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PERSPECTIVES

Ocean Sciences in Relation to Living Resources

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The Intergovernmental Oceanographic Commission's Resolution XI-17 on Ocean Sciences in Support of Living Resources specifies that programs should be formulated in applied ocean research related to fishery problems. In this report we identify some types of needed research. We discuss the relative importance of the various life history stages to the question of resource variation regarding difficulties in sampling or studying on relevant scales. Our report stresses identification and accounting for causal climate-driven ambient variations. Some testable hypotheses relating the larval stages are given as examples of useful research. We also describe research needed on predation and species interactions. Examples of specific systems where important ecological processes need intense study are given. Upwelling areas, coral reefs, tropical and shelf demersal fisheries, and the open ocean fisheries each require different types and scales of study. The importance of data accessability and multidisciplinary research activities, beginning with dialogues between the ocean research and fishery resource scientists is paramount to successful completion of these tasks. The examples provided may stimulate further effort to identify resource research problems and programs for resolving them.

Key words: ocean science, living resources, life history cycles, fishery recruitment, predation, species interactions, fish eggs and larvae, vertical stability of the ocean, advection, convergence and divergence, upwelling systems, coral reefs, tropical demersal fisheries

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La résolution XI-17 de la Commission intergouvernementale d'océanographie concernant les sciences océaniques à l'appui des ressources vivantes spécifie qu'il faudrait formuler des programmes de recherche océanologique appliquée axés sur les problèmes de la pêche. Le présent rapport identifie quelques genres de recherches nécessaires. On traite de l'importance relative des diverses étapes du cycle évolutif dans la variation de la ressource, en ce qui a trait aux difficultés d'échantillonnage ou d'étude sur une échelle appropriée. Le rapport met l'accent sur l'identification et l'explication des variations ambiantes causales qu'entraîne

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le climat. Quelques hypothèses vérifiables établissant un rapport entre les stades larvaires sont donnés comme exemples de recherche utile. On décrit aussi la recherche nécessaire sur la prédation et l'interaction des espèces, et on donne des exemples de systèmes spécifiques nécessitant une étude intense des principaux processus écologiques. Les zones de remontée d'eau profonde, les récifs de coraux, les pêches démersales dans les tropiques et sur la plate-forme continentale, et les pêches en haute mer nécessitent des recherches de types et d'échelles différents. La facilité d'accès des données et des activités de recherche multidisciplinaire, débutant par des dialogues entre les scientifiques en recherche océanique et les scientifiques en ressources halieutiques, sont d'une extrême importance pour l'achèvement de ces tâches. Les exemples fournis peuvent stimuler des efforts supplémentaires pour identifier les problèmes de recherche sur les ressources et les programmes pour résoudre ceux-ci.

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Background to the Report

At its 11th Assembly the Intergovernmental Oceanographic Commission (IOC) passed Resolution XI-17 on Ocean Sciences in Support of Living Resources (OSLR). The purpose of this resolution was to promote development of plans for major oceanographic studies of the physical–ecological interactions of importance to fishery resource-related problems for submission to the 12th Assembly in 1982. IOC and the Food and Agriculture Organization (FAO) appointed two rapporteurs, Dr T. Austin and Dr J. A. Gulland, respectively. In consultation with the IOC Secretariat, they decided that the most useful approach was to convene a small group of individuals actively involved in research on multispecies and climate–environment physical processes applied to fisheries problems, which could provide a useful survey of present-day thinking on how to begin formulating such plans. This document, originally identified as the Report of the "Group of Four," was circulated widely throughout the oceanographic community as a stimulus for comments and a basis for thoughtful progress toward the objectives of the OSLR resolution.

The fact that both distributions and abundances of resource species are related directly to environmental properties such as temperature, food, and oxygen is of primary importance. However, few well-defined examples are available of direct causal relationships between variations in abundance and environmental processes beyond the seasonal "displacement" of the above properties or observations of nonusual events relative to some geographic base (i.e. North Atlantic cooling trend and cod occurrence).

Much of our ignorance in this regard can, I believe, be attributed to wrong-scale thinking. For example, studies of recruitment of fishes often integrate the entire early life history of these fishes into a single prerecruit class, and the relations between recruitment and subsequent production are sought from trying to match up only spawning biomass and recruits, with the residuals or deviations from any one of the numerous available stock–recruitment formulations being attributed to "environmental variations." The major proportion of the mortalities in most oviparous species occur in the prerecruit stages. The order of magnitude of the recruitment is therefore primarily dependent upon variations in about the 4th or 5th decimal place in these day-by-day, stage-by-stage probabilities of survival.

The single, most important distinction in the recently emerging approaches to these problems of recruitment is the idea that there are very important processes at scales relevant to survival of *individual* fish larvae and juveniles which must be encountered, or the larvae cannot survive. This implies that there are hierarchic hurdles to be faced resulting in variable and discontinuous mortalities rather than averages or constants.

Much of this current thinking is described for the problems of dealing with only first feeding of pelagic fish larvae in IOC Workshop Report No. 28 on the effects of environmental variation on the survival of larval fishes (1980). Increasing our knowledge of the trophic levels supporting this single stage and beyond will require intense multidisciplinary study.

The significance of environmental variability on the numerous trophic levels is the subject of many biological oceanographic studies. These often elusive intricacies of marine ecosystems are driven by solar energy which generates climatic events arising from diurnal, seasonal, and epocal processes of energy absorption, transfer, and dissipation, often months and thousands of kilometres away (i.e. El Niño) as well as daily, local events (i.e. insolation, wind, rainfall).

One major problem is our need to develop methods for measuring and monitoring directly or via proxies (i.e., upwelling or stratification indices) the directly causal processes important to the variations in survival of the numerous fishery resources. This means that appropriate scales need to be defined, that appropriate measurements be identified, and that sensors and equipment should be designed and employed to resolve these processes into useful signals.

