MODELLING FISHERIES: WHAT WAS THE QUESTION?

by

Gary D. Sharp, Jorge Csirke and Serge Garcia

Marine Resources Service
Fishery Resources and Environment Division
Fisheries Department
FAO, Via delle Terme di Caracalla
00100 Rome, Italy

Resumen

En este trabajo se revisa la evolución de los modelos matemáticos empleados en la evaluación y ordenación pesquera, tanto desde el punto de vista histórico como desde el punto de vista conceptual. Se subrayan los problemas que han surgido durante esta evolución tales como las variaciones en las capturas, la mortalidad, distribución, crecimiento, reclutamiento, escalas de tiempo y estructuras por edades. Se pone también énfasis en problemas de particular importancia, tales como el muestreo, el origen y la estructuración de hipótesis, así como los conceptos relacionados con los stocks, incluyendo la caracterización de los mismos. Todo esto lleva a la pregunta en forma de conclusión de ¿por qué modelar las pesquerías? Se revisa la evolución y las diferentes alternativas que se han presentado y se presentan en el campo del modelaje en pesquerías. Se revisa el esquema conceptual, se compara el enfoque tradicional en los modelos de pesquerías y se dan algunas sugerencias en cómo pueden ser mejorados. Se hace una revisión de la perspectiva histórica y después se discuten algunos aspectos relacionados con los estados de no equilibrio de las poblaciones de peces, tales como las variaciones en las capturas, las variaciones en mortalidad, cambios en la distribución de las poblaciones, los cambios en crecimiento, la variabilidad del reclutamiento, las variaciones en las escalas de tiempo, variaciones en la estructura por edades, cambios en la captura por unidad de esfuerzo, la abundancia, etc. Se dan algunos ejemplos de cómo la selección de un determinado modelo tiene una influencia grande en los resultados y conclusiones que se pueden obtener de un determinado conjunto de datos. Se agrega un anexo donde se discuten los métodos empleados en la caracterización de poblaciones de peces.

INTRODUCTION

The mathematical models used in conventional fisheries science are abstract, simplified representations of the processes governing growth, decay and reproduction of exploited populations as well as their reaction to exploitation. As all models, they are only special cases of particular scientific theories. At any point in time they reflect, at best, some part of the knowledge and understanding we have been able to reflect, at best, some part of the knowledge and understanding we have been able to integrate in order to try and answer a specific question. Models must, therefore, change and new dimensions must be captured in the representation when our knowledge improves or when a different problem must be addressed. Many aspects of the models available to us for the last 3 decades are more and more often said to be unsatisfactory and it is probably time to check their appropriateness in face of the knowledge accumulated since their inceptions, but it is also time to ask whether the model is being applied to a situation which corresponds to the special case for which the model was developed.
A model can be a useful tool only when the problem addressed is well formulated for numerical analysis. It is therefore, useful to consider classical formulations of each fishery problem in order to compare the advanced point of view with the previous ones. It is important to recognize that the scientists who developed the original production or yield per recruit models based their work on the observation that the economically and biologically depressed resources of the North Atlantic recovered noticeably during the 1st and 2nd World War periods when fishing effort declined considerably.

The rapid development of fishing effort in the fifties rapidly raised questions about inherent limitations of resources particularly about the necessity to regulate fishing mortality. It was largely accepted that unregulated fisheries lead to economic, and possibly, biological overfishing. The problem to be solved was therefore, that of optimizing captures while conserving the resources by regulating fishing. Essential questions had to be answered such as: How do growth and mortality interact in the development of population biomass and production? What is the effect of additional mortality by fishing at different ages? How much can be extracted from a given stock? What is the relation, if any, between parental and progeny abundance etc.? Therefore, models had to be designed to investigate these since experimentation was and remains hardly feasible.

The same problems have still to be faced today but with new knowledge additional dimensions need to be added. The climate driven environment has been recognized as an important causal factor of variability of pelagic stocks, with or without intensive fishing, through changes in both recruitment success and geographic distribution. This has created the need for more reliable predictive "tactical" models usable in the short term for deciding on management measures in order to cope with continuous environmental changes. Of course ecological perturbations due to fishing are also likely since the removals are often selective and can be large proportions of major populations.

In this paper we try to retrace the evolution of modelling from the historical as well as from the conceptual point of view, underlining the problems that have been raised during that evolution such as variations in catches, mortalities, distribution, growth, recruitment, time scales and age structures. Emphasis is given to problems of particular importance like sampling, causality and hypothesis structuring as well as stock concepts including stock characterization which then lead us to ask again as a conclusion: "Why model fisheries".

**FISHERIES MODELLING: EVOLUTION AND ALTERNATIVES**

**The Conceptual Modelling Framework**

Our knowledge of species specific biology or understanding of ecological interactions has improved with time although most fisheries models basically rely on Russell's (1931) and Graham's (1935) original conceptions that the state of a single species population at any time was the result of growth, mortality, recruitment and migration processes. This has clearly been the basis for historical elaborations of all the presently available models including the most sophisticated ones. The different directions taken by fishery modelling stem from different perceptions about the key factors responsible for population changes, namely fishing effort, physical environment or predation.

The classical theory of fishery science has been based for a long time on a series of elementary models where natural mortality (M) is usually considered as an exponential process, constant after recruitment; growth (G) is represented by various continuous or discrete functions of size or age. Fishing mortality (F) is supposed to be proportional to fishing effort (f) and therefore catch per unit effort is equally taken as proportional to abundance. Biological production is mostly considered as a function of biomass and recruitment is often represented as a function of stock size.

Additional basic concepts or assumptions underlying the classical modelling of fisheries are those of steady state and homeostasis. It is believed that a given population is in permanent dynamic
equilibrium with its environment and therefore, limited by some feature of it which defines a specific carrying capacity (K); that population abundance is significantly affected mainly by fishing; that a new steady state is reached when fishing is stabilized; and that the observed declines in productivity and economic conditions (attributed to excessive fishing) are almost certainly reversible (homeostasis).

The original conception of fishery systems models as closed1 steady state systems was quite in line with the conceptual framework of other branches of ecology and science in general at that time.

Modern science is however discovering that systems (and more typically biological systems) are more often likely to be open and affected by non-linear, non-equilibrium and often non-reversible processes, characterized by threshold limits and discontinuities. As the available data base builds up it becomes more and more evident that recruitment variations cannot be considered as random noise, but that this variation is an essential signal, input into the adult population system (the only portion of populations usually modelled). Recruitment is the ‘output’ of an adjacent system (the nursery) about which our understanding has been poor and therefore, usually neglected in general fishery modelling. It becomes clear that, at least for quite a number of stocks, a drastic revision of the ‘original’ models is necessary and, for instance, that the concept of “carrying capacity” of the environment applies probably more often at the larval stages of a population than at adult stages, and that recruitment may be affected by stock size but is certainly affected at least as strongly by environment.

The Classical Modelling Approach

Within the above conceptual framework the precursors in biological fishery modelling integrated the elementary submodels on growth, mortality, production, etc. in the two most widely used surplus production and analytical approaches of fishery science in order to predict fisheries performance. These approaches have therefore the defects of the elementary models and assumptions employed, aggravated by the effects of their combination. The limitations of these higher order models are well known and the literature is crowded with theoretical considerations about the possible effects of density dependence of growth and mortality, or about the effect of seasonal or long term variability of the subpopulation component interactions as well as trophic factors. However, because such effects are difficult to isolate and measure, they have generally not been taken into account in modern decision-making processes related to fishery management.

These models were constructed to investigate steady states of self-contained mono- specific “unit” populations (as nearly closed systems) and their reactions to fishing. Density dependence was implicitly accounted for in production modelling and could be introduced in analytical modelling as shown by Beverton and Holt (1957) themselves.

Despite their obvious limitations, the models traditionally used for management have had their indisputable usefulness. The Production Model was important in providing convincing arguments that resources are limited and that effort needs to be controlled if any conservation objective was to be reached on the long-term.

It can be said that production models should also have been strategic models (helping to identify possible objectives and ways of action). They have, however, been used with little success for year to year implementation of effort reduction policies or quota regulations and may be said to have often failed as tactical models.

______________________________

1 In the sense that the species and its predator (the fishermen) were isolated conceptually from other species interaction or from the environment
Yield per recruit models gave clues about the puzzling problems of balance between growth and mortality and of the effects of ‘thinning’ of adult populations by fishing under different exploitation patterns. They have helped us to understand the effects of management measures as changes in mesh size and closed areas or seasons which, by the way, is what management has been about for decades. They finally showed, by omission, that recruitment was crucial to understanding and prediction of year to year variations of stock sizes.

Towards Improved Modelling

Tersely stated, the problem is to either be simple or to be realistic. The situation described above is neither specific to fishery science nor to quantitative ecology in general. The fishery system is a very complex one. Modelling is necessary and, as always, compromise needs to be found between holism and practicality; between intractable sophistication and oversimplification. There will always be a need for partial analysis and modelling of the fishery systems, including in models the processes which are understood and documented, leaving out of the model (as externalities) the processes which are still beyond understanding and beyond control. The resulting simplification makes models more understandable but poses immediately the problem of interactions. As soon as it is recognized that the effect of externalities on the modelled sub-systems are far from negligible, it must be recognized that that specific approach is too narrow.

For example, in spite of the recent discovery and attention to relevant small time and space scales, proper modelling of recruitment will need to also involve observations of large time and space scales to take into account the phenomena of cross-oceanic or inter-oceanic teleconnections as well as low frequency signals like “sunspot cycles” and other related cosmic factors. However, it is quite evident that it is pointless to model recruitment without taking into account microscales (metres/days) in order to resolve particular time-space “survival windows” for the analysis of the mechanisms directly affecting larval survival.

In some cases a more comprehensive and realistic model would have to take into account species interactions as well, especially as far as food relationships are concerned, particularly when it is anticipated that predator-prey effects may be just as important, if not more so, than fishing effects.

Care must be however taken because there will also always be the tendency to develop as many holistic models as possible (energetic, trophic-dynamic, or self-generating models) trying to circumscribe in the model all the essential processes. The risk here is just as Hedgpeth (1977) states: “the construction of elaborate diagrams and mystic- mathematical representations of assumed relationships powered by selected values is a favourite pastime of many ecologists and environmental engineers and a model which is simply an elaborate mathematical summary of a textbook does not tell us more than we already know.” Erwick et al. (1979) remind us that a model can be made so sophisticated as to produce outputs resembling closely the real world. However, because the underlying assumptions are so complex and their interdependence so obscure the model may not be easier to understand than the real process was (Bonini's paradox).

The very complex models such as the trophic-dynamic (Andersen and Ursin 1977) ones have a high number of dimensions and therefore, their data requirements are high. They use numerous coefficients and involve quite a lot of measurement and estimation. As proposed by Fedra (1980), they will certainly have a role in the development of fishery science but their usefulness for management can be questioned because their complexity and number of dimensions prohibit analysis of their sensitivity to variation and hence evaluation of their ability to reflect biological responses.

The goals of model building, namely realism, precision, and generality seem therefore just as conflicting as management objectives generally are. A trade off has to be made when modelling fisheries. The energetic (Paloheimo and Plowright, 1979) and trophic- dynamic models being still too far from any practical application to fishery management, they will have to be further developed as experimental exercises, in order to try to gain some understanding on the mechanism of
biological production of complex multispecific systems and to identify the most likely key factors responsible for year-to-year variations, and the most useful data to be possibly collected economically in the future.

This will be a long process and in the meantime we have to adopt a practical approach. We still need models but they have to be simple, (lower predictive value but lower risk of error) and enable the right choice be made between management options, within some tolerable limits of uncertainty. The precision required must be adapted to the objectives of management and unnecessary (overvalued) predictive reliability or precision should be avoided, because of the underlying costs or mistakes. For instance, it may be important to understand the mechanism of recruitment survival but it is essential only to know which parameters govern year class strength and supply predictive capabilities (see Csirke 1980 for the Peruvian anchoveta recruitment or Garcia and LeReste 1981 for predictive models in penaeid shrimp).

It is quite clear that, in contrast with the past, a strategy has to be adopted for management, under varying environmental conditions, for many stocks, but the cost of doing so in the future should be lower than the present losses by not doing so and the overall efficiency of management should increase. One obvious consequence of dropping the steady state hypothesis is the great increase in the need for monitoring (of species distribution, species composition, recruitment survival factors, etc.) in order to increase the short-term forecast capabilities of models. It will always cost a lot more to predict accurately next year's catch than to detect the most likely trend or sign of variation for a more or less near future.

Another consequence is the need to introduce the concept of risk management. It must be clear that the models cannot be deterministic and that there is no single answer to a given problem. It must also be clear that introducing a random factor (stochastic elements) into a model is not very useful for short-term management as most of the environmentally induced fluctuations are autocorrelated. It has been recently proposed to use decision theory (Lord 1976, Laurec and Maucorps 1981). Applied decision theory depends very much on the weighting of the various outcomes, and these will vary greatly among various interest groups. The uncertainty of the environment, biological responses, market fluctuations, and other often neglected control mechanisms make the first steps into a modern “decision theory” based management system difficult to implement, but this is an obvious requirement for progress toward proper system management.

