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**REPORT OF THE ICES-IOC STUDY GROUP MEETING ON MODELS  
FOR RECRUITMENT PROCESSES**

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# **1 INTRODUCTION**

## **1.1 Terms of Reference**

Council Resolution 1989/2:21 states that a Study Group on Models of Recruitment Processes will be established and convened by Dr M.P. Sissenwine, USA (later changed to Mr J.G. Pope, UK). The Study Group will meet at IOC Headquarters in Paris from 7-11 May 1990 to:

- a) formulate models of recruitment processes that can be used as a basis for future recruitment research;
- b) consider alternative objectives for recruitment research relative to short- and long-term fisheries management needs, likelihood of success, and appropriate research strategies, and report to the Inter-Committee Recruitment Group and relevant Committees.

## **1.2 Change of Convener**

Due to pressure of personal recruitment processes, Dr M.P. Sissenwine was unable to convene the Study Group and Mr J.G. Pope, therefore, took over on a caretaker basis.

## **1.3 Participants**

The following participants took part in the meeting. Annex A gives addresses.

Dr A. Bakun	USA
Dr J.E. Beyer	Denmark
Dr J. Boucher	France
Mr J. Cabanas	Spain
Dr P. Cury	Senegal
Mr A. Dommasnes	Norway
Dr M.J. Fogarty	USA
Dr M. Heath	UK
Mr T. Jakobsen	Norway
Mr C. Koutsikopoulos	France
Mr M. Lanteigne	Canada
Dr B.A. Megrey	USA
Dr R.A. Myers	Canada
Prof. T. Osborn	USA
Dr P. Pépin	Canada
Mr J.G. Pope	UK
Prof. B.J. Rothschild	USA
Mr C. Roy	Senegal
Dr R. Sánchez	Argentina
Dr J. Shepherd	UK
Mr I. Somers	Australia
Mr K. Sunnanå	Norway

## **1.4 Strategy and Tactics**

The justification given by the Inter-Committee Recruitment Group (IRG) provided a focus for the work of the Study Group. They stated:

"The indeterminant relationship between recruitment and spawning population size and environment is a critical problem that constrains management options. The IREP Steering Group, the IRG, and the Larval Fish Ecology Working Group identified conceptual problems and lack of theory as impediments to research progress".

Clearly then, the strategy of the Study Group needed to be aimed at clarifying conceptual ideas and developing theory rather than providing an up-to-date review of the field. Such objectives are often finally achieved by individuals rather than by group discussions so the tactics of the meeting were to encourage, provoke, or annoy individuals or small groups into attacking these needs. This was done firstly by group discussions of the background and problems of recruitment modelling research. These are reported in Section 2. Secondly, by splitting into smaller "think tanks" to address the problems in more detail. The reports of these groups were all very useful, particularly in the elucidation of concepts, and are reported in Section 3. Finally, individuals were encouraged to submit prototypes of models, *etc.*, that they hope to develop further, or thoughts on concepts. These are reported in Section 4. This section is the responsibility of individuals rather than a consensus view of the problem, but should provide ideas for the future and perhaps some contributions to the proposed ICES Mini-Symposium for 1991 on "Models of Recruitment Processes Relevant to the Formulation of Research Strategies".

### **1.5 Acknowledgements**

The Study Group would like to thank the IOC Secretariat for their help during the meeting in Paris and the ICES Secretariat help before and after the meeting.

### **1.6 Recruitment Report**

The 1990 Sissenwine cohort is:

a girl

## **2 RECRUITMENT MODELLING PROBLEMS**

To orientate itself to recruitment modelling problems, the Group first had an overview discussion reported in Section 2.1 and then heard presentations of various papers and programmes provided by Study Group members. These are reported in Sections 2.2 - 2.4.

The objective throughout these discussions was orientation to the Terms of Reference rather than to provide a detailed review of the subject areas. They are thus reported here as a record of discussions, not as a review.

### **2.1 Objectives and Overview of Recruitment Modelling Report Introduction**

Recruitment processes represent a dynamic interplay between population regulatory factors and environmentally-driven variability. Understanding the factors which stabilize recruitment is central to the development of effective fishery management strategies and to determining the resilience of the population to exploitation or other perturbations. An important objective of recruitment research is to extract the population signal from the noise introduced by random fluctuations in biotic and abiotic environmental variables affecting recruitment. The role of the biotic environment places the recruitment problem explicitly in the context of multispecies interactions (with the early life history stages as both predators and prey). These diverse considerations provided the framework for the deliberations of the Study Group on Recruitment Processes.