Equally important is the training of fishery and oceanographic scientists in the principles and use of the sensors and equipment, long-term data collection, and the employment of cause-and-effect (or rational) hypothesis testing. This will certainly include experimental research in the laboratory as well as on the sea so as to provide evidence that there are true cause-and-effect linkages between the various important signals.

For example, without the fruitful, diligent research of many of the co-workers in Lasker's Laboratory, his hypothesis regarding the importance of small-scale phytoplankton stratification in the larval habitat to the survival of the California Anchovy (Lasker 1975) and other important pelagics might have remained speculative. However, the laboratory studies of Hunter (1972, 1976), Hunter and Thomas (1974), Arthur (1976, 1977), Lasker and Zweifel (1978), O'Connell (1976, 1980), O'Connell and Raymond (1970), and Methot and Kramer (1979) have provided supportive evidence for Lasker's hypothesis. They have also helped further define appropriate scales of sampling at sea and in the laboratory for improving our understanding of the conditions promoting survival of individual larval fishes in the sea.

From this same research group we have learned about rates of important egg and larval fish mortality processes due to cannibalism (Hunter and Kimbrell 1982), spawning site selection and predation (Alvariño 1980), and the significance of batch fecundity (Hunter and Goldberg 1980) to the interpretation of conventional egg and larval surveys.

In particular the California northern anchovy (*Engraulis mordax*) examples are stimulating, formative observations, employing new and classical methods yielding interactive research results from which we can begin to challenge the overintegrative "conventional wisdoms."

This extreme case of "focused" research could lead one to conclude that to investigate each important commercial species would require unlimited resources and expertize. In fact, this is not true. These examples provide numerous opportunities to test quickly or evaluate generalities of such fundamental processes as first feeding which must certainly be a common property of newly hatched fishes, onward through ecological and environmental properties which promote, or subsequently fix the limits of survival into the following stages or ecological challenges. Once a decision regarding causal processes has been reached, appropriate proxies can be identified and monitored on relevant scales.

These and many similar experiences have led to the formulation of this report.

As the experimental research activities in the world ocean become more restricted because of conflicts of interest and jurisdictional progress, it seems that both the applied and academic scientists will of necessity recognize their interdependence, even to the point of initiating required dialogues and mutual-objective research. The relative isolation which has been characteristic between marine science and fishing-related problems needs to be diminished. This has been said by so many for so long that it must be a real problem. OSLR is an opportunity for scientific collaboration, mutual dialogue and familiarization, and resolution of important worldwide problems. OSLR is both challenging and sobering. Perhaps OSLR will provide stimulus for the maturity of marine ecological research into the fruitful and valuable applied science it should become.

The Group met at FAO Headquarters, Rome, Italy (Fisheries Department), from October 14 to 17, 1980, and included the following persons: A. Bakun, J. Beyer, D. Pauly, and J. G. Pope (Chairman) as members of the 'Group of Four Scientists.' The two previously mentioned rapporteurs; G. Tomczak, IOC Secretariat; G. D. Sharp, FAO Fisheries Resource and Environment Division; H. Austin and FAO staff also took part in the discussions.

Obviously readers will recognize that so few people in so short a time could not address the problem in more general terms and still have something tangible for others to add to, or assault, as the case might be. Stimulation was the objective; problem definition and resolution is the product expected from the readers.

G. D. SHARP

The Report

Introduction

The Group decided to confine its discussions to ocean areas between 45°N and 45°S to focus attention on the fisheries problems of the developing world. This document was an attempt to identify gaps in our knowledge of important fisheries-related processes which might be closed, given the attentions of the ocean sciences, in the broadest sense. The Group saw many areas where research would be valuable. However, we noted that for this research to be useful in understanding fisheries problems, it would need to be conducted on a time-and-area scale appropriate to the fishery in question.

The Group agreed that oceanic research of all sorts was potentially valuable; however, for direct use, ocean research in support of resource science argues for close collaboration between fisheries and other ocean scientists at all stages of research.

Problems of fishery science arise from the need to answer questions posed by the fisheries management community, particularly in the face of the numerous conflicts of interests, i.e. among different methods of commercial fishing or commercial fishing vs. sport fishermen, or subsistence fishermen vs. public opinion, and, most important, restrictions imposed as conservation measures vs. exploitation interests. Some of these questions can be answered by the collection and interpretation of fisheries data (catch, effort, age structure data, etc.) but others have proved intractable on this basis. From experiences in well-studied areas such as the North Sea, California, and the waters around Japan, it is clear that problems of recruitment, availability, and species interactions cannot be solved from fisheries data alone.

Some conventional fishery-related questions generally asked and the problems posed are set out below:

Management tasks from the FAO perspective	*Empirical approaches and scientific problems*
1) For a region where fisheries are not fully exploited: identify the resource(s), describe their seasonal and long-term distribution patterns, and evaluate possible effects in neighboring fisheries.	Survey or exploratory fishing, comparison with data sets from known area, identify unconventional resources, identify efficient harvest methods.
(2) For a growing fishery: determine potential yield and its likely variability.	Identify population characteristics and population structure, estimate present abundance, investigate ecological interactions, compare natural and man-induced variations within and outside of area.
3) For both developing and developed fisheries: improve operating efficiency.	Locating fish stocks and their seasons and areas of vulnerability; investigate source of variance in vulnerability, including those that are due to environmental fluctuations; predict catches.
4) For a fully exploited fishery: set suitable constraints to achieve rational exploitation:	
a) For single species with uniform recruitment.	Estimate population parameters such as growth rate, onset of maturity, mortality rates at various stages.
b) For single species with variable recruitment.	Factors affecting recruitment, including minimum spawning biomass. Early estimation of year-classes.
c) For fisheries on several species.	Effects on one species of changing patterns of fishing on other species.

The problems relating to the first two questions are concerned with fisheries development. They are thus transitory problems which need coarse but timely advice. In many cases order of magnitude answers would be sufficient. Questions of operational efficiency and management, however, are permanent features of fisheries requiring more accurate advice which may be developed over a longer time frame. Operational questions may need to be answered to within a factor of 2 while management questions ultimately need to be understood with greater precision.