The Historical Perspective

A brief review of past fisheries investigations helps to give some insights into possible trends and alternatives for fisheries sciences in the future, particularly in relation to the problem of modelling exploited fish populations.

The origins of fisheries modelling can be traced to the beginning of the century, and the available literature provides important landmarks in the history of fisheries sciences that will help in understanding why we are where we are now, what alternatives have been used and which ones have still to be explored.

The first landmarks in the history of fisheries science are those of Hjort (1914) and Baranov (1918). Both were compilers of the “pre-World War” knowledge in fisheries sciences and inspirers of the succeeding generations of fisheries scientists; and not surprisingly most of their basic concepts are still fully valid today.

It is not our intention to review the work of Hjort and Baranov but it is worth mentioning the main characteristics of their work and their general approach to fisheries sciences. This can probably be well-described by just the titles of their respective two main papers: “Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research” and “The question of the biological basis of fisheries”. They both looked into the biology of fishes as the major issue when
trying to solve fishery questions. Fishing itself was considered as an important factor, but the hydrographical and biological conditions were considered to be at least as important as fishing, with respect to the fluctuation of fisheries and of fish stocks. Already in 1914 Hjort concluded that, in the case of the few species he investigated, recruitment was highly variable and that this was the major cause of the fluctuation of fish stocks. While pointing out that variability of the strength of year-classes was the main cause of fluctuation of fish stocks, Hjort also indicated that these fluctuations were driven primarily by the conditions prevailing at the time at which the development of the early life history stages of fish were taking place.

If we are to make an inventory of the alternatives presented by Hjort (1914) and Baranov (1918) we will certainly find that these were quite ample. All factors that we consider important now were probably mentioned and proper justifications for investigating most of them were given. Moreover, in light of what we know now, we can probably conclude that the relative importance assigned by Hjort to each of these factors was probably well balanced. Great importance was assigned to the investigation of environmental and biological factors and of the effects of fishing, but what is most significant is that great importance was also assigned to the investigation of the relationship between these three groups of factors.

This was more or less the situation in the so-called “pre-World War” era, but then came the two World Wars which changed the course of civilization and also the course of fishery sciences.

The First World War (1914–18) caused fishing activities to be suspended for four years in the North Sea, and when fishing resumed in 1919, there were the results of the first large-scale non-voluntary experiment which demonstrated that fishing was in fact a major cause of fluctuation of exploited fish populations. These results were particularly striking in the case of some highly valuable fisheries that before the war were heavily exploited, such as cod, haddock, halibut, turbot, etc. Catch rates were higher, fish caught were bigger and total landings augmented during the few years after the war, but all these started to regress to pre-war levels as fishing intensity increased.

These series of events are the source of inspiration for another generation of fishery scientists, amongst whom the most representative are E.S. Russell and M. Graham. From this generation those classical papers that can also be considered as landmarks in fisheries literature are the one on “Some theoretical considerations on the overfishing problems” by Russell (1931) and the ones on “Modern theory of exploiting a fishery” and “The sigmoid curve and the overfishing problem” by Graham (1935 and 1939).

These were the first real attempts to represent the dynamics of an exploited fish population through a mathematical model, and it is noticeable that their subject matter was the same, the overfishing problem, although their approaches were different. Russell set up the foundations of what we commonly define now as analytical model, while Graham started another school of analysis based on the global production model. The works of these two authors also reflect the general concept that has lasted for many decades with regard to the most likely cause of fluctuation of exploited fish populations to be analysed and incorporated into fisheries models: the effects of fishing.

The Second World War (1939–45) gave a further large scale demonstration of the severe effects of fishing on exploited fish populations, and particularly demonstrated that the effects of fishing were reversible. This gave new impetus to the development of theories and models of population dynamics as well as new concepts of alternatives for exploited fish populations. The major factor remained fixed, i.e., the fishery.

The potential role of environmental and biological variability as major causes of fluctuations in fish populations was never completely ignored, but was conveniently relegated to just a potential role. In fact there were very few experimental observations to counterbalance the well accepted evidence that fisheries accounted for substantial amounts of the observed fishery and fish stock variabilities.
The works by Beverton and Holt (1957), Ricker (1958) and Schaefer (1954) are probably the best examples of the bloom in the development of post-war fisheries modelling. The models proposed were based on the assumption that fishing or fishery related factors (fishing mortality, average size of individuals, spawner stock size, size at first capture, etc.) accounted for most, if not all, of the variability of fish populations. A well founded concept if we take into account the events that affected fish stocks and fisheries in Northern Europe in the first half of the century. If the Northern European fisheries had been hit by a series of “El Nino” type of short-term climatic events instead, it is certain that the evolution of fisheries science would have been completely different, but that would have been true for world history as well.

The developments introduced by Beverton and Holt (1957) and Ricker (1958) to analytical modelling of exploited fish populations, and the ones introduced by Schaefer (1954) to global production modelling contributed to building an entire theory about how fish populations behave and on how to manage fisheries. There have been some later refinements and descriptions of special applications of these two schools of analysing and modelling fisheries for the purposes of fisheries management, but in general terms these developments can be considered as the ultimate steps in modelling the effects of fishing on fish populations. These two types of models do provide a reasonable framework for the development of fisheries management strategies as they stand now, provided that (a) the effects of fishing on the population can be measured and controlled, and (b) it still holds that most of the variability of the population characteristics is due to fishing. Beyond what has been achieved so far probably little more can be added to fisheries modelling by further efforts to improve modelling the effects of fishing, unless the effects of hydrographical and biological factors are brought into the picture with considerable effort to inter-relate each to the others.

It is certainly not fair to say that the development of fisheries science and of fisheries modelling have been slow, but it is true that although it had developed in both theoretical and practical aspects, most of this development has been concentrated on only one of the three possible sets of alternatives that were identified almost 70 years ago. The investigation and modelling of fishing effects on fish populations have developed, but the investigation and subsequent modelling of environmental effects and biological reactions and interactions has been disregarded for a long time.

Major attention has been paid to factors other than fishing in relation to the fluctuation of fish stocks only after the collapse of several important pelagic fisheries. The collapse of the California sardine in the 1950's; the collapse of Japanese sardine in the 1940's and sudden recovery in the 1970's; the collapse of the North Atlantic herring in the late 1960's; the collapse of the Peruvian anchovy in the early 1970's and the associated increase of other pelagic stocks, all contributed to more attention being paid to “the other” possible causes of changes in the fish stocks, although in most cases the first act was still to blame the fishery for the collapse of the fisheries.

Although it is true that no fishery will collapse in the absence of fishing, in most cases it seems that other (i.e. environmental) factors had either favoured the over- development of fisheries prior to the collapse or had complemented the negative effects of heavy fishing by reducing the growth potential of the subject populations.

Changes in recruitment are the major cause of fluctuations in fishable populations. Although normally more attention tends to be paid to downward than to upward changes, in fact, attention should be paid to both. The successive failure of recruitment has been identified as the most immediate cause of reduced stock size and subsequent collapse of the fisheries, but in most cases these have been preceded by a series of increased recruitments, that increased both stock abundance and subsequent fishing activities, thus magnifying the downward changes in the fishery resources when or if more usual recruitment levels resume.

Although the potential effects of change in growth rate and natural mortality (e.g. the post-recruit stages) are not as great as those caused by changes in recruitment, these can still play an
important role in fish stock variability and attempts should be made to model their fluctuations for incorporation into fishery models.

Probably the most striking example of recruitment failures and subsequent collapse of the fisheries is that of the Peruvian anchovy in the early 1970’s. The collapse occurred in 1972, but the conditions for it started building up at least two years earlier. The Peruvian anchovy also provides a good example of the potential effect of changes in growth rate. In fact a good recruitment entered the fishable stock in 1976, raising the total biomass to 11 million tons at the beginning of the year. However, reduced growth rate (and heavy fishing) contributed to reductions in stock size by the end of the year to around 3 million tons, thus extinguishing the expected recovery of the stock. It is worth noting that both series of events were linked to changes in the environment that respectively affected either reproduction success or adult feeding success, hence lowered growth in numbers and biomass.

Efforts need to be made to model changes in recruitment, growth rates, natural mortality, etc. and to relate these with environmental factors, but for this to be successful further investigations are needed on the relationships between these factors and, of course, on the factors themselves, how they work, how to measure them, particularly since most data available to date was collected to answer the question of how fishing affects fisheries.

SOME ASPECTS OF NON STEADY STATES IN FISH POPULATIONS

When trying to internalize in the models more externalities than in the past, essential phenomena have to be considered, like patterns of variations in catches, mortalities, distribution, growth, recruitment and time scales.

**Catch Variations**

Caddy (1983) has provided an assortment of examples of four classes of fishery resource behaviours: I) Steady state fisheries; II) those with regular periodic fluctuations; III) fluctuations with irregular periodicity; and IV) irregular or intermittent production. Many examples of each type are available. Classical production models and age structured models may suffice to portray types I and II adequately for most management purposes. However, types III and IV will certainly require far more extensive information pertaining to causal, environmental and ecosystem related effectors.

**Mortality Variations**

All mortality is “event” controlled; a series of hurdles or irregular filters imposed at each stage, differing drastically from point to point in space. Much as fish school sizes are often distributed in a negative binomial fashion, predators are also often “aggregated” this way. There are also density related thresholds of abundances of egg-larval fishes and their prey which are important for feeding, hence survival. The predator relying on egg-larva sized prey, or larvae feeding itself, requires encounter threshold densities in order to affect survival/mortality of their prey.

Much of the earlier modelling effort has been based on “average” information or probability estimates based upon over-integrated data sets rather than relevant scales of interaction such as those employed in the studies of Vlymen (1977) and Beyer and Laurence (1981). The hurdle concept evolved by Beyer (1976, 1980) has a very strong probabilistic component, but is at least intuitively satisfying in this regard as presented. This type of modelling needs to be merged with data on the distributional properties of predator fields, their sources, etc. But, quickly one arrives at the point that it is the universe needing described and modelled. What should be done? What is sufficient information, where should one start and when should one stop?

The search for precision has always had its advocates, and it should never be given up. However, in fishery related field research the available tools are simply too coarse to yield other than rough
indices at present. The most productive use of day to day research resources would be on gathering basic information about where, when and what is caught by various gears; where and when reproduction appears, where and when young stages are observed, particularly if it is possible to have precise ages of these. Time series of climatic conditions on a daily basis would be useful over the region their fisheries occur. Ageing via daily growth rings in pelagic fishes; larval blooms and juvenile migrations in estuarine fisheries; and general age-specific geographic distribution time series probably tell more about the present status of a fishery than most other information.

For example, the hypothetical annual and interannual variability in eggs produced and subsequent recruits realized shown in Figure 1 gives far more information than, for instance, simple egg-recruits tables. Seasonal changes in survival rate of progeny are not unusual in many species. However, it would be even more useful to have the time series data on both the egg-larval distributions (see Santander et al., Watanabe, this volume), and adults (see Kondo, 1980) in order to better understand their trends and possible interactions (Csirke 1980, MacCall 1981).

Once a time series of data of these sorts is available it is quite obvious why the simplistic “stock-recruitment” relationships can be both incomplete and uninformative. Even in some cases poor knowledge of the whole system can lead to erroneous interpretation, for example, Figure 2 drawn from Garcia (1983) for depicting seasonal changes in recruitment survival in shrimps has been modified in order to show the kind of year-to-year changes which are often “projected” into artefactual stock recruitment curves, without regard to system variables.
Fig. 1. Three hypothetical examples of monthly egg production and subsequent realized recruitments are shown. Note that although either total eggs produced or total recruitment may not be very different there is no suggested relation between either, or when survival, hence recruitment is determined.
Fig. 2. Sequential changing population fecundity and recruitment are often compressed into presumed stock-recruitment relations by projection. One should recall the message by projection. One should recall the message in Figure 1 which suggest no apparent direct relation between eggs produced or recruitment in time. Artefactual stock-recruitment relations are often produced without necessary evidence (from Garcia, in press).

Modelling of non-equilibrium populations is slowly coming of age. Age structured models are commonly employed in which size-age data are arrayed in time-series such that from total catch and estimates of M and F, recruitment can be estimated. Assumptions are made about the relation between fishing intensity (f) and relative fishing mortality (F) i.e., fq = F, and either f or q (the so-called catchability coefficient) are held relatively constant. These models are appropriate for small regional fisheries with relatively direct concurrence between the population being exploited and fishing effort distribution. However, if there is emigration or migration such that the effort distribution is not concurrent with the resource, then knowledge of the In and Out proportions need to be known. If these estimates or assumptions are invalid then the model results are simply artefactual.

Species with diverse discontinuous fishing effort applied to them are certainly not easily modelled and this is a problem where population structure is vague and unknown. Age structure changes need to be evaluated from knowledge of both the distribution in time and space of the fishery and the age groups of the fish.

Distribution changes

Csirke (1980) was able to model the dynamics of recruitment in the Peruvian anchoveta utilizing catch and effort data as a measure of density and the relation between this and independent population size estimates as a measure of area, hence volume of the occupied habitat. The density dependent mechanism (density per unit volume) for recruitment modification can be attributed to
density related cannibalism of the eggs and larvae by adult anchoveta (Santander et al. this volume).

