species for genome studies of a map-poor species. Knowing the location of genes in a well studied species such as a related model species like zebrafish, one can ask if the genes are arranged similarly in the same chromosomal locations. Comparative mapping is still at its infancy stage in aquaculture species, but hold great promises for the identification of candidate genes responsible for important economic traits.