For these reasons the problems associated with questions of fisheries operations and management seem the most appropriate for the inputs of longer term scientific advice. The problems of (1) Availability (distribution, abundance, vulnerability to gears), (2) recruitment and life cycle or natural history variations, and (3) species interactions are the problems which seem most pressing in well-studied fisheries; however, this may not be the case for all systems. Therefore, the report considers questions arising from various stages of fish life cycles and also problems arising in the major ecological systems associated with the developing world. The proposed types of research at the locations suggested are in no way intended to be exhaustive. Rather they are in the nature of examples of what might be done.

Life History Cycle

Definitions of Life History Stages

The common denominator in the world major food fish resources is that oviparous fishes dominate the catches. Only a few exceptions are notable, i.e. *Sebastes* species, elasmobranchs, *Zoarces* species, etc. Therefore, in portraying a typical life cycle pattern it is appropriate to start with the egg in the water column and proceed by stages of development and characteristics of these stages toward the deposition of eggs in the subsequent generation. A simple circle diagram can be used to describe this pattern.

Stage I comprises entry of the egg into the environment (A), fertilization and subsequent prehatch larval development; hatching of the larvae (B) and subsequent development up through metamorphosis (C — loosely defined here as the time scales form or when dominant respiration switches to the gills).

Stage II includes the posttransformation developmental stages of juveniles (D) which precede entry of the fish into vulnerability to fishery operations (E). This is the least-understood stage in the life history cycle of many fish because there is no appropriate gear to sample them effectively during this stage.

Stage III includes the period from initial entry of the fish into the fishery or sampling operations (E), of juvenile to adult fishes before the onset of gamete maturation (F).

Stage IV is defined as that period from the onset of gamete differentiation and maturation (F) to the end of the reproductive period of the individual. This may be seasonal, annual, or continuing over varying time scales, depending upon the species. Also, egg maturation and subsequent spawning may happen once or several times in a lifetime, i.e. iterative within any year (Hunter and Goldberg 1981) or annual.

Life cycles determine susceptibility of the populations to short and longer term system variations, physical and/or ecological in nature. Early life history stages exhibit variations based on, for example, temperature or food conditions.

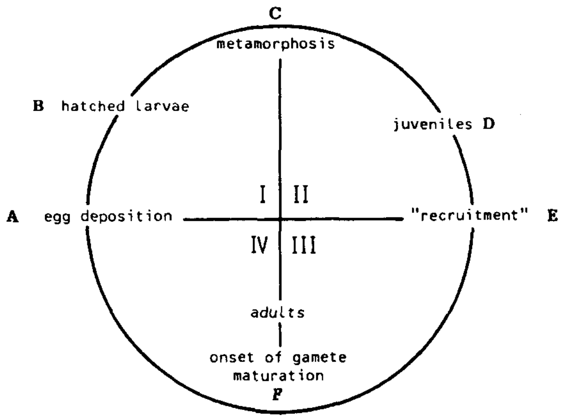

FIG. 1. A schematized life cycle of fishes.

"Ecological positions" shift continuously as fish grow, but these shifts are different, i.e. have differing rates of change, within and among species, and represent responses to system changes. Obviously death may occur at any point in the diagram.

A common starting point for oviparous species is the hatched larvae's need to encounter appropriate densities of appropriate foods to stimulate first feeding (from B on the diagram). The larvae that are *not placed* into the appropriate environment do not survive. Appropriate survival environments are 'windows' in time and space. They are probably not forecast by the adults in any direct sense in many coastal fishes. This is evidenced by their long or continuous spawning seasons. Other species having localized spawning (e.g. homing) and short reproductive seasons are tuned to relatively stable systems which are found to vary on the decade time scale as these populations also do (Iles and Sinclair 1982). More complicated reproduction behaviors are expected in the open ocean (oceanic) species because the patchiness and availabilities of species-specific "survival windows" may be on different and probably extensive time and area scales in the oceanic systems (Sharp 1981). These species must have a more definite ability to identify "appropriate larval survival habits" than the other species or there are more of these densely populated larval fish nurseries than is presently suspected.

The upper quadrants (I and II) of Fig. 1 represent stages in which survival is only rarely affected by man directly (except for pollution and habitat destruction). All stages are directly affected by environmental variations and this is the basis of several problems which could be tackled by scientific researchers.

Stage I — egg and larval survival — Extreme vulnerability and high rates of mortality characterize the egg and larval stage; this stage is considered the most critical to eventual recruitment. There are multiple interacting processes involved including feeding, growth, predation pressure, etc. at various substages. Because most of the available data are from the adult stage which is sampled by a fishery, it is a common practice to integrate the processes of Stage I, and of the juvenile stage (II) as well, by means of empirical stock–recruitment functions. Unfortunately these functions often provide poor fits to the observed data. The deviations are commonly attributed to environmental effects.

One way to view the problem is in terms of a multiple regression in which stock size (S) is included with environmental terms (E_i) as explanatory variables. For example, the formulation:

$$\log R/S = a_o + a_1 S + a_2 E_1 + a_3 E_2 + \ldots$$

is a Ricker (1975) function modified by environmental terms.

Obviously, if the dependence on S is less important than the environmental dependence, neglecting environmental terms leads to a poor estimate of the dependence on S (which is the only term that can be influenced by management). However, there is always an extremely limited number of data points available. Thus, the number of explanatory variables must be reduced to a minimum. This should be done on rational grounds, based on the best available understanding of cause–effect relationships between recruitment and environmental factors. Terms relating to multispecies interaction (for example, the size of a predator stock) might be incorporated similarly.