Growth Changes

In many studies (e.g. Jones and Hislop, 1978; Zijlstra, Dapper and Witte 1982) there are clear examples showing modification of growth at various ages/stages, from early juvenile (prerecruit) to adults. In adult stages these changes in growth are related to changes in individual fecundity and often age of first spawning, all of which need careful analysis in order to understand the resulting reproduction success and subsequent recruitment. (Fontana 1981).

In the younger stages, the variables affecting growth reflect both biological distribution variations and also physical-chemical ones. Temperature, food particle distributions and predation appear to dominate larval growth and survival parameters (Theilacker and Dorsey 1981, and others - see IOC Workshop No. 28).

Changes in growth with time, associated with changes in either the overall abundance or the environmental conditions are also important and need to be given careful consideration when modelling non steady state fisheries. For instance, Zuta, Tsukayama and Villanueva (this volume) show that in the Peruvian anchoveta there were drastic losses in weight (of up to 36% for a given length) associated with abnormal environmental conditions and due to the high concentrations of the population that occurred in 1976–1977 and 1982–1983 even though there were no indications of changes in growth in length (Pauly and Tsukayama, this volume). Changes in growth with time and space are also shown for the Pacific mackerel and anchovy of California (Parrish and Mallicoate, this volume).

The variable Recruitment Issue

As most population variation is explained by changes in natural mortality (M) at some stage in the life history, it should be asked where this might be accounted for. Of course, the usual mechanism involved is “a change in recruitment” which involves changes in either M or fecundity-related potential recruitment. Actually it is due to convenience of data availability that fishery models have to-date depended primarily on the post-age-at-entry portions of populations, and that these groups are assigned constant M values. This latter assumption is among the more troublesome in interpreting, for example, cohort analyses or other age structured models, and is simply blurred in the production models to such a degree that any changes in size-age structure for whatever reason and subsequent changes in “intrinsic rate of increase” (i.e. growth rate and mortality) are confounded.

There are several logical issues which should be examined in this set of “conventional explanations” before applying these models. These derive from a cursory understanding of fish life histories and an emerging literature on what comprises natural mortality at various stages. The fate of most dead fish is to be consumed by other organisms. The capture and engulfing of a fish is direct predation (M_{p1}). This is enhanced by the prey being debilitated through disease, poor nutritional condition, or senescence. However, good predators also consume healthy, viable prey, but may have to work harder to obtain their meals. There are secondary forms of predation (M_{p2}) such as scavenging, fungal or bacterial actions. Of course, this brings up the size hierarchy of direct predation, which often breaks down in secondary predation. That big fishes eat little fishes is no surprise, but it does appear that it is often forgotten that big fishes start out as little fishes, i.e. that the proportion of little fishes during their progression toward larger sizes is controlled by the amount of predation and therefore the abundance of predators in the system at various sizes.

Without fisheries operating, natural populations comprise a larger proportion of larger, older fish. The relative stability of such systems depends nearly entirely on the predation/consumption rates on smaller individuals somehow balancing losses at the larger sizes, i.e., lost due to senescence, disease or the limited predation by very large predators. The bulk of fecundity is usually bound up
in large-old individuals in such systems. Once a fishery begins the older, larger individuals are preferentially harvested, and a flood of "uneaten" small fish is left to grow into older, larger individuals. However, under exploitation of the larger predators, not only do we expect a surge of survival in the intermediate sizes, but we also expect an increased predation upon the smaller individuals due to this removal of the larger, more ecologically efficient classes, i.e., fish generally have lower per-unit-weight nutritional demands as they grow. Remembering that these are system processes, rather than single population characteristics, we should find that the prey species preferred by the juveniles or pre-recruits (intermediate sized fishes) of each exploited population should be subject to increased mortalities, while these intermediate sized fishes' natural mortality should actually decrease in the exploited system from which their predators are being removed.

In any situation where cannibalism plays a major role, i.e., filter feeders and many opportunists like tunas, gadoids, etc., the fishery related changing predation rates represent variable M at age-size. In complex ecosystems comprising vast species arrays and diverse behaviours it is not so easy to pin-point which fishery is affecting, secondarily, which age-size-species, but the obvious point is that M values are neither stable, nor only a "species specific" character, they will depend to a great extent upon the ecosystem and its exploitation modes.

By definition the recruitment (R) criteria are fishery and gear specific, but the fluctuations in R will also reflect system variation of the sort just described. Any population can be said to have a finite recruitment potential in the numbers of viable, fertilized eggs it introduces into the sea. Of this potential, only some very tiny fraction will reach maturity, and contribute to the potential of subsequent generations.

**Time scale variations**

The difficulties with estimating natural mortalities are immense. The recent approach by Csirke and Caddy (1983) to equilibrium systems would permit estimation of M if a low variance, steady state system could be identified. However, the probability of any fishery resource being in relative steady-state changes with the number of species it might interact with and their (the predator's) mobilities; the reciprocal of the distribution area compared to its potential habitat; as well as the reciprocal of the number of age classes within the population. This latter problem is particularly relevant in that for descriptive expressions employing differential equations (dx/dt) where t is time, the time frame needs careful consideration. Differential equations refer specifically to time intervals where dt is small, i.e. \( t \approx 0 \), whereas t is often expressed as months or year long periods in fishery formulations. The assumption of year-wide responses, to say decreased adult abundance in recruitment process applications, is that for each species, and population component, the expected response time t is a reproductive life-span. For example, a fish living up to 13 years with maturity at age 6 has eight years to "reproduce itself" whereas our fishery models often expect any responses to perturbation to occur "instantaneously", i.e. in one year. Simulation modelling has shown us that when employing simplistic density dependent self generating models there is a resonance period of several reproduction cycles before "steady-state" is approached. This implies that perhaps only short lived species can "live up to" the assumptions of such models, and long lived fish cannot be adequately portrayed using models with only annual or shorter response time increments. It does seem rather foolhardy to expect that a population whose age structure is being collapsed due to fishing pressure will respond in the same fashion as the unfished or lightly fished one might. The "survival insurance" of many age classes is being harvested also, from which it is obvious that any selection over time for a minimum longevity guaranteeing persistence beyond long term perturbation processes can be reversed, i.e. early maturation and shorter, slower growth may be selected for by removing individuals of above average sizes from the virgin populations. Certainly changes in growth rate and age structure need to be accounted for, while the significance of the time increment should be considered in regard to the intensity of fisheries operating on the population or in regard to the intensity and variations of seasonal and epochal anomalies affecting local hydrography, and the behavioural characteristics of the population, i.e., its distribution, aggregation and migration characteristics, among many other ecological details.
All of these variables can and do affect natural mortality in a population, leading to variations or oscillations throughout the ecosystem.

Ursin (1982) has provided an exceptionally insightful discussion of the relative stability of marine ecosystems, based primarily on North Sea studies. His studies of predation (starting with Andersen and Ursin, 1977) lead him to look for stabilizing mechanisms such as the “triangular meshes” of a food web which he describes in some detail. Ursin’s Table 2 (p.65) gives an interesting summary of Pauly’s (1979) study of Gulf of Thailand trawl survey results, which can be contrasted with other systems.

Table 1: Changes in stock sizes of commercial species in the Gulf of Thailand, (Ursin 1982 - from Pauly 1979). Two significant digits retained.

<table>
<thead>
<tr>
<th>Ecological group</th>
<th>Units of 1000 metric tonnes</th>
<th>Virgin stock</th>
<th>Exploited stock</th>
<th>Exploited Virgin stock</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Large benthos feeders</td>
<td>150</td>
<td>1.3</td>
<td>0.0087</td>
<td></td>
</tr>
<tr>
<td>2. Small demersal prey</td>
<td>830</td>
<td>21</td>
<td>0.025</td>
<td></td>
</tr>
<tr>
<td>3. Intermediate predators</td>
<td>620</td>
<td>74</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>4. Large predators</td>
<td>21</td>
<td>5.3</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>5. Pelagic fishes</td>
<td>13</td>
<td>5.7</td>
<td>0.44</td>
<td></td>
</tr>
<tr>
<td>6. Flatfish</td>
<td>3.5</td>
<td>7.6</td>
<td>2.2</td>
<td></td>
</tr>
<tr>
<td>7. Squid and crustaceans</td>
<td>30</td>
<td>90</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td>Depleted stocks (1–5)</td>
<td>1600</td>
<td>110</td>
<td>0.066</td>
<td></td>
</tr>
<tr>
<td>Replacing stocks (6–7)</td>
<td>33</td>
<td>97</td>
<td>2.9</td>
<td></td>
</tr>
</tbody>
</table>

Ursin concludes: “Obvious collapses of exploited stocks are few and limited to heavily schooling pelagic stocks, mostly or exclusively clupeoids. Most other fishes of temperate seas and of subtropical upwelling systems appear to be to a large extent ubiquitists and ‘opportunists’. Contrary to this, the demersal fisheries of the tropical Pacific interfere with an extremely old and highly specialized ecosystem. In these, large long-lived demersal feeders as well as short-lived pelagic feeders maintain large stock sizes in spite of heavy fishing. In the demersal fisheries of the Gulf of Thailand… both of these groups collapsed quickly under fishing pressure whereas large pelagic predators were reduced only to half their former stock sizes.”

From Table 1, it is obvious that populations of flatfishes, squids and crustaceans grew in the face of the decreases in the other groups. One should wonder what the usual pattern of variation might be in the Gulf of Thailand, with or without fisheries. Assuming stability is certainly questionable, but it would be nice to know just how much fishery operations perturb or contribute to natural fluctuations.

Age structure changes

Since we know already that an unexploited (by man) system will tend to comprise many older, high fecundity individuals with low-specific consumption requirements, it would appear that each species would tend to respond through long term selection to system perturbations such as changes in primary production rates, changing temperatures or even predation due to sporadically appearing nomadic predators, by promoting larger-older individual’s abundance, increasing age classes, and generally shortening smaller, immobile stages as much as possible, i.e. maximizing growth rate and efficiency. Fisheries operate in opposition to this set of characteristics.

Whereas many pelagic fish species have managed to accomplish only the latter few things, many cannot reach large size and thereby decrease their predator field. Clupeids, engraulids and numerous bathypelagic species are in this group. However, some other species have evolved not
only rapid growth, older-larger age classes, but also formidable sizes, i.e. the large sharks, the genera *Seriola*, *Scomberomorus*, *Thunnus*, *Coryphaena*, the istiophoridae and *Xiphius gladius*. These species are usually apex predators of omnivorous habit, high activity and mobility, and can be extremely ecologically inefficient (Sharp, 1983) in contrast with demersal or sedentary predators.

The opposite extreme is the situation for substrate specific populations, i.e., tropical reef fishes or tidal zone inhabitants where the populations are smaller in absolute numbers, life times are fairly short and even the size of potential predators is limited by the environment, i.e. refugia. Here the physiological and morphological adaptations for surviving the rigours of the environment are prerequisites. Variable growth or limited size, territorial behaviour, brooding or rearing of younger stages in those species with low fecundity, etc. are all demanded by “the Environment” if a species is to thrive. Yet the absolute adult population sizes are set by the number of appropriate home “sites”, or substrate occupied, because any other than those individuals “on site” and actively maintaining their tenancy will be washed away, preyed upon or otherwise kept from occupying permanently “a site”. What is interesting in this case is that exploitation of such species will open sites and tend to decrease natural mortality in the population at large, up to the point where fishing mortality is greater than the limiting “site” recruitment rate which will depend both on females “on site” as well as their abilities to produce sufficient young to fill any available sites. A reef fish assemblage may actually vary primarily in response to the very sporadic reductions of individuals in localized contexts which can also be subsequently recolonized by other, locally abundant species. This would make modelling reef fish communities very much more “fragile” than modelling either pelagic or demersal communities, due to the fact that as available substrate varies, reproduction rate varies as a function of “on site” individuals; natural mortality rate would tend to fluctuate as a function of fishery intensity and local predation intensity; and overall mortality would depend upon “open site” recolonization related to the number of species and recruiting individuals competing for the “sites”. This involves extremely complex feedback loops. It might well be more useful to assume that reef fishes of various habitats have tended to achieve similar growth and recruitment potential, and that knowledge of size-age structures and substrate area might actually give the best estimates of turnover rates, hence fishery potential in these cases.

**BUILDING THE “UNDERSTANDING MODEL”**

A numerical model is nothing else then a representation of an “understanding model” in the sense that it simulates and integrates our knowledge on the modelled processes. It will take into account the available facts and put in equation the hypotheses put forward in order to explain these facts. It will therefore be just as good or bad as our knowledge was. There is very likely a marine population to fit most conceivable models. We do not believe, however, that there is any single model to fit all fisheries, or that there is an available model for all fisheries.

The common denominators of neritic resources are difficult to identify, although some certainly exist in smaller time-space references. Our problem is that starting with any single resource upon which a fishery develops, how much and what kind of information is necessary to adequately and effectively “manage” both the distribution of fishing effort, and monitor the resource such that the effort appropriately tracks any changes in the resources’ distribution, potential, or position in its milieu, the ecosystem?

This is not a simple question and there is no simple answer. The elements need to be examined in perspective, leaving only specific examples of individual species aside so as not to clutter the discussion with anecdotal material.

There is a fairly extensive historical log of the efforts of scientists (and philosophers) to unravel the marvels of the sea, e.g., Pliny and Aristotle’s writings; the studies of Linneaus; and records of the age of exploration of the seas, culminating in Darwin’s treatise on speciation. Astute marine biologists flowered at the turn of the twentieth century. Early insights of the Norwegians were documented by Hjort in his treatise of 1913–1914, and Graham’s (1935) development of fishery
statistics and continuing efforts to understand environmental effects of feeding, growth, maturation and early life history of fish are remarkable. It seems that few of us today have progressed beyond their insights. Of course, there have been remarkable re-developments of basic concepts, and subtle mathematical expressions devised to express them, but the problem of obtaining better insights into what causes the variations and how to cope with them has not been resolved, although we may be getting closer in solving some of the intermediate questions.

Early pioneers in fishery-oceanography like Kishinouye (1923) and Uda (1927, 1952) had already formulated relations between, for example, species morphology, physiological capabilities and oceanic variations, hence zoogeographic and fishery related behaviour. The importance of system variables, currents, temperatures, oxygen, food abundance, etc., although certainly recognized, have too often been taken in gross forms, i.e., average surface temperatures for a series of months, and these values have been “regressed” or “correlated” with fishery yields or recruitment. Short series containing correlated trends have been identified for numerous data pairs. Skud (1982; this volume) has also pointed out that they actually reverse under certain conditions, usually involving a change in dominance of one species with another, and the second species often takes on the response pattern characteristics of the first species upon which the correlations were based. This speaks clearly for opportunism in the face of a system-wide change of state.

Meanwhile, it is also important to recognize early on that fish are very much part of a larger system, loosely termed an ecosystem, which they, in turn, support various components of, and from which they extract their needs. The ecosystem is constituted of intrinsic (internal) components, and extrinsic ones. Time and distance scales are very significant in interpreting changes in the fishery catches, particularly as they might reflect effects of factors extrinsic to specific fishery geographies. Fisheries do not reflect only local events, but also climate-ocean and solar system driven changes, which induce biological ones. It is important to realize that within even these eco-system constraints the basis of all present modelling of populations is the “unit stock” assumption for each resource under study. Eventually, the questions arising from observed variations must be addressed with regard to any potential non-homogeneity, or non-uniformity arising from sub-population level components. This should be the starting place for modelling resources, but usually is lost in the manner of most assumptions.

In the following sections some of the key difficulties encountered when trying to build our understanding model of exploited fish population will be discussed, starting by the basic problem of collecting information on the population/sampling problems. The concept of unit stock will be relatively extensively discussed because of its overwhelming importance in modelling. It will be followed by a discussion on the use of CPUE as a measure of abundance in schooling fishes.

The two last sections of this chapter will deal, through illustrative examples on larval survival and stock-recruitment relationships, with the problems of causality and hypotheses structuring on the one hand, and of preconception of results on the other hand, both processes leading to slower progress in understanding and therefore in realistic modelling of exploited populations.

**Sampling Problems**

**Sampling the Sea**

Since the advent of the age of exploration of the seas there have been relatively few innovations in biological sampling of the sea. We still use filtering, via towed nets, as a primary sampling tool, with some relatively recent advances made on how to capture more synoptic time-space frames from relatively controlled monitorable devices such as the Batfish (Dessurault, 1976) or Undulating Oceanographic Recorder (Aiken, 1981) for fine (meter) scale resolution; BIONESS (Sameoto et al., 1980) and the Longhurst- Hardy Plankton Recorder (Longhurst and Williams, 1976) for slightly increased scales; and the standard arrays of plankton nets for larger, more integrative scales (see Fasham, 1978 for review of net sampling scales and their resolution limitations). For studying
larger, mobile species we are still pretty well limited to fishing gear or experimental versions of these.

On the other hand, the physical oceanographers and climatologists have taken advantage of the increased technologies of the electronics industry by deploying deep sea pressure-tolerant encasements, buoy suspended or free floating (e.g. SOFAR) gear, as well as airborne or satellite-borne sensing and information transmitting technologies. This has allowed them to obtain synoptic measurements with deeper as well as broader temporal and spatial resolution of the seas. Biological sampling is still in very primitive condition in contrast, although even the satellite-scanners can yield rather important information on fronts and eddies, phytoplankton distribution patterns, etc. (Pingree, Holligan and Mardell, 1978). The fishery resources are simply irresolvable with present techniques. Such contrasts in technology must some way be diminished if fishery biology is ever to fully mature into anything beyond empiricism and anecdotal time series. The major point being that the improvements in sampling and monitoring technology have not been parallel in the various realms of ocean research.

Recent attempts to employ high frequency sonar scanning technology for monitoring the plankton and calibrate these signals with multiple sample plankton nets showed that the daytime signal variations were due to large copepods and small euphausiids, while at night the signals indicated changing small fish, squid and larger euphausiids (Greenblatt, 1982). Patchiness in these signals differed very little diurnally, but the patch contents were indeed different. The importance of collaborative sampling in contrast to total reliance on any one technique is evident. Any proxy technique will need continuous “subsampling” and calibration in order to be useful in studying resource behaviour.

Sampling of Fisheries

A major problem in approach to fishery resources compared with terrestrial populations is that fisheries can only rarely sample in an unbiased manner the populations upon which they operate. Size-age, migrational, and other stratum limitations confound the basic sampling which the fishery scientists must again subsample in order to draw inferences. Figure 3 from Caddy (1983) shows the effective differences between various fishing gears in a Caribbean reef fishing area. However, it is still necessary and possible to study and draw inferences from these catches, and their associated fishing efforts, provided each element is accounted for. From studies of size (length and weight) and age we can obtain growth estimates. From sampling length frequencies in catches we can infer age structure, i.e. relative abundance by size-age. From a time series of these we can begin estimating total mortality (Z), and estimating natural mortality (M) and fishing mortality (F).

Through various methods, some employing fishery statistics, others utilizing independent survey methods, biomass estimates are obtained, along with age structure data. Time series of these data can give estimates of numbers of individuals at different ages or sizes and then estimates of recruitment, mortalities and effective fishing mortality can be made. The availability and accessibility of these data have lead fisheries scientists to look into the yield-per-recruit (Y/R) relations and stock-recruitment (S/R) or dependency between adult biomass and subsequent recruitment.

The problems of fishery scientists do not end here, and in fact, have proven to often begin once these data are available and their analytical results are in hand. What is usual is that every parameter is found to vary such that it becomes impossible to pinpoint with reasonable accuracy just which variables are responsible for observed variations in age distribution, catch rates, or total biomass of a resource from these data.

For most fisheries, research has evolved to include fairly precise descriptions of the fishing effort itself, through log books for example, such that the distribution of effort, catches, size-age groups are recorded. This step, it appears, is very important to even cursory understanding of any variations in the catch statistics, as we will see.
Stock Concepts

The objective of the following discussion is to review the stock concept, definition, and applications in fishery management.

Various stock characterization techniques and their relative merits and weaknesses are reviewed and these are summarized in table 2 for ready reference.

Recently Booke (1981) defined the word stock for the Stock Concept International Symposium for application in fishery science. The general definition (i.e. vague) he gave was that “a stock is a species group, or population of fish that maintains and sustains itself over time in a definable area. In a more precise manner, stock can be defined, where genotype is known, as a population of fish maintaining and sustaining Castle-Hardy-Weinberg equilibrium. Where no genetic basis is available for characterizing a stock, then phenotypic definitions need to be recognized so that a population of fish would maintain these characteristics and therefore could be called a stock”.

The latter case is the one generally applied today. Booke also emphasizes the need to recognize stock genetic variability and measures of it in management, given the guardianship implication of fishery management.

Probably more familiar to the usual stock assessment community is the assignment of stock labels by convention, based on fishing gear, geography, i.e., ocean hemisphere, or simple species designations, i.e., South Atlantic albacore, Baltic herring, etc. The numerous very tenuous stock structure hypotheses for most fish species have tended toward hemispheric or large regional approaches to stock definition.

![Diagram](https://example.com/diagram.png)

Fig. 3. Species classified by availability to gear, (From Caddy 1983).
Table 2: Methods, utility and data sampling characteristics for population discrimination.

<table>
<thead>
<tr>
<th>Technique</th>
<th>Method</th>
<th>Relative unit cost</th>
<th>Data Type</th>
<th>Determination of population characteristics</th>
<th>Definitive or not in discrimination</th>
<th>Weaknesses and Strengths</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1 Protein characterization</td>
<td>a. electrophoresis</td>
<td>low</td>
<td>non-parametric</td>
<td>sample size dependent</td>
<td>yes</td>
<td>sampling difficult, genetic basis</td>
</tr>
<tr>
<td></td>
<td>b. electrofocusing</td>
<td>high</td>
<td>non-parametric</td>
<td>sample size dependent</td>
<td>yes</td>
<td>procedure slow, highest resolution</td>
</tr>
<tr>
<td></td>
<td>c. purification and functional analysis</td>
<td>very high</td>
<td>parametric</td>
<td>sample size dependent</td>
<td>can be</td>
<td>technique difficult, great sensitivity</td>
</tr>
<tr>
<td>A2 Chromosomal comparisons</td>
<td>a. karyotyping</td>
<td>low</td>
<td>subjective</td>
<td>can be useful</td>
<td>can be differences</td>
<td>requires big, genetic basis</td>
</tr>
<tr>
<td></td>
<td>b. banding studies</td>
<td>moderate</td>
<td>subjective</td>
<td>can be useful</td>
<td>yes</td>
<td>requires large chromosomes, genetic basis</td>
</tr>
<tr>
<td>A3 Mitochondrial DNA</td>
<td>a. isolation and fractionation</td>
<td>moderate</td>
<td>non-parametric</td>
<td>sample size dependent</td>
<td>can be for familial studies or differentiation by area</td>
<td>tedious procedures inherited, maternally inherited</td>
</tr>
<tr>
<td></td>
<td>b. pigmentation patterns</td>
<td>low</td>
<td>non-parametric</td>
<td>can be useful</td>
<td>can be</td>
<td>basis needs determined i.e. ontogenetic or hereditary, usually genetic basis</td>
</tr>
<tr>
<td>A4 Color patterns</td>
<td></td>
<td></td>
<td>non-parametric</td>
<td>can be useful</td>
<td>can be</td>
<td></td>
</tr>
<tr>
<td>A5 Immunology</td>
<td>a. tissue typing, i.e. blood</td>
<td>low</td>
<td>non-parametric</td>
<td>sample size dependent</td>
<td>yes</td>
<td>sensitive to ambient, genetic basis</td>
</tr>
<tr>
<td></td>
<td>b. microcomplement fixation</td>
<td>moderate</td>
<td>non-parametric</td>
<td>too sensitive</td>
<td>yes</td>
<td>very sensitive, species level tool</td>
</tr>
<tr>
<td>A6 Numerical or Metrification studies</td>
<td>a. hard part dimensions</td>
<td>low</td>
<td>parametric</td>
<td>can be useful</td>
<td>yes</td>
<td>basis needs determined samples must have common expectation, usually regionally specific, often genetic basis</td>
</tr>
<tr>
<td></td>
<td>b. morphometrics of body dimensions</td>
<td>low</td>
<td>parametric</td>
<td>can be useful</td>
<td>can be</td>
<td></td>
</tr>
<tr>
<td>A7 Growth and life history</td>
<td>a. age-growth by</td>
<td>can be high</td>
<td>parametric</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>parameters</td>
<td>1. annual ring on hard parts.</td>
<td>often useful</td>
<td>corroborative</td>
<td>subjective</td>
<td>ease of collection</td>
<td></td>
</tr>
<tr>
<td>------------</td>
<td>------------------------------</td>
<td>--------------</td>
<td>---------------</td>
<td>------------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td>2. daily growth rate</td>
<td>high</td>
<td>parametric</td>
<td>definitive</td>
<td>can be useful</td>
<td>needs calibration</td>
<td></td>
</tr>
<tr>
<td>3. tagging- recovery</td>
<td>high</td>
<td>estimation</td>
<td>not usually</td>
<td>corroborative</td>
<td>tagging changes natural patterns on short term</td>
<td></td>
</tr>
<tr>
<td>b. onset of maturity</td>
<td>low</td>
<td>parametric</td>
<td>useful</td>
<td>corroborative</td>
<td>differences can be induced by environmental changes,</td>
<td></td>
</tr>
<tr>
<td>c. fecundity</td>
<td>moderate</td>
<td>parametric</td>
<td>useful</td>
<td>corroborative</td>
<td>difficult to evaluate true number of eggs produced or hatched</td>
<td></td>
</tr>
</tbody>
</table>

| Distribution studies | a. mark and recapture | high | point A to B | can be useful | corroborative | needs substantive |
| 1. tags and markers | | | | | support data of A type |
| 2. hooks | low | point A to B | can be useful | corroborative | for assessing movements |

| Natural tags | a. parasites | moderate | non-parametric | can be useful | corroborative | can be lost or |
| b. chemical/hard parts | high | parametric | can be useful | corroborative | transferred can be transferred or source can be spuriously distributed i.e. currents |
| Meristic | c. gillrakers or | moderate | parametric | not useful in tunas | no | highly variable in |

569
<table>
<thead>
<tr>
<th>counts</th>
<th>vertebrae</th>
<th>some species due to ambient</th>
<th>some species differences.</th>
</tr>
</thead>
</table>

570
Applications of Stock Concepts and the Underlying Causality Problem

The simple panmixis hypothesis, welded together with the assumption of constant or average parameters in fishery models has led to the long-term failure of “conventional” fishery stock assessment and management procedures in many species, including tunas, and has retarded applied ecology in general. The common denominator is a logical error inherent to the assumed simple stock hypothesis.