Such a procedure is an example of the combination of the rational (cause–effect) approach, which is based on understanding of the physical and biological processes involved, and of the empirical approach in which the functional relationships are defined by analysis (e.g. by regression) of available data. A strictly rational approach is usually not feasible. The complex linkages between environmental processes and biological consequences are extremely difficult to observe or to investigate experimentally; the quantitative information needed to construct rational models of those linkages is most often unavailable. On the other hand, the empirical approach is hampered by a lack of sufficient data points. Fishery data characteristically yield one estimate of stock size and recruitment per year; the available time series rarely exceed several decades and most often are of the order of 10–20 yr. To sort out a multitude of possible environmental effects by statistical means from a series of 10–20 data points is not possible. Moreover, the time series often contain significant autocorrelation, indicating a lack of independence of data points, which further reduces the limited degrees of freedom.

It is also important to realize that the concept of one single recruitment graph (deterministic approach) needs to be replaced by stochastic approaches that are based on probabilistic formulations of the endogeneous variables such as stock size variation, age structure variation, hence fecundity variation, etc. This is in contrast to exogenous stochasticity (i.e. forcing functions in terms of independent, random variations such as temperature patterns or turbulence-inducing events) which is useful for sensitivity analysis but otherwise usually of little value. The stochastic formulation allows for the possibility of expressing statements on recruitment in terms of probabilities.

Generally, a combination of the rational and empirical approaches allows a great amount of the limited information available to be incorporated. Often, the rational approach is used to generate hypotheses and to test and quantify those processes which can be measured or addressed experimentally. Then the empirical approach, i.e. experimental study, is used for testing, calibration, and verification. Further progress in fishery science requires advances in both approaches. A better rational, i.e. causal, understanding would allow us to predetermine the shape and properties of the function which will best describe the available data points. More data points allow a better and more detailed evaluation, revealing more aspects of functional relationships and thereby lead to increased understanding of the actual process involved.

Of course the classical rational method of hypothesis formulation and testing, leading to a mechanistic model, should be encouraged; however, it is recognized that useful application to real world problems will involve a considerable degree of integration of complicated process by means of simplified empirical transfer functions, i.e. simplified mathematical relations such as average values or linear equations.

A set of promising rational hypotheses are now available and these involve processes capable of exerting sufficient control on reproductive success such as to be discernible through the noise level of the multitude of additional processes. The following list is arranged in terms of physical processes, because both eggs and posthatch larvae are very much part of local physical processes, with the four categories containing results of recent research activity and interest and which are considered very promising avenues for further research.

(a) Vertical stability processes — Recent work (Lasker 1975; Hunter and Thomas 1974; IOC Workshop Report No. 28) has indicated a dependence of larval feeding success on fine-scale layers of food particles. These layers can be destroyed by vertical mixing (Kullenberg 1976; Owen 1981). Information on the structure, accumulation rate, nutritional suitability, and resistance to dissipation of such layers is required. The processes of sighting, approaching, attacking, and capturing appropriate prey organisms by larval fish take place on the microscale (millimetres to centimetres) and are believed to be strongly affected by turbidity and turbulence conditions. The interaction of water column stratification with turbulence generation is a key problem area. It is necessary to know how to formulate available wind data to indicate space–time windows sufficient for reproductive success (Bakun and Parrish 1981).

(b) Horizontal advection — Reproductive strategies often appear to be keyed to larval drift or passive transport mechanisms (Parrish et al. 1981). Larvae must be able to reach favorable nursery grounds. There appears to be a pattern of strong avoidance of offshore loss of reproductive products in the reproductive characteristics of stocks of coastal upwelling regions. Reproduction in areas of closed gyral circulation appears to be common. Where spawning is distributed in time and space or the larvae occur in the plankton over substantial time periods, very short-scale flow variations may tend to be integrated by the continuum of drifting larvae; thus a simple Ekman–geostrophic flow description may be adequate. Research on the use of established time series, such as sea level measurements or standard meteorological analyses, as indicators of flow variations should be encouraged. Variations in exchange of localized gyral circulations, which appear to be utilized in spawning strategies, within the larger-scale flow system should be investigated.

(c) Temperature — Rates of biological processes are controlled by temperature; extreme temperatures can be lethal. Thus temperature can usefully be used to define limits of occurrence. Anomalous temperature conditions, by changing growth or maturation rates, can cause disruptions and mismatches in time of critical life cycle events. A commonly cited example is the necessity for the production cycle of suitable food organisms to overlap with larval food requirements. In addition, temperature is a readily measured signal of important ocean processes (for example, in eastern boundary current regions, cool sea temperatures are often related to coastal upwelling and to horizontal advection from higher latitudes).

Temperature time series (depth profiled) which are characteristic of the space scale of reproduction are needed. Estimates of probable error are also required.

(d) Surface convergence or divergence — Horizontal structure (patchiness of larvae and their food organisms) is affected by convergence or divergence and associated frontal formation (Simpson and Hunter 1974; Owen 1981). Food availability and vulnerability to predation may increase in convergent fronts. Wind-driven Ekman divergence or convergence, which is controlled next to a coastal boundary by the alongshore wind stress and in the ocean interior by the wind stress curl, determine the vertical advection (upwelling or downwelling) in the upper ocean. Ekman suction and pumping can change slopes of ocean density structure and thereby alter current patterns. For example, in the California Current system the wind stress curl distributions coincide with the subpopulation structure of the major pelagic fish species (Parrish et al. 1981). This might also be the case in other areas.

Time series of ocean surface divergence processes and patterns should be developed and interpreted in a biologically relevant sense (Parrish and MacCall 1978). Error estimates are a particular requirement because a gradient of uncertain flow velocities is involved; errors are amplified in a derivative field of this sort. Horizontal mixing which would destroy spatial structure should be investigated. Linkage of frequency and intensity of frontal occurrence with large-scale surface convergence needs to be demonstrated.

The list could certainly be continued. For example, solar radiation is important to the production cycle as well as being a dominant stratification and turbulence energy source (i.e. winds). The biological interactions and their relationships with the physical variations should be studied. Any increase in rational understanding will allow better use of the very limited degrees of freedom in the available data.