“Use of average parameters is non-conservative during times of population stress”.

Although a mathematical average will always be obtainable from a sample, that “average” individual or condition may not exist at any specific moment. This is the essence of the problems with application of mathematical theory and the theories of population genetics, evolution, and ecology as a subset of general biological science. Also there are few environmental characteristics which can be shown to be constant, or near “average” more than two short periods every year or so.

“Evolution of individuals, species and systems are continuous, i.e. progressive.”

As a starting point in delineating “stocks” it should be obvious that the geographic location of reproduction is an important criterion, but that species may have variable geographic and temporally stratified reproduction, sustaining more complex rather than simple panmictic populations within any geographic context. These complex age-structures imply complex temporal and spatial patterns of reproduction.

The recent advances in thinking regarding marine teleost larval fish requirements (Hunter, 1980; Lasker, 1975; Sharp, 1981a, 1981b) have provided considerable basis for changing the usual premises applied to fish reproductive success. The concept of a “survival window” in time and space, arising from studies of the critical energetic requirements of larval fishes and the processes which promote them, is the key to better understanding the multiple cohorts of recruits entering most fisheries.

If we start with the basic premise that it takes nutrients to sustain marine life, and “new” nutrients to either sustain or increase biomass, then clearly one needs to examine the basis of nutrient sources and their availability to larval fishes, and their eventual conversion to biomass in various forms. These are processes determined by energy input and form, i.e. light, turbulence, terrigenic and biogenic nutrients, etc. Starting with photosynthesis, by definition driven by light, the presence of nutrients, and catalysts in the form of organisms, it provides the initial hierarchic step in a long chain of energy transfer and transformation leading up to fishable resources. The larvae must be placed into the appropriate milieu (Sharp, 1981a, 1981b). Until they transform into mobile post-larval stages they are directly influenced by local physical and density dependent requirements in regard to their food sources.

The necessary conditions are not universally or evenly distributed so that each larval group or “cohort” is the evidence for a “survival window” which generated the opportunity for their successful development. That proportion of eggs sown into the sea which will encounter the appropriate conditions, i.e. high food availability and low predator abundance, must be highly variable and likely accounts for the absence of a clear relation between adult biomass and subsequent recruitment in most fishes, but particularly in the nomadic species such as tunas and other oceanic species.

The numerous species of scombrids and their diverse distributions is a clear indication of the complexity of their habitats. The evidence from even cosmopolitan species, like yellowfin and skipjack tuna, supports a localization and differentiation hypothesis for population structures.
The relative amounts of mixing of population components in various regions very likely accounts for the differences in relative abundance and productivity among regions, and in seasonal and annual patterns of vulnerability to various forms of fishing. Many species are fished during or just prior to their reproduction aggregation. In these instances stock structure studies may be unimportant. However, many species have less well defined reproductive behaviour, and better understanding is required.

The problems of oceanic species compared with neritic species are worth considering before proceeding on to techniques for discriminating populations. For example, the major difficulty with obtaining any rigorous kind of stock identification of or labelling device for tunas is the very cryptic nature of their reproduction. For most tunas we have little or no knowledge of the relation between those individuals recruited to the various fisheries, the adults in major ocean areas and the eggs, larvae and prerecruitment juveniles.

So far in the world's tuna fisheries we have only a few examples where less than 40 cm (or 9–12 month) fish are abundant in commercial catches. The Philippine payao fisheries yield abundances of small skipjack, yellowfin tuna and occasional bigeye, as do the surface fisheries for tunas in the Gulf of Guinea and West Africa. Occasionally similar phenomena are observed in the transition zones in the eastern Pacific Ocean fisheries.

Although there is little evidence for or against localization or very small population ranges in the genus *Thunnus*, or for the Thunnini in general, it is likely that the smaller, less mobile stages are indeed more influenced by "local", i.e. metre to kilometre scale, current or water mass phenomena, whereas the 10 cm and greater stages become more and more independent of these "local" features of turbulence, eddies and advection (Sharp, 1981b).

Nakamura (1969) published his anecdotal correlations between apparent abundance, as measured primarily by longline catch and effort, and the current and/or water mass structures. Given this basis, in light of the studies of Saito (1973; 1975) Hanamoto (1975) and Suzuki and Kume (1982), as well as the improved understanding about the physiological ecology of tunas (Sharp and Dizon, 1978; Sund et al., 1981) it is moot that the physical environment hierarchically molds or forms the potential for all fisheries, particularly tuna fisheries. These processes are neither mystical nor particularly untenable, given that one does not expect to predict, sensu strictu, the presence and abundance of fishes in the ocean. The manifold solutions to environmental and ecological challenges to biological persistence are met in the sea by the behavioural and physiological plasticity within and among species.

Except for a few areas, the year to year catch variations for tropical tunas are on the order of 1 to 5 times, low to high, with smaller geographic reference areas exhibiting variations of the order of 20 x, or more (Sharp, 1981b). The relative independence of the larger tunas from local ambient conditions due to their high mobilities can be used to explain some of this variation, the rest is tied up in population structure, component mixing and density dependent schooling dynamics (Sharp, 1978; Sharp MS - What is a tuna school?). To ignore these processes is to ignore the basic tenets of biology, and evolutionary processes.

Other species, as are documented throughout this consultation undergo similar and even greater year to year abundance changes.

To expect less than continuous, slow changes in ecological systems is to be unaware of normal system variations in both ambient energy-nutrient fluxes and subsequent biological responses. These happen on both long and short time scales, affecting local and wider areas. Stock assessment in most cases is still based upon equilibrium states which are not only unlikely, but also misleading. The stock concepts have evolved around this equilibrium assumption and can hardly cope with the processes evident in today's fisheries, i.e., the numerous blooms and recolonizations by species for which we have records of previous fisheries, or the new development of fisheries in areas where these have not been observed before.
In fisheries where fleets are mobile and catch variations are minimal, there is an inherent urge to assume stability of the underlying resource, i.e. unit stock. What this can often be attributed to is that the “stability” is an artefact of “too broad” a definition of the unit stock. In fact the underlying genetic units may indeed be sequentially decimated, without signals from the catch statistics.

Given that speciation is an extreme form of population differentiation in response to environmental changes, the lesser scales of changes and characterization of these processes within a species needs to be understood before a useful stock concept can be clearly defined.

Population Variation and Characterization

The individuals of a given species are the fundamental units of biological evolutionarily significant selection. The low fecundity species such as mammals have little chance of having identity in chromosomal-gene level structures, or their expressions. This, and the effects of differing environments produces the nearly infinite array of effects and characteristics in even closely related individuals. Fishes, with superior fecundities, and facing quite extreme selection, have evolved a more near uniformity in many cases, but individuals are still usually distinguishable, if enough characteristics are examined.

The most recent survey methodologies applied to characterization of the genetics of species, which are considered to be relatively sensitive, hence definitive, are:

A. 1. Protein or enzyme characteristics  
   2. Chromosomal comparisons  
   3. Mitochondrial DNA comparisons  
   4. Colour patterns  
   5. Immunological reactions  
   6. Numerical or metrification studies

Methods 1, 3, and 5 are quite discrete and can be categorized as being useful for both differentiation and consolidation of identities. Methods 2, 4, and 6 are fraught with subjectivity and integrative, hence less definitive, except for differentiation, where they are adequate inferential tools.

Another list of inferential tools can be constructed which permit various levels of inference to be made, but which alone cannot be definitive. Unless far more data are collected or spawning populations and/or heritability are known and studied extensively, their uses are primarily for estimation, but all population structure conclusions based only on these data are tenuous.

B. 1. Growth and life history parameters  
   2. Distribution studies through mark and recapture  
   3. Natural tags  
   4. Meristic counts

Because this important domain of knowledge is often only partially available to classical fishery biologists, a short series of discussions of each kind of data is given in the Annex 1 on stock characterization.

Catch per Unit of Effort and Abundance

Effort distribution in relation to the resource distribution, availability and vulnerability needs to be carefully evaluated before fishery data are informative, i.e. interpretable. This usually implies that fishery independent sampling has been initiated (e.g. research programmes or fishery monitoring programmes). The difficulty is to know the true distribution of the resource population, and monitoring this single parameter may tell more about the status of resources than most other statistics.
The first of many sampling problems in fishery research is, therefore, to determine the distribution properties of the subject resource. The aggregations of resources in marine environment are complicated by the three dimensional, highly dynamic transport properties of the water column, seasonal distribution discontinuities and the behaviour of the size-age groups in a population. If the "recruits" to a fishery school, or the aggregate for spawning are diffuse, yet contagiously distributed, sampling inter-predations change. Of course, the vulnerability of fish, particularly schooling fishes, can vary tremendously in time and space, in response to numerous variables. Since this is the case, tremendous biases can and do result from fisheries sampling these populations. To try to portray the numerous variables in this complex of interactions it should first be recognized that there is a distinction between available resources and vulnerable resources.

The available resource comprises the whole, finite, abundance of the resource, including all recruited individuals. The space frame of the available resource is the total area or volume inhabited by the resource. Depending on the distribution and migration pattern of the subject species and the space constraints of the fisheries, we may find that only a portion of the available resource will occur within the range of the commercial fleet or gear being used. The combination of these two characteristics will define the accessibility of the resource to the given fisheries. Furthermore, only part of the individuals will be vulnerable to specific fishing gear, and will be subject to being caught, either because they are found in relatively big schools, are ready to bite, or show low mobility. For instance, most neritic fishes will be accessible to almost any type of pelagic fisheries provided they are reasonably close to the surface and within reasonable navigational distance from a fishing port, but they will only be vulnerable to purse seine fishing if they are part of a commercial size school. In the simple catch equation

\[ C = qfP \]  

q is the purveyor of this information. This coefficient can be broken into gear (man), behavioural (biological) and physical (environmental) components which yield perhaps the most dynamic aspects of this simple view (equation 1) of how fisheries operate. Whereas in the past the catchability coefficient (q) has been held "constant" in deference to the nearly measurable C and f parameters so as to determine P; in a number of cases it has become clear that this "convenient" approach can lead to erroneous interpretations (Garrod, 1964; Paloheimo and Dickie, 1964; Clark, 1974; Pope and Garrod, 1975; Francis 1977; Sharp, 1976, 1978, 1979; Clark and Mangel, 1979; Csirke, 1980; Pope, 1980) and a non-useful approach as to the evaluation of the dynamic aspects of both fisheries and schooling resource populations.

While it is fascinating to consider the variability of each of the coefficients in the simple catch equation, it is more important to consider the sources of the variation. What is measured in a typical fishery is the total catch (C) and the fishing effort (f). The total catch has errors in the 5–20% range depending on reporting, species identification, and proportion of the fish entering controlled markets and fishing effort, has all the associated uncertainties of the catch composition plus a number of other sources of errors related to changes in efficiency, technological improvements, learning changes in target species, etc., which vary widely from one fishery to another.

A list of the variables contributing to C as implied from the three variables q, f and P are given below with contributing variable properties following each parameter.

P, population size, is characterized by

1. Age structure
2. Geographic distribution by size-age
3. Differential ecological interactions by size-age
4. Differential potential for reproduction by size-age

f, the effective effort varies with:
1. Gear type (hooks/day; bait utilized; mesh size; etc.)
2. Relative efficiency (functions of saturation, effectiveness, etc., position on learning curve of gear, competition or interference of effort, etc.)
3. Distribution of effort over the resource range

\( q \), the catchability coefficient is a “fudge factor” affected by:

1. Availability (function of \( P_2 \) and \( P_3 \))
2. Vulnerability (function of biological properties and ambient properties in relation to \( f_1 \) and \( f_2 \))

The biological properties having a direct impact on CPUE as a measure of abundance are:

a) schooling or aggregating behaviour
b) willingness to “bite” bait or to “stay put” for gear effectiveness
c) seasonal density dependence of \( P_2 \)

The ambient properties affecting CPUE are:

a) sea state, visibility of cues, gear appropriateness, which affects vulnerability of fish
b) depth of limiting features, i.e. thermal, oxygen profiles, bottom topography, etc., which affects habitat size of the available resource and
c) proportion of local population drawn or concentrated into area where fishery is located, i.e. accessibility

Until most properties of these parameters are understood, we will not have enough understanding to explain the variations in catch, relative to effort or any other parameters with sufficient confidence to consider the standard management options a variable resource will offer.

The environmental dependences of variations in \( q \) are quite well evidenced in the tuna fisheries of the world. A complete description exists for surface gears, particularly purse seine operations on “school fish” (Sharp, 1978, 1979). Francis (1977) examined \( q \) variation in the eastern Pacific Ocean yellowfin purse seine fishery with respect to size recruitment period (semestral groups), geography (nearshore to offshore) for “average” annual data. His table 2 (page 241) shows that there are marked differences between “catchabilities” of tunas by size in the three areas, up to 20 times the “average” annual data. Given this “smoothing procedure” one could expect at least five times this variation in the individual area annual values, and perhaps several orders of magnitude more from monthly, inter-annual evaluations. Total catch varies on the order of percentages from year to year, local catch varies by orders of magnitude from year to year. Fishing effort varies only in quality and location. This is not unique, but an example of the variations to be expected in schooling fishes.

It appears that many of the problems inherent to the interpretation of fishery data are the result of extrapolation and integration of data beyond their limits of representation. Assumptions are necessary, but their appropriateness, rather than their convenience should be the first consideration. Clearly fishing effort on schooling species is operational only because the fish aggregate. These aggregations have finite distributions or ranges, which vary considerably among species and size age groupings within species. The units of effort are simple predator analogues, which are effective only when a school or an aggregation of schools is behaving appropriately so as to become vulnerable to the gear employed. These schools are not the basic units of the underlying population in most cases, but composites of what are described as core units (Sharp, 1978) or elementary populations (Lebedev, 1970). The study of the properties of these fundamental building blocks which must converge, merge and redistribute themselves to varying degrees is not part of the “conventional wisdom” of population dynamics, but some believe it holds the key to many important questions.

Clark and Mangel (1979) have given a preliminary description of the Michaelis-Menten, enzyme-substrate analogue models which we feel best represents the important “schooling” dynamics.
Their proposed models have definite limitations in application, due primarily to our ignorance of the
effects of 1) density dependent schooling dynamics, 2) distances over which the attractions
between aggregators and schools operate, (3) size specific behaviour of schooling fishes with
respect to same species and multispecies aggregations and 4) the distribution properties of the
size similar, core schools which are the building blocks of the underlying population fished by the
various gears. The important questions are the dynamic ones, but a fundamental basis for our
understanding of these depends more on the validity of the “core school” concept.

Fishes with some dispersion in their occurrences provide even more intriguing problems,
particularly if their habitat of life history includes a gradient in vulnerability and a substantial portion
of the resource can be considered to have a “refuge” against fishing effort, i.e., \textit{Trachurus} species
in the Eastern Boundary Currents, some flatfishes, oceanic species, etc. Other examples are
species associated with kelp beds or rock piles, where usual trawling effort is not effective or
practical. What is needed is some estimate of “recruitment” to and from the refuge. The problem is
that sampling and monitoring is far more complex than a “normal” fishery sampling programme can
provide for, hence we can lose track of substantial population elements. This phenomenon could
account for a large amount of unexplained “stability” of some resources in the face of intense
exploitation.

Fishery resources can be found in innumerable distribution patterns, from windrows (i.e.
invertebrates) to schools on through relatively uniform dispersion over a habitat. It does not matter
so much which pattern is prevalent, as long as it is known to some degree. Schooling fishes are
often aggregated in density dependent, size (length) determined groups, usually with a negative
binomial aggregate-size frequency. Fisheries select for intermediate to large schools for obvious
reasons, and this confounds interpretation of catch and effort related statistics. The distribution
frequencies of individual schools would better reflect local abundance of density than the integral
catch rate statistics, except when a resource is very disperse (i.e. not aggregated). Only careful
records of time and space related catches (e.g. via precise logbook reports) can help one interpret
such interactions.

\textbf{Causality and Hypotheses Structuring in Larval Survival}

Continuous studies have sought to close one of the most important gaps in fishery science, the
one which stands between a cohort of fertilized eggs' entry into the sea and the recruitment of the
subsequent group of fish at some later date to fisheries. The problem hinges around the
observation that some 5 to 6 orders of magnitude losses are realized during this period, and
usually estimates of year to year recruitment variation for natural, not heavily exploited fish
populations range from about 2 or 3 $\times$ to about 500 $\times$ or about 2.5 orders of magnitude (Ursin,
ecosystems suggests that even this variation is small compared to what might be expected unless
there are considerable stabilizing influences.

Rosenthal (1970), Jones (1973) and Lasker (1975; 1978) have each rediscovered the early life
history as the most sensitive period, as proposed by John Hjort in 1913–1914. The modelling
studies of Vlymen (1974; 1977), Beyer (1980) and Beyer and Laurence (1981) provoke one to
consider that spatial distribution and quality of esculent particles in nature control the first in a
sequence of hierarchic hurdles to be cleared if any larval fish is to survive to reproduction ages
(Sharp 1981a).

While theory, modelling and restructuring of research plans and activities have taken some years,
recent reports (O’Connell 1980) and research in progress (Theilacker, personal communication)
have given adequate support to this concept that to ignore it is futile. Likewise the importance of
predation cannot be in any way ignored, as clearly natural mortality is either due to direct or
secondary predation ($M = M_{p1} + M_{p2}$). The problems of monitoring directly either $M_{p1}$ or $M_{p2}$ are
formidable, and to-date are not well documented for larval fishes in nature except by inference
(Alvariño 1980). Sampling post-larval pelagic fishes is sufficiently difficult that quantitative studies
of distributions and abundances are nearly non-existent. Demersal post-larvae of some species are somewhat less difficult to sample, and Zijlstra, Dapper and Witte (1982) offer again remarkable insights into variations in growth, mortality and early life history related density dependent processes for one demersal species.

Meanwhile other researchers (Owen 1981, Mackas and Boyd, 1979; Sameoto 1981, Smith et al., 1981, and Coombs et al., this volume) are finding that the stratification and densities of organisms, larval fish food particles and larval fishes are indeed related on scales predictable from models and laboratory physiology and behaviour studies. These studies are the necessary logical feedback into the Restructuring of research programmes and continue to add fuel to the efforts of climate-ocean researchers to find linked cause-and-effect relations between climate-weather-ocean variability and subsequent larval and small juvenile fish survival (Bakun and Parrish 1981, Bakun et al., 1982, Parrish et al., this volume).

Platt and Denman (1975) have given a fair representation of the expected biomass spectrum (particle size frequency), and a good example of a “bolus” of energy passing upward through this spectrum. The point that needs considered is that the distribution of volume densities (contagion) are greatly affected by the negative binomial distribution at each and any size range, i.e. it takes several orders of magnitude more individuals of 50–200 μm phytoplankters to reach a mass equivalent of even a fish larva, but we only rarely observe via sampling naturally occurring densities of phytoplankters of this size range in sufficient relative abundance or concentration to support feeding fish larvae (e.g. 0.8 to 3.0 times the larval fish biomass per day, depending upon species, temperature, and activity of the larva).

The concept which is often neglected is that where the lower densities prevail, none of the predators in the milieu can operate in a positive energy balance. This leads one to reason that larger individuals need to be mobile in order to survive, and that the smaller predators, i.e. fish larvae, must either be situated in or very near appropriate densities or they will indeed starve, and become subject to predation (Sharp 1981b).

Simpler, single cell organisms have evolved stasis mechanisms such as encystment and dormant phases which preadapt them to nutrient poverty periods of relatively long duration. Settling out of the upper water column, into cooler waters, slows basic metabolism to some degree, but to be successful, i.e. persist and reproduce, single cell organisms or small predators must either be transported or swim upward into photic, productive waters again, or be able to somehow persist on the rain of detritus and debilitated organisms from above. Those that cannot will themselves become detritus.

Since it is also certain that nutrient and particle injection into the photic zone that is sufficient to stimulate primary productivity is neither uniformly nor stochastically distributed in regard to location, timing or amount, then it is nearly certain that the sequential processes of colonization, predation, growth and reproduction by each oviparous fish species contains a series of low frequency-of-occurrence requirements which cannot be attributed a priori probabilities or even averages. Hence stochastic, process models might only be useful to represent known distributions and occurrences. This also implies that only causal ecological modelling based on directly linked processes or localized interactions can be expected to be predictive in any realistic sense. Probabilities of interaction are therefore, only interesting on very small scales, i.e., meters/minutes (see Vlymen 1977), whereas above these scales they approach zero very rapidly. The only reprieve in this case is the increased mobility of larger predators which expands the probabilities of interactions over larger scales, i.e., km-days, between larval fishes and their more mobile predators. However, as the larvae develop, their numbers decrease and even though total biomass goes up, their tendency to aggregate also increases, decreasing a predator’s opportunity to encounter them. (Further evidence that this is a problem is the fact that the first schooling phases and their predators are poorly known for most marine fishes due to their infrequent occurrences and patchy distributions (Hewitt 1982, Smith et al., this volume). This decimation and biomass increase is an ever upward spiralling continuum which ultimately results in the various observed distribution patterns and characteristics of adult fishery resources, i.e. solitary to schooling, sedentary to highly mobile;
abundant to rare; small size to larger size; homing reproduction to opportunistic reproduction; wide distributions; or limited distributions. What is important is that the eggs be placed into sufficiently amicable environments to begin development; that upon hatching they find themselves in the “rare” high density portion of the distributions of their food; that they find themselves in a null or near null abundance of their respective predators; and that they manage to develop rapidly enough to mobile stages, perhaps even to schooling stages, so that they can begin searching for the even rarer abundance distributions of their, now somewhat larger prey.

The picture culminates in the simple realization that the distributions of all the lower trophic components are discontinuous, that these species are characteristically opportunists with high production rates, and that these species have evolved in harmony with discontinuities in the physical environment which promote their regular, i.e. serial bursts of productivity, hence persistence.

It is certain that monitoring only larval fish distributions and food particle stratification/destratification processes will not be adequate to allow complete explanations of recruitment in any “larger” system today. However, it is also certain that unless these basic measurements are included in the data proposed to monitor or explain recruitment, there can be no progress. The predator-prey research and technology for sampling post-larval and juvenile fishes up through about 5–20 cm lengths needs a lot of improvement before the complete logical bridge is made between eggs and recruits to fisheries. Methods for measuring organism size distributions in relatively large volumes of open ocean need to be developed so that eventually any major effects of harvests by man or major predation might be measured. It appears that in spite of our zealous efforts to understand the spectrum of fishery resources above “recruitment” sizes, the most biologically important and dynamic changes all occur well below this threshold, while these changes may well be influenced by climate-ocean phenomena many thousands of kilometres and months to years away.

Preconceived Results In Stock-Recruitment Relationships

Perhaps the most common difficulty in which fisheries scientists find themselves when trying to apply their knowledge to fishery data, in contexts of available tools and methodologies, is how much data can or should be “averaged” or integrated to adequately represent a resource. For example, the simple portrayal of Population Fecundity (viable egg production) in any given year and potential recruitment resulting sometime later usually takes the form of a table of figures as shown below:

<table>
<thead>
<tr>
<th>Year</th>
<th>Estimated total eggs produced</th>
<th>Resulting recruits in year (+n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$t_X$</td>
<td>$14 \times 10^{13}$</td>
<td>$8.6 \times 10^6$</td>
</tr>
<tr>
<td>$t_Y$</td>
<td>$15.5 \times 10^{13}$</td>
<td>$6.0 \times 10^6$</td>
</tr>
<tr>
<td>$t_Z$</td>
<td>$22 \times 10^{13}$</td>
<td>$10.2 \times 10^6$</td>
</tr>
<tr>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>$t_N$</td>
<td>i</td>
<td>j</td>
</tr>
</tbody>
</table>

A simple plot of $j$ against $i$ for a sequence of years is the usual end point. Some assumptions about a model/form are made and some sort of estimate of the relation between the two estimates is produced. Even less elegant is the use of biomass of adults in the place of total population fecundity, as integrated by use of the biomass figures.

Recent insights about engraulid populations and sequential or iteroparous reproduction shows that for some populations a biomass estimate cannot really be used by itself as an estimate of recruitment potential (Hunter and Goldberg 1980, Parker 1980, Hunter and Macewicz 1980, Alheit
et al., this volume). Except for a few “homing” populations with precisely determined reproduction periods, it is most that such attempts to portray potential recruitment are futile exercises.

However, another question can be answered from estimates of egg abundances in the sea. The question is what is the minimum biomass of the females producing the eggs observed? If the data are collected over sufficiently extensive time-area strata to extend beyond the range of reproduction, and if the population is somewhat conservative in its reproduction behaviour, i.e. not too large a variance in either proportions of females spawning, or eggs produced per female biomass, then a reasonable and useful estimate of spawning biomass can be made (Alheit et al.; Smith et al.; Watanabe; all this volume). It is quite a bit less complex to make these calculations for species with either direct (linear) relations between size-age and eggs produced than it is for a population with allometric fecundity and many size-age classes.

On the other hand, knowledge of only the eggs produced will not result in a reasonable “prediction” of the amount of recruits. It is the sequence of events beyond the egg's production and release into the sea which determine this, and these are not events which are uniformly or stochastically occurring (see Kawai and Isibasi, this volume).