Comparative studies appear a promising avenue for increases in understanding of processes that are difficult to address experimentally. For example, if there is a pattern of spawning by analogous stocks in semienclosed coastal gyres, one can reason that natural selection has operated to generate the pattern. Because natural selection implies reproductive success of preadapted individuals, it would be reasonable to assume that subsequent confinement of reproductive products within such a gyre is indicative of a significant survival factor. This provides a logical basis for development of a time series of variations in the strength of the gyre as an explanatory variable to be included in an empirical model and from which the contribution of such phenomena might be evaluated.

Explanatory index series should probably always be tailored to the scale of the reproductive process involved, although minimum scale may be dictated by data availability. Where possible they should be associated with a data source that can be continued for a reasonable period and preferably be hindcast over past periods of fishery operation. Thus experiments and new types of technology will be most profitable where they can be used to 'calibrate' an existing time–series data source. Time scales of interest will correspond to spawning frequencies, although the controlling factor may be rather short-scale events; for example, in the case of the effect of wind mixing on larval anchovy first-feeding success, a relevant series would be the interyear variability of the occurrence of space–time 'windows' during which storm events above a certain threshhold intensity are absent (Lasker 1975; IOC Workshop Report No. 28, 1981, p. 15–104).

Stage II — Juveniles — Juveniles are here defined as young fishes, from metamorphosis to those stages where they live in the same place (time and space) as the adults and become available to fishing.

Little is known about this stage even in well-studied areas because: (a) there is a lack of good gear for sampling them; (b) they do not usually occur where the adults and the larvae occur.

It is at the juvenile stage that the 'fine tuning' of the recruitment numbers occurs. During this stage the fish actively move into the area occupied by the adults, where they must learn to survive or in which they must establish a territory, e.g. as in coral reefs. As compared to the situation in the larvae, where starvation or predation might be viewed as largely nonselective, predation on juvenile fishes may have a strong 'selective' component, with mainly unfit or smaller, slower growing fishes being removed from the system.

Juvenile growth is often seasonal (Brett 1979; Ricker 1979). Fish typically spawn prior to the onset of a "growth season." Thus, ambient temperatures and anomalies have a strong effect on juvenile growth and on the resulting length of time they stay in size-related predator fields, which are themselves temperature-dependent. Density-dependent growth is often evident at this stage.

Problem-solving for this stage will also follow a pattern of rational understanding of processes including testing and calibration against empirical data similar to that described for Stage I.

Example hypotheses of particular interest are:

a) that recruitment is limited by niche availability in the case of reef fishes;

b) for demersal fisheries an important hypothesis would be that predation by adult demersal fish is a strong and varying source of juvenile mortality which modulates recruitment;

c) for upwelling systems hypotheses about predation and mortalities related to advection need to be tested.

Research requirements would therefore differ among these various systems. A common problem, however, is the general lack of suitable gear for sampling this stage of the life history and development of suitable gear would seem urgent. The study of the ecology, distribution, movements, and interspecies interactions of juvenile fish (especially of commercial species) could help in closing a gap in our understanding of fish population dynamics, especially in establishing whether there are monitorable mechanisms which contribute to the suggested 'fine tuning' of recruit numbers, of which the order of magnitude will likely have been determined during Stage I.

Data requirements need to be closely related to the timing and scales of distribution of posttransformation small fish patches. These vary from metres to kilometres and have time scales of perhaps weeks to months. General ocean circulation patterns may be useful in developing an understanding of this life history stage. Distributions are in some cases localized and the causes of this need to be explained by examining features of the physical oceanography (fronts, gyres, etc.).

Stage III — Non-reproductive adults — Stage III is defined as the non-reproducing adults, including juveniles or maturing stages which have recruited into an exploited resource.

Although fishery biology is at its best when adult fishes are discussed, there are several areas where the OSLR Programme could help gain new insights, generate new hypotheses, and provide opportunities to test them. These relate to:

a) The spatial distribution of fish, i.e.:

i) with regard to fishes currently considered more or less limited to certain characteristic marine habitats (e.g. tuna species, or age-classes within species);

ii) with regard to the general rule that bigger (often, but not necessarily older) fish of a given species tend to occur in water deeper and/or cooler than the smaller (often younger) stages.

In both cases explanations have been provided which relate the temperature and depth of occurrence and/or water mass characteristics, including particularly oxygen content.

b) The natural mortality of fish. Natural mortality comprises both species-specific endogenous properties as well as exogenous causes, and both may be linked with environmental temperatures (and anomalies), and certainly with changes in the biological milieu.

c) Growth is strongly temperature-dependent, and both the zoogeography of fishes (occurrence of various species at various places — long-time scale) and the growth parameters at a certain time of a given stock (short-time scale) can be linked to changes in ambient temperature. Temperature would thus influence such things as population structure, size at first spawning, and fecundity and quality of gametes.

The OSLR Programme, by refocussing attention on the influence of long- and short-scale oceanographic phenomena on adult fish could help explain adult distribution, abundance and vulnerability to fishing gear (availability), and many growth-related phenomena (e.g. maturation, migration).

Stage IV — Maturing and spawning adults — Stage IV in the life cycle of fishes is defined by the onset of the reproductive cycle in the adults. On a population level this cycle can be seasonal or continuous. Recent observations, on *Engraulis mordax* for example (Hunter and Goldberg 1981), confirm the continuous population spawning (or batch spawning of individuals). The "fecundity" of such species thus becomes a concept that is difficult to evaluate. This single parameter, fecundity, has often been used to calculate biomass of spawners from egg and larval survey data. It is important, therefore, to investigate more thoroughly the ability of populations to spawn continuously, and individuals repetitively.

There is little known regarding internal and external clues which initiate egg differentiation and maturation. Several effects appear to be related to temperature, among these differences in egg size and 'fecundity.' The thermal history of the juveniles and adults prior to Stage IV results in varying growth parameters and subsequently in varied fecundity, egg quality, and size. There are also apparent size−age effects on time of spawning and egg quality which are independent of temperature.

Little is known about how fish identify appropriate areas or locations for reproduction. There are several alternative strategies ranging from continuous sowing of gametes over the spawning season, to discrete, short-term spawning events (Sharp 1981).

Predation and Other Interactions Between Species

Species interaction is mainly caused by predation which here is interpreted in the most general sense, including man as the climax predator (Laevastu and Larkins 1981; Clepper 1979). Most management questions in some way relate to the concept of species interaction because it is only few stocks that, in practice, can be considered as isolated.

Our ability to predict short-term (1 yr) changes in stock composition to a large extent depends on our understanding of the mechanisms that govern predation on postrecruits. Possibilities of making probabilistic predictions of long-term (1−10 yr) changes in the stock compositions depend on our understanding of the predatory mechanisms as well as of recruitment.

Quantitative knowledge of predation mechanisms is still scarce, in particular, for the egg stage, the larval stage, and the juvenile stage. It is imperative, therefore, that as much information as possible on predation is extracted from available stomach content data. The few available stomach data sets can be used for making population level inferences in the sense that the stomachs from specimens of the same size sampled over broad areas and extended time represent predators that have been feeding in different geographic habitats. Data on the accessibility of various prey types during foraging is equally important as data on actual prey selection (stomach contents) to infer properties of the mechanisms governing food selection. Thus, stomach data sets, in particular for pelagic species, should be evaluated along with corresponding ecological data sets from the appropriate habitats. Approaches to bypass this problem are being developed based on Virtual Population Analysis or Cohort Analysis extended to account for species interaction (J. G. Pope, ICES CM 1979/H:16, ICES CM 1980/G: 19, unpublished data). There, total mortality for each entity of prey is partitioned into fishing mortality and natural predation mortality, and a 'residual' mortality (a coefficient accounting for mortalities due to causes other than predation).

Natural predation mortality is the fishery independent part of predation mortality, and is calculated by evaluation of an interlocking series of Virtual Population Analyses. This approach is necessarily based on various assumptions regarding the monthly or annual food consumption of each predator type (species, age, and size group) to reduce the number of unaccounted for variables.

Realistically, multispecies Virtual Population Analysis is a retrospective estimation of stock sizes that are in accordance with the observed stomach contents information. Evaluational classification of the relative importance of the various underlying assumptions is needed. For example, the derivation of reliable selectivity indices should probably not be done exclusively based on stomach data. This would require a prohibitive amount of stomach sampling. There is a need to combine the empirical approach with rational models of size selection (Beyer 1980). The only hypotheses presently available refer to size selection. One is the Andersen and Ursin (1977) log-normal selection model. There, it is assumed that a preferred prey size exists and that the ratio of predator size to preferred prey size remains the same throughout a predator's lifetime. This log-normal size-selection model is completely specified by two parameters — the relative measures of preferred prey size and selectivity broadness. No general hypotheses seem to be available with respect to interspecific differences in vulnerability to predation. Differences in vulnerability or desirability may be caused by differences in the external protective structures and avoidance behavior of the potential prey types.

Rational models will help in identifying data requirements and designing experiments on various scales to improve understanding of species interaction as well as help in utilizing the already available information on predation.

The complete story of predation is about why most fish die and why some of them survive. Predation is simply a sequence of perceptions, decisions, and actions of predators about their prey. This is, however, oversimplified. Apparently predators often encounter prey organisms one at a time. Their feeding strategy and success depends on several factors including their state of hunger, experience or skill level, adaptation to certain prey types, and probably many other factors apart from their size or species. Filter feeders depend on similar recognition and reaction to their prey, depending on their hunger state and other stimuli.

The degree to which it will prove necessary to distinguish between different predators — sometimes considered as identical — and to incorporate knowledge of their various feeding strategies depends on the marine ecosystem in question and the nature of the problem to be addressed. At present, however, it is not even clear what the basic differences in feeding strategies are that allow closely related species to coexist. In the first instance, there is a need for observations of individual feeding behavior. This type of process-oriented data collections must to a large extent be carried out *in situ* for juvenile and adult fish. Additional studies in tanks or enclosures of sufficient size to avoid behavioral or activity constraints may help in clarifying concepts. Other fields which clearly require more experimental studies are digestion and gastric evacuation. Basic principles of the digestive process are not yet understood and this limits understanding of the relationship between stomach contents and actual food consumption.

The possibilities of evaluating causal aspects of vulnerability to predation by comparing characteristics (e.g. condition or parasite burden) of freshly caught prey found in the stomach with live prey of the same characteristics, i.e. specimens of the same length, could prove important.

In the early life history stages experimental studies may be of considerable help in identifying feeding mechanisms, requirements, and limitations for growth and survival. These studies would be most informative if performed in simulated mini-ecosystems (or laboratory microcosms). This, among other things, requires the ability to measure and perhaps control the species, size, and spatial distribution of plankton. Nearly all experimental studies with larval fish have been carried out at food densities in great excess of what is usually found by integrative measurements taken in the sea via nets, pumps, or other techniques. Intensive studies of growth and survival of larval fish, with and without larval predators, with interpatch zooplankton densities in the order of 10 plankton per litre are needed. To be useful such studies need to be carried out so that there is enough data collected to permit alternative, statistically testable hypotheses on growth and survival to be resolved. This is not possible with current measuring techniques. Techniques are needed for precise and automatic detection and monitoring of local (centimetre to metre scale) densities and sizes of plankton (10 μm–3 mm) and fish larvae (3 mm–30 mm) without disturbing the system. The usefulness of optical or acoustic techniques for this purpose — for application both in the laboratory as well as in the field — needs further investigation.

Major Systems of Interest

Systematic ordering of the stages in the life cycles of fishes leads directly to scaling problems and to questions of appropriate research methodologies which might be used to study these different stages and scales. There are other important considerations which are also very restrictive in the sense of scaling and approach, namely biogeographic or ecosystem considerations. In the higher latitudes, which have been purposefully deleted from detailed discussions, seasonality of production is the dominant variable, with a resultant selection in evolutionary contexts for annual cycles and longevity in the dominant fish species. In the tropical and subtropical regions a full spectrum from seasonal to nearly continuous production patterns are observed. Also, much of the biomass comprises large numbers of small, short-lived, rapidly responding species (Pauly 1979), whereas the larger, longer-lived species, although present, tend to be of relatively low abundance in most systems, because of their relatively high position in trophic webs.