The examples provided by Shelton and Armstrong (this volume) on both the anchovy, *Engraulis capensis* and the pilchard, *Sardinops ocellata*, from two fisheries (South Africa and Namibia /Southwest Africa) can be useful in illustrating some of the questions we are trying to address. Figures 4 and 5 show for the pilchard the annual figures for potential spawning biomass and subsequent recruitment. By connecting segmented points starting with the earliest years for which both estimates are available, we have a new insight into the recruitment story. The longest series is that for the South African fishery (1950–1982). The 1950 through 1954 points are clustered about 500–750, 000 ton spawning biomass and recruitments are estimated to have been over the range from 8 to 16 × 10⁹ individuals. Comparable recruitments occur for the years 1971, 1973, 1974, 1975, 1967 and 1968 when spawning biomasses were relatively stable at about 100, 000 tons. Of greatest interest, of course, are the years 1955 to 1962 when the recruitment and subsequent adult biomass bloomed. The surges of recruitment in 1955 to 1957 lead to the adult abundance increases in 1958, 1959 and the 1960 peak of over 1,400,000 tons. Subsequent to 1960 there was a steady decline in both adult abundance and recruitment. While in fact only 1962 recruitment falls within the range of the 1950 to 1954 levels, and from 1963 to 1966 recruitment was quite low but stable, i.e. on a par with recruitment observed since 1976.

This suggests that the system controlling recruitment went through a sequence of state changes, the earliest ones 1955 to 1957; 1958 to 1960; and 1961 to 1965 where the population size changed dramatically in response to several variables: 1) recruitment enhancement, 2) declining but large recruitment and increased abundance of older age classes due to the previous recruitment, and 3) decreased recruitment as well as senescence and fishing induced biomass declines. Since 1966 the population is small, relatively stable, and the responses of recruitment are obvious. However, the most interesting message in this series is the relatively ‘stable’ recruitment since 1962–1963. This feature implies that there are “other” limitations on recruitment beyond biomass of spawners.

The sequence of information on the Namibia - Southwest African pilchard fishery is shorter, 1970 to present, but can be contrasted to the situation described in the South African fishery. It would be better if a longer time series were available, but the catch records clearly indicate a northward shift of the abundance of pilchard in response to the massive growth of the population of South African pilchard in 1958–1959. The catches of pilchard peaked in the north in 1968, while the catches were returning to pre-bloom levels (pre-1958) in the south. Clearly the sequence (1970 to present) portrayed in Figure 4 is only part of a complex story in which the sequence preceding it must also have been analogous to that in Figure 3 with a recruitment bloom starting in about 1964–1965, ending in 1967 or 1968 and then arriving at the lower 1970 series of Figure 3.
This set of scenarios compels one to consider that the system-wide patterns of recruitment, from setting adjacent geographic bits together in temporal sequence, to be perhaps the following:

1. While fisheries were developing in both areas from 1950 to 1958, catches stabilized over a narrow, low range.
2. In the south recruitment bloomed in 1955, and resulted in increased subsequent adult biomass, inducing further fishery development.
3. Some of this biomass was displaced northward inducing development of catches in the years 1961 to 1965.
4. In about 1965 the recruitment to the north also bloomed, while in the south it had already declined steadily since 1960 to stable, usual levels in 1962–1963. The population abundance centre had shifted north, while resuming usual levels in the south.
5. The recruitment bloom of 1965 in the north lead to shifting effort and abundance hence catches, which peaked in 1968.
6. The population recruitment declined and the fishery and natural senescence induced a decline in adult abundance through 1970, at which time another short pulse of recruitment (1971–1973) once again boosted the abundance, hence catches, and subsequently both northern and southern fisheries have declined due to both low recruitment and fishery induced lowered abundance.

Fig. 4. The South African pilchard recruitment-spawning biomass data from Shelton and Armstrong (this volume) with the fitted curves removed can be quite informative if arrayed in sequence. Note that the entire fishery from 1955 to 1962, 1971, 1973–1975 and 1967–1968. Poor recruitment does not appear related to spawning biomass, although that biomass certainly reflected previous recruitment success.
Fig. 5. The Southwest Africa/Namibia pilchard data on recruitment-spawning biomass (from Shelton and Armstrong, this volume) shows a similar spiralling diminish. There is a clear indication that the population density-centre changed in the sardine fishery during the years 1960 to 1970, with recent years in both fishing areas being poor since 1975 (see Figure 4 and next).

The anchovy examples are shown in Figures 6 and 7. The South African anchovy population shows a series of bloom and recession cycles in the period from 1964 to present. A minor bloom is evidenced in 1966 to 1967, a major bloom occurred in 1973, then a series of years of relative stability are observed from 1975 to 1980. In 1982 another major bloom is indicated. All of this is in the face of increased fishery removals.

The Namibia/Southwest African population information sequence is again very short, i.e. 1972 to present, making it difficult to compare directly with the South African information. However, the recruitment has been relatively stable between about 55 and $7 \times 10^9$ individuals per year over a range of about 100 to 340,000 tons of spawners, with a trend in low years (1976, 1977 and 1979) where lower biomasses yield lower recruitment. In direct contrast with the South African situation, 1982 recruitment is estimated to be very low. Both data sets imply little relationship between adult biomass and recruitment enhancement.

Another useful data series is that from Watanabe (this volume) where he explores the relations between eggs produced in each year, and the eggs subsequently produced by the progeny of that year. Figure 8 shows this pattern for the sequence of years 1951 to 1976 for the common mackerel (Scomber japonicus) population of the northwest Pacific. Note the sequences of cyclic blooms and recessions commenced with a bloom observed in the years 1951 through 1963. The first collapse cycle begins in 1964 and by 1968 is complete. The subsequent bloom starts in 1969, from a relatively low production of $200 \times 10^{12}$ eggs, rising steeply in 1970 and 1971 from similar egg production until recruitment to the spawners ensues in 1972 through 1976. The decline in egg production, hence potential recruits begins in 1974 and continues despite high egg production through the end of the series, in 1976.

This double cycle of bloom and recession shows, once again, an independence of implied causality between eggs that generate a given year class and subsequent eggs produced by that year class and in fact shows that these are two periods with entirely unrelated abundance cycles.
which are more likely due to changes in ambient conditions and distribution than to adult abundance, per se. A feature already demonstrated to be a major cause of variability of recruitment in the Peruvian anchovy by Csirke (1980).

Fig. 8. The data on egg production in any year versus eggs produced by the progeny of those year classes (from Watanabe, this volume) shows a series of complex bloom and recession periods for *Scomber* around Japan. The importance of sequential year class survival and subsequent egg production cannot be ignored, but fitting lines through each time series (i.e. period 1) 1953 to 1964, or 2) 1969 to 1974) does not help one understand or imply any stock-recruitment relation.
Fig. 6. The South African anchovy recruitment-spawning biomass data (from Shelton and Armstrong, this volume) indicate that this resource is still in a positive state with respect to recruitment. The spurt of recruitment success in 1973 resulted in a biomass increase which was sustained up through 1980, but the lower recruitment from 1979 to 1981 tended to shift the biomass back toward earlier levels until the 1982 bloom.
Watanabe (this volume) also presents similar data for the shorter time series, 1960-1978, for *Sardinops melanosticta*. There are two short cycles again indicated with a low period of abundance from 1960 which subsequently declines to inestimably low levels until about 1970, when a new "abundance" cycle began, attaining the heights described in various reports (Tanaka; Hiyashi; and Kawai and Isibasi; all this volume). The egg production cycle began declining again in 1976, and will be an interesting feature to monitor, as suggested by Watanabe (this volume), as an indicator of future stock potential, but not predictive until the recruitment and mature stock abundance is obvious from other measures (Figure 9).
Fig. 9. Similar egg to egg production data for the Japanese sardine (from Watanabe, this volume) shows once again the futility of fitting "mean" stock-recruitment lines to such data. Clearly any implied relation severely over-estimates the likely recruitment or egg production for poor years while a time sequence plot can yield useful insights into likely trends.

The value of this approach is that clear indications of changes in system state are evidenced, lower abundance bounds are made more obvious, and declines are signalled, indicating periods when care should be taken and monitoring of other indicators such as age structure, distribution and abundance blooms of predators should be more closely monitored.

A series of abundance-increase data (which normally compares increased recruitment, increased catches, increased fishing effort, etc.) can easily generate a done shape curve with a form resembling some presumed stock-recruitment curve, a yield per recruit curve, and even a surplus production curve, all depending on what is the source of the basic data and mostly on what interpretation is being given to it. Fitting a model can therefore be purely artefactual and will normally tend to give the wrong answer to key questions such as: 1) What spawning population abundance will provide for persistent, relatively high potential reproduction? 2) What is the lower level of population which can be expected to support a substantial bloom given the appropriate conditions?

This latter question is posed only by considering these observations and concluding that the bloom cycles are stimulated by non-fishery related phenomena, and are relatively short term. The subsequent increases in distribution and overall abundance, each act to increase potential reproduction, although not necessarily determine their realization. The collapse cycles, on the other hand, do indeed reflect major components of causality in some studies (Csirke 1980;
Santander et al., this volume) and warrant further investigation of such features as cannibalism, disease and other density dependent phenomena.

CONCLUSION: WHY MODEL FISHERIES?

In the absence of clear objectives for fishery and fishery related ocean science, there have been significant changes in general attitudes about what these objectives might be. Tautological dialectics about promoting stable fishery production and maintaining species in perpetuity, etc., hardly represent all realistic objectives in the “real-world” of societal demands, growing populations, political economic decisions regarding exploitation and distribution of benefits from renewable marine resources, particularly while facing the perpetual climate-ocean variability which affects each of these.

The main biological variables surveyed here will all need to be considered as potentially strong affecters of fishery models. The simplified models which have evolved have had their utility, and certainly, their severe short comings. The problems of population definitions, basic biological units of interest, and their interactions with other ecosystem components, biotic and abiotic, need to be kept in perspective, and resolved to adequate degrees. Adequate, meaning in this case sufficiently well to be useful in forecasting or predictive models. Hindcasting or historical monitoring models can be (and usually are) less rigorous since they are not critical as bases for immediate decision making.

Even with exploitation unit concepts and resource definitions clearly in hand, modelling has yet to evolve toward a level suggesting the reality of the many changing population responses such as those discussed. Changes in: growth rate; natural mortality rates and sources; carrying capacity at all life stages; distribution and relative abundance; hence density at each stage; all affect the future status of any resource. The changes in age structure, available refugia or determinant processes leading to mortality at any life history stage severely influence any potential to resist either natural or man induced perturbations in the ecosystem.

We are not advocating modelling of the Universe, but only that if any resource is truly important that there be given due consideration to the observations that traditional or conventional fishery models have yet to prove adequate, or even appropriate in many cases. There are obvious exceptions, for example the amazingly stable North Sea plaice, upon which many leading fishery scientists have based their enthusiasm for both age structured and production models. But, … it should be kept in mind that only diligence by marine ecologists and oceanographers has kept at least one of the major nursery areas (The Wadden Sea) from joining other “industrial wastelands” and thereby insuring, at least temporarily, a future for this component of the production from the North Sea (See Wadden Sea Working Group Reports 1–11, 1982).

It is likely that specific bivariate plots of each pair of fishery-biological variables will or can hold answers to dynamic fishery questions? Even if the answer is “No” they might and have proved to serve as useful aids in evaluating the appropriateness of many conventional questions. If, no matter how precisely the information gathered, the variables do not give indications of any direct relation, then it is appropriate to declare the question inappropriate, null and void. Reformulation of the question is in order. This is progress. This is what we hoped to achieve during this Consultation.

Other questions needing answers have been discussed here and in other fora (i.e.; Caddy 1983), and two that need particular attention in regard to man's role as major predator are:

1. What are the ‘population dynamics’ of fishing fleets?
2. What are the determinants of fishery planning on the short and long term, particularly related to econometrics of fishing and dependent, subsequent operations?
If these were well known, it would appear that perhaps managers and decision makers would learn what are appropriate biological questions to ask, and we, as scientists, might be able to formulate and execute research and monitoring schemes to answer them in reasonably synoptic fashion.

Much of marine science can be said to be answering questions for which answers would be nice to know. More important in applied fishery research is that there be more attention paid to formulating answerable questions which need to be known. This is particularly true if we intend to involve other disciplines and fields of interest which have their own immediate problems.

By focussing attention on such phenomena as El Niño, it is possible that there is a misemphasis of important alternative states of the ecosystems involved. Where many are still trying to attribute the demise of the Peruvian anchoveta to the mythical El Niño of 1971–1972, the processes were already well in gear prior to this ‘event’. Glantz (1981) has addressed the societal benefits of an El Niño forecast, and inter-governmental bodies have made efforts to not only define El Niño (SCOR Working Group No. 55) but also now scientists have attempted to discover their underlying causes and predict them. Because of the immediacy of the effects droughts and floods, which are among accompanying symptoms of El Niño, are given more attention. However, the fact that El Niño is not regional, but an oceanwide process has only recently been generally recognized. As yet no one has responded at National levels to the consequences of Guillén's “Anti-El Niño's” on fisheries. Kawasaki (this volume) has provided an interesting correlation between fishery processes across the Pacific Basin which would suggest that modelling and predicting fishery responses has indeed longer term components than only today's fishing effort or today's habitat and ecological status. There is a history and a future which, although they might cycle about some median state, do not permit the broad handed “averaging” of information.