In an attempt to focus attention on systems likely to be important to developing countries, four basic regimes were selected as representative of characteristic habitats. Certainly there are distinct differences among the several manifestations of these types or systems, but because of overriding physical biological effects, similarities have emerged which make generalization within each type of system possible.

Upwelling Systems

The upwelling regions of the world are characterized by high productivity and massive pelagic fish stocks which exhibit extreme fluctuations. Recent research indicates that coastal upwelling can be driven both by local wind forcing and by disturbances propagating from elsewhere. On experimental time scales (fractions of a day to several weeks), propagated effects seem to contribute relatively greater variance in tropical systems than in subtropical or temperate systems. Thus the collapse of the California sardine stock has occurred in a system that appears to be predominantly locally wind-driven. Collapses of the anchoveta in the Peru Current, and the sardinella in the Guinea Current, have occurred where at least the shorter-term fluctuations are uncorrelated with local wind variations.

The upwelling system off southwest India appears to be an extreme case of noncorrespondence to local wind forcing. Here the upwelling season coincides with the southwest monsoon, when the prevailing wind tends to be directly toward the coast. Thus the offshore surface Ekman transport which would drive locally produced upwelling actually vanishes at the very season when upwelling is most evident. Possible explanations include coastal trapped wave propagation around the southern tip of India from an area of offshore-directed surface transport on the east coast. It is also possible that the Somali Current circulation, which leads to a southwest current off southwest India during the southwest monsoon, may be contributing to the observed upwelling through interactions with bottom topography (onshore-directed bottom Ekman layer, etc.). The stock of oil sardine off southwest India has been subject to extremely wide long-period variations, appearing in such large numbers during the upwelling season as to constitute the major single-species fishery resource during certain groups of years, while being virtually absent over other multiyear periods.

The particular massiveness of the fish stocks inhabiting upwelling regions suggests that upwelling is a basic mechanism in maintaining them. Most of the recently developed understanding of the dynamics of upwelling systems concerns the shorter time scales which are most readily addressed by experiments. However, the observed stock variations occur on long (seasonal and interyear) time scales. Even off Peru, the Coastal Upwelling Ecosystem Analysis (CUEA) studies suggest that the quasisteady upwelling which may underly the energetic shorter scale fluctuations may actually be locally wind-driven. Understanding longer term variations in the upwelling system could lead to insights into the interacting effects of exploitation and environment on stock variations which would yield improvements in the management and exploitation of these resources.

Coral Reefs

Coral reefs contribute significantly to the world's total fishery catch. Yet the overwhelming part of coral reef research is ecologically oriented and conducted predominantly by marine biologists, ecologists, and ethologists, with very little input going into applied questions relevant to fishery biology and resource management.

Among the more urgent questions pertaining to the exploitability and long-term productivity of coral reefs are those relating to the recruitment of young fish to the coral reef populations. In this context, emphasis should be given to the separation of reef systems which produce their own recruits from those which receive their recruits from neighboring reef systems, and to the transport mechanisms by means of which recruit transfers take place. Answers to these questions, which could help in the identification of suitable areas for underwater national parks or broodstock reserves, would be of considerable interest to countries whose reef resources need protection. An interesting question for fishery science would be an assessment of the range of influence of such reserves.

The study of the interactions between coral reef fishes could also help in elucidating the process of predation and its possible role in stabilizing and structuring reef populations. The study of fish predation in reefs would also help to answer questions pertaining to energy transfer between trophic levels and to the role of large predators in relation to a fishery.

Likely areas in which to conduct such research are the Caribbean, where previous research has laid a solid groundwork to start from, and the Great Barrier Reef, where the replication of experiments would seem easiest.

Tropical and Shelf Demersal Fisheries

Catches from tropical shelf demersal fisheries are characterized by large numbers of species. There is great difficulty in obtaining fisheries data at the species level. In some areas research surveys have provided useful time series of abundance changes by species groups and these suggest a greater stability with respect to the environment than temperate systems exhibit. This may, however, be simply an impression created by ignorance of such factors as recruitment or catch of each species, or even due to the behavior of the fishermen themselves.

The development of fisheries research in these areas will probably be dominated by surplus production models for some time in the absence of data for more analytical approaches. An approach to analytical techniques may be made by estimating growth, mortality rates, and recruitment for certain representative species. Until this is done, it may be premature to initiate major programs aimed at understanding the biology of, for example, the early stages of the life history.

More pressing scientific problems would seem to be a comparative study of the factors that effect productivity (primarily of fish) in these areas. A comparative study might, for instance, be carried out in the South China Sea area with the aim of explaining abundance or yield in terms of environmental features. Because the demersal fisheries there seem to operate in semiestuarine systems, it seems probable that runoff may be a key factor. Such a study might enable surplus production modeling applications to be generalized over this area and might also enable species successions resulting from fishing pressure to be predicted. The time scale of such an investigation might be by month and the size scale by about 50-nautical-mile lengths of coast. These scales would doubtless need to be adapted to fit with topographical details.

Results from the Gulf of Thailand, Indonesia, and elsewhere suggest that fish stocks in the area may be rather localized. Various groundfish surveys indicate different trends in abundance in different areas. If the fisheries in such areas are based on various small substocks this will have important implications for the management of these fisheries. Scientific studies of stock divisions in such areas may therefore be of value. Tagging/meristic/genetic studies would seem indicated in the first place but studies of ocean circulation processes and larval transport may be indicated to back these up. The size scale of these studies might be of the order of 100–200 nautical miles of coastline.

Certainly given the contribution of mangrove and other brackish-water systems to coastal fisheries, a tremendous research effort is required to evaluate the dynamics and dependencies in these complex ecosystems which affect subsequent production. Here again, scale will be of great importance.

Oceanic Pelagic Fisheries

The oceanic environment is perplexing in that there are many broad provinces with physical–chemical–climatic properties which can be labeled, but the occurrence of resource is patchy within these provinces. The major apparent abundances and vulnerability zones of the resources are often at interfaces of the physical–chemical provinces, including the thermocline. There are examples of unconventional resources which have recently come to our attention (e.g. Antarctic krill, mesopelagics off Oman).

There are undoubtedly others. With ever-increasing insights arising from marine exploration (for example, recent location of deep-water thermal and freshwater vents), new potentially interesting sources of productivity are being identified, and in some cases commercial species are found associated with them. Often only the knowledge of the sources of the productivity helps to dispel some of the uncertainties in fishery resource contexts.

Important questions still exist about the transfer of energy in deep ocean systems to the larger, but not particularly numerous apex predators.

Tunas and their kin (the genera *Thunnus, Euthynnus, Katsuwonus, Auxis*) are special cases requiring specific modes of study. However, considering that they are presently under investigation by large bodies with diversified interests, other open ocean resources can be identified which should perhaps receive more attention. At least three — rainbow runner (*Elagatis bipinnulata*), dolphins (*Coryphaena* spp.), and oceanic sharks — seem to be of sufficiently greater potential commercial interest than presently exhibited that they certainly warrant further attention in this context.

The deployment and monitoring of open ocean-aggregation devices for the explicit purpose of concentrating relatively diffuse, but not particularly abundant individuals or small schools of oceanic predators (including the species mentioned above) could provide both scientific insight into aggregation cues and improved utilization of these resources. In a broader context, studies of these predators' behavior and ecological properties could also help in determining their impact on pelagic and coastal ecosystems.

Suggested Studies

Two approaches to fishery/environment studies are possible — detailed studies of particular situations (e.g. anchovy in the California current), and comparative studies of similar systems (e.g. coral reefs). The latter has two aspects. There is the direct practical aspect in which a fishery scientist working in a poorly studied area can obtain some insight into how his or her questions might be answered (and possibly also some of the answers) by analogy with a better-studied area. The other is of more general scientific interest and results from examination of data from a number of similar systems (no one of which may have been studied in depth) to identify patterns and differences and thus obtain insights into how each system operates.

These approaches are all valuable, but it is important that a proper balance is maintained. In particular the Group felt that it was vital to have high quality in-depth studies of at least some representative examples of each of the main systems discussed in this report. Such studies cannot be done for all examples in each system and some selection must be made. In the context of OSLR it is fortunate that there are examples of most systems of interest to developing countries off the coast of, or close to, developed countries with high-quality expertize in the marine sciences (eastern boundary currents off California and Portugal/northwest Africa; coral reefs off northeast Australia; tropical shelves in the Gulf of Carpentaria and the Gulf of Mexico). Many of the necessary detailed studies might well be conveniently carried out in these areas. Participation by scientists from developing countries in these studies should be encouraged and facilitated, e.g. through cooperative research programs and fellowships, though this should not rule out the execution of detailed studies off developing countries where sufficient expertize can be brought to bear. At the same time assistance should be given to developing countries with respect to their own systems, especially in the compilation and analysis of data that might be used in comparative studies, and in the identification, formulation, and pursuit of relevant research topics.

Access to Data

The participants noted the instructions to the IOC Secretary (IOC Resolution XI-17 to "... develop through correspondence an inventory of information ..." on subjects of marine ecosystems.

Dissemination of data and information is not a new problem, but the multidisciplinary studies that will be required in OSLR add a new dimension to the problem. Not only must, for example, data on physical oceanography be available to fishery scientists, but they should be available in a form that the fishery scientist can readily interpret and employ by combining it with fishery data to study the effects of varying environment on fisheries. The same is true as regards the possible use of fishery data by oceanographers and others.

Many of the basic environmental data (e.g., sea surface temperatures) can be located through the World Data Center System, the IOC Marine Environmental Data Inventory (MEDI), and both national and regional oceanographic data centers; marine meteorological and climatological data can be obtained through the World Data Center System and the World Meteorological Organization (WMO).

The products of these data centers are often not in the form that a fishery scientist can conveniently use, even when the figures presented are the ones of interest. There is a need for presentation of the relevant oceanographic data in a form and on a time and area scale that are directly applicable to fisheries. It might be a later task of OSLR to identify more closely what the relevant data and the appropriate time and area scales are, as well as to identify the locations where such data would be most useful. In addition to the basic data stored in the Data Centers there are quantities (e.g. wind stress curl) that can be derived from these — and may be directly relevant fo fisheries, but which are not generally available. These need to be calculated, and an appropriate format will be required for each study program depending upon time–area scales of interest.

The problems of making fishery data available to non-fishery scientists are even more difficult. Basic fishery statistics (particularly of fishing effort and corresponding catch) are the most widely used source of data in monitoring the abundance of fish stocks. However, the interpretation of the types of data generally available is full of potential pitfalls (much of the work of fishery scientists is concerned with the suitable adjustment and interpretation of this type of data) so that they are not generally suitable for direct incorporation in data centers, to be used by the unwary without further guidance. Nevertheless, there is a large volume of fisheries data which could be most useful to environmental scientists if they were aware of them and could be guided in their use and interpretation by someone familiar with the fishery concerned. It was therefore suggested that it would be useful if a catalogue or inventory of such data could be developed (perhaps by FAO), setting out for each country and fishery for which data series exist: the nature of the fishery (major species and methods of fishing), the period over which data exist; the nature of the data (e.g. units of fishing effort used); the form in which the data are recorded (e.g. annual statistical reports, unpublished notes, files on magnetic tape); and the institution to which enquiries should be addressed.

Concluding Remarks

Regional or fishery scale multidisciplinary scientific fora for the exchange of information, formulation of projects, and coordination of activities will be of primary importance to the success of the OSLR programs. Equally important will be the individual and institutional efforts necessary to disseminate and apply existing knowledge and techniques for resolving questions relevant to living resources. These efforts need no further justification; what is needed is dialogue and action.

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