The time to begin facing these problems, reformulating questions and developing new techniques to answer them is now. There is little need for new theory. What is needed is clear headed, pragmatic science of the sort everyone talks about but too few are ready to do, for whatever reasons. The major stumbling blocks to progress usually involve persistent optimism about technological or simple, quick-fix solutions. The solutions lie in hard work at sea, in the laboratory, by innovative multidisciplinary study and gathering of long time series of information, and on a precise knowledge of what are the questions that need answering. The questions needing answers will be posed in a changing societal milieu, and will certainly become more demanding than ever before. If it is recognized that the equilibrium or averaging concepts have proven to hinder rather than help in facing the problem of variations in climate-ocean processes, and their products, fishery potential; and if it is also recognized that the fishery is just one of the many elements to be considered in modelling fisheries, then we may find this to be the age of rediscovery in fishery science.

In the meantime, as fishermen need to fish and resources need to be harvested, sources and patterns of variations should be identified and taken into consideration when interpreting the output of classical models. What is even more important is to evaluate the amount of risk involved by not taking, or not being yet able to take, important externalities into consideration. This will be carefully considered, and any obvious concerns explicitly stated. Until these uncertainties are accounted for it cannot be said that “fishery management” works. It can only be said that there is a lot to be learned before we can be sure we are even approximating adequate monitoring of the complex fishery systems we are charged with sustaining.
ANNEX 1

DISCUSSION OF METHODS OF STOCK CHARACTERIZATION

A1. Protein and enzyme characterizations are possible through a number of techniques which range from electrophoresis and histochemical staining techniques, electro-focussing to chemical purification, and thermodynamic-biochemical function studies. The latter types are extremely costly in time and materials, and are usually only effective at species, or in rare cases at sub-specific levels, for identification of sub-population distinctions. The rare cases would include species isolates with clear distinctions and no mixing.

Protein electrophoresis is the presently dominant technique for rigorous population discrimination procedure in studies of avian and terrestrial vertebrate populations with clearly distinctive barriers to interbreeding, even where some parts of life history stages are coexistent. The applications in the marine environment have been of mixed utility primarily due to misjudgement of the nature of intra-species or sub-population differences.

The statistical requirements and sampling strategies are determined by the non-parametric nature of the data due to the discrete nature of the variation, and the behaviours of the species' populations in reproduction. If a species does not "home" or obviously isolate itself at reproduction, or at some opportune moment for sampling then it is very difficult to obtain sufficient evidence to rigorously define population structures. However, far more inferential power is available in the face of even this problem than is available from category B methods, given the same problems of reproduction behaviour.

A2. Chromosomal comparisons are now classic in species such as *Drosophila* and *Chironomids* which have few, large and highly structured chromosomes. Fishes do not exhibit obvious stratifications from this perspective as their chromosomes are numerous, small, and not yet well described, except for a few species.

The techniques available for studying chromosomal variation are tedious and time consuming, and non-parametric data results, so that these are not promising in studying any but isolated reproductive groups or known spawning fish. Finding no differences cannot, however, be interpreted as being definitive in species with numerous small chromosomes due to the resolution problems described previously.

A3. Mitochondrial DNA is maternally inherited and could be quite useful in studying relations or affinities within and among schools, as hypothesized to exist within similar size fish within schools (Sharp 1978, 1981b). The technique is recent (Giles *et al.*, 1980; Avise *et al.*, 1979; and Lansman *et al.*, 1978) and is useful for relatively limited and intensive studies until better characterized. The absence of a discrete functional quality or character other than size or weight of DNA fragments makes comparisons essentially one of analogy to meristic measures, although heritability is implied. When possible this should be shown rather than assumed. It will be at least a decade before this technique will be evaluated for utility in discriminating breeding units of oceanic species.

A4. Colour pattern and pigmentation studies fall into several categories. Where pigmentation is often a developmental (sequential) process, there are often neotenic arrests, or slow downs in individuals within distinct geographic regions. Atlantic albacore exhibit these processes (Aloncle, personal comm.). Whether these are population characteristics or only developmental anomalies due to environmentally induced processes is not likely to be known until culture and laboratory breeding studies of marine fishes is well advanced. On the other hand Perrin (1975) and Evans (1975) have shown that the study of colour patterns are useful genetic tools. At present colour patterns appear to have limited potential in this area for most fish species.
A5. Immunology has receded from favour in applied studies since the late 1960’s because the results of various studies tended to imply far more complexity than was expected in and among species (Deligny, 1969; Sprague, 1967; and Sprague and Fujino, 1965).

The procedures are not difficult and they are both economical and rapid, but the interpretation of results is tedious, often complicated by the effects of ambient conditions where the immune assays are performed, i.e. temperature, light, contaminant aerosols, etc. If a better controlled environment, a special chamber or other mechanisms could be employed to remove these variables, an at-seas sampling programme could be devised to re-evaluate the utility of this tool.

As in electrophoresis, the data are non-parametric, and therefore sample sizes and sampling strategies would need to be rigorous, and these studies are therefore demanding. Breeding studies would be extremely valuable in conjunction with this approach.

A6. Numerical or metrification analyses, as defined here, are multivariate morphometric and/or growth pattern related studies, as opposed to meristic counts. Numerical techniques comprise primarily tedious multivariate data analysis of suspected related groups, contrasted among themselves in order to determine the affinities or levels of relation. Except in clear-cut divergences, close sub-specific groups are likely to be given greater or lesser affinity than closely related but even obviously different species. Numerically derived cladograms can give very opposite results from those based on clearly defined process-related studies of morphology, genetic characters, and even behavioural information (Sharp and Pirages, 1978; and Le Gall et al., 1976). However, to find clear, slightly or non-overlapped morphological properties among samples of a species with uniform expectation is a powerful inferential tool even if rarely encountered. The key is in the knowledge of when and where to look. For sub-specific groups which potentially mix, the sampling problems are formidable. For widely distributed species with simultaneous occurrences at extremes of the species habitat, sampling at these points can yield useful and stimulating sampling insights, particularly if studied concomitantly with other category A and B methods.

B1. Growth rate, respiration and developmental sequence are all population specific properties, with great overlap and graded variation within and among populations. In the nomadic species like the tunas, with their great diversity of environmental options, physiological and behavioural responses are also quite diverse; growth rate and onset of maturity studies are still developing, but there are clear dichotomies arising. The studies of Cayré (1981, 1982) on skipjack behaviour and fecundity in the eastern Atlantic indicate at least two different physiological/behavioural groups are frequently encountered where both differences in fecundity at size and school specific fecundity and ovarian state at size are observed.

The importance of population parameters in characterization of resource parameters is fundamental to evaluation of the fishery potentials of the various populations, but such observations as highlighted by Josse et al. (1981), show the great differences and confounding features of studying opportunistic species such as tunas in contrast to localized or homing species (Sharp 1981b).

B2. Mark and recapture studies are good for primarily one definitive aspect of “stock” characterization; fish can be shown to move from the point of receiving the mark to the point of recapture. Other inferences will depend heavily upon other data. Since recapture in most fisheries is dependent upon environmental characteristics and the distributions and kinds of fishing effort, unless the entire habitat is fished, the results are often severely biased, hence of limited value to population structure studies.

The application of mark and recapture experiments in defining “stock structure” depends solely upon the supportive data set accompanying the studies. It has not yet been proven for any fish that tagging alone has had a definitive role in determining stock structure, it is solely an inferential aid. Albacore crossing the North Pacific or a codfish crossing the Atlantic does not prove the single genetic stock hypothesis, or panmixia, it only suggests that some population components are
actively making transoceanic crossings. Whether there is a single, simple population or several is only proved through characterization studies based on genetic information, principally from A1, 3 and 5.

B3. Natural tags fall into two types, those obtained from the environment which are permanent and those which can be transferred and/or lost. Of the first category we have examples of chemical isotopes which arise from point sources in the environment, and incorporated by individuals either directly from solution in the water column, or by dominant food organism concentration, and assimilation, or both. The studies by Calaprice (1971) and Calaprice et al. (1971) have shown useful examples of this type of natural tag in salmonids species arising from known spawning grounds, with characteristic chemical patterns.

Of the second category there are distinctly conflicting possibilities which confound the interpretation of the results, hence diminishing the utility of the tools. Parasite- specific studies fall into this category. If a parasite is carried specifically by a host with a limited geographic range, delimiting the distribution of that parasite, then the parasite is a good marker or natural tag, comparable to those in category B2 for studying the distribution of the host species arising from the parasite's habitat.

However, if the host or the parasite can be separated (lost) or transferred (by predation of the host) by a species with a broader range, then the utility of the parasite as a definitive label, as contrasted to a "distribution" indicator, is lost too. The use of parasites to determine population structure depends heavily upon supporting information and can be corroborative, but is not alone definitive.

Chemical tags have to be evaluated in the same light as parasite information. If for any reason one suspects that the chemical tag can be lost or transferred, then its utility as a delimiting character is lost.

Natural tags in hard parts can act as records of life history processes. Oxygen isotope ratios can yield information on temperature exposure, and the changes of habitat, i.e., fresh to saline, saline to freshwater, can certainly be observed. Fishes with complex life history patterns in local regions could be studied quite usefully in this regard, while mesopelagics and most tunas, with their subsurface, thermocline centred habitats, prove more of a problem both logically and realistically.

The problem reduces to one of observations on Lagrangian water motion and water mass parcel distributions in the ocean. Rossby, of the Woods Hole Institution of Oceanography, has studied for several years the Lagrangian transport of SOFAR floats through acoustic methods across the North Atlantic from the mouth of the Mediterranean to the west across the Atlantic Ocean, throughout the Sargasso and Gulf Stream related water masses. The complexity is astounding. The upper and lower thermocline transport is relatively independent. Studies of chemical tags could be quite misleading.

B4. Meristic counts, like life history patterns and natural tags are due to local, but short-term exposures, with genetic underpinnings. The causal studies of Lindsay (1961) and Taning (1952) show extreme meristic variation. Differences are primarily dependent upon such variables as temperature exposure and development time. These are neither definitive nor inferential data without several concomitant information sets. For example, if one could use oxygen isotope ratios from chemical tag studies of hard- parts to characterize temperature epochs of early life history stages along with meristic counts, perhaps single populations spread over broad geographic ranges (latitudinal or depth) could be interpreted to comply with a simple stock concept. The important initial data would be category A studies. Without those data the meristic sampling observations could be entirely misleading and illogical bases for drawing conclusions on population structure. Gibbs and Collette (1967) show that meristics are barely useful as species identification tools for the genus *Thunnus*.  

587
For opportunistic and widely distributed species it is unlikely that any of these data sets (A or B) will, alone, be adequate. Other sets of data which can be useful are length-age frequency data and sex ratio with size. These permit an evaluation of a few behavioural parameters, as yet not given appropriate attention in population studies.

REFERENCES


Alheit, J., B. Alegre, V.H. Alarcón and B. Macewicz. (This volume). Batch fecundity and spawning frequency of various anchovy (genus: Engraulis) populations from upwelling areas and their use for spawning biomass estimates.


Cayré, P. 1982. Qu’est-ce qu’un banc de listao (Katsuwonus pelamis)? Quelques réflexions à partir des observations faites lors des campagnes de marquage. ICCAT, col.vol.of scient. papers. 17(2), doc SYMP/81/5:467–470.


Coombes, S.H., J.A. Lindley and C.A. Fosh. (This volume). Vertical distribution of larvae of mackerel (Scomber scombrus) and microplankton, with some conclusions on feeding conditions and survey methods.


590
Hiyashi, S. (This volume). Some explanation for changes in abundances of major neritic-pelagic stocks in the northwest Pacific Ocean.


Kawai, T. and K. Isibasi. (This volume). Change in the abundance and species composition of neritic pelagic fish stocks in connection with larval mortality caused by cannibalism and predatory loss by carnivorous plankton.

Kawasaki, T. (This volume). Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis of fluctuation from the viewpoint of evolutionary ecology.


Parrish, R.H. and D.L. Mallicoate. (This volume). Analysis of fishery data from the California anchovy fishery. The role of adult processes in population fluctuations.


Santander, H., J. Alheit, A.D. MacCall and A. Alamo. (This volume). Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*).


Skud, B.E. (This volume). Interactions of pelagic fishes and the relation between environmental sections and abundance.

Smith, P.E., H. Santander and J. Alheit. (This volume). Comparison of egg sample probability distributions of the anchovy (Engraulis ringens) and sardine (Sardinops sagax) off Peru and the anchovy (E. mordax) and the sardine (Sardinops caerulea) off California.


Tanaka, S. (This volume). Variation of pelagic fish stocks in waters around Japan.


Watanabe, T. (This volume). Stock assessment of common mackerel and Japanese sardine along the Pacific coast of Japan by spawning survey.


Zuta, S., I. Tsukayama and R. Villanueva. (This volume). El ambiente marino y los fluctuaciones de los principales poblaciones pelágicos de la costa peruana.