The Study Group considered several interrelated objectives of recruitment research which address these issues including: (1) prediction of annual recruitment, (2) understanding the factors that stabilize recruitment, (3) understanding the factors that cause variability in recruitment, and (4) anticipating long-term changes in

recruitment. The Group felt that the first objective addresses an important pragmatic need, but that this issue was of less general importance than the remaining three objectives. The interrelationships among these objectives are examined below.

### 2.1.1 Population regulation and environmental variability

The appropriate null model for the relationship between stock and recruitment for a closed population is a straight line through the origin representing a purely density-independent process. A population with little or no compensatory capacity will be particularly vulnerable to exploitation or other disturbances. Accordingly, it is essential that the relative importance of compensation in exploited fish populations be understood. Populations characterized by high levels of recruitment variability may also have relatively low compensatory capacity and resilience to exploitation. It is, therefore, critical that the stock-recruitment relationship of these populations be studied in detail.

The classical stock-recruitment relationships treat recruitment as a univariate function of stock size (or preferably, egg production). Clearly, environmental factors play an important role in recruitment and the full multidimensional nature of the recruitment process must be recognized. It is perhaps more appropriate to consider a family of recruitment curves representing different environmental regimes. A simple hypothetical example of a stock-recruitment-environment relationship is provided in Figure 2.1.1 (Fogarty *et al.*, 1990). Consideration of the relevant environmental factors would allow both fuller understanding of the underlying population dynamics (by permitting the environmental effects to be filtered) and greater predictive capability.

Random fluctuations in biotic and abiotic environmental variables affecting recruitment obscure the form of the stock-recruitment relationship and complicate the determination of fishery management reference points [ $F_{rep}$  (or  $F_{med}$ )]. A more insidious difficulty, however, can result from sustained trends in important environmental factors. Environmental changes can act synergistically with other perturbations such as harvesting to destabilize the population. Consider the recruitment curves depicted in Figure 2.1.2 for two environmental regimes. At low fishing mortality rates, stable equilibria exist for both the "favourable" and the "unfavourable" environmental conditions. However, for the higher fishing mortality rate, a stable equilibrium is possible only under the favourable environment; a stock collapse is predicted for the combination of high fishing mortality and unfavourable environmental conditions. These considerations assume particular importance with the prospect of global climate change.

### 2.1.2 Compensatory processes

The role of size-dependent processes in recruitment dynamics received considerable attention. Models coupling density-dependent growth with size-dependent vulnerability to predation (Shepherd and Cushing, 1980; Beyer, 1989) provide plausible compensatory mechanisms and testable hypotheses that are amenable to field and experimental studies. It was noted that the von Foerster model could provide a convenient framework for modelling and observational studies of this mechanism.

The possibility of deriving recruitment models based on first principles and estimating the parameters of the model in process-oriented studies was discussed. This approach might offer a way to eliminate the difficulties associated with attempting to interpret the relationship between empirical estimates of spawning stock size and recruitment with their attendant problems of measurement error and environmentally induced variability. It appears that field and laboratory studies could be used to examine specific mechanisms and to estimate the appropriate rate constants. This would permit a general examination of the shape of the stock-recruitment curve. It is less certain that this approach would allow a sufficiently accurate estimation of the slope of the recruitment curve at the origin to permit inference regarding the resilience of the population to exploitation. The primary elements controlling the slope at the origin are the population fecundity and the survival rate at low stock sizes; estimates of survival rates under realistic conditions could be difficult to obtain in laboratory conditions and field observations would be subject to substantial sampling error.

It was noted that the role of compensatory maturation and fecundity in the reproductive dynamics of fish populations has not been sufficiently studied. Although the scope of compensatory response based on these mechanisms would appear to be insufficient by themselves to account for the apparent capacity of some stocks to withstand high levels of exploitation, they may contribute to the overall compensatory reserve of the population in important ways. It would be desirable to devote greater attention to reproductive biology and to consider making routine measurements of fecundity and maturation to track changes in these variables as population size varies. In principle, these measurements could be made relatively inexpensively and with reasonable levels of precision.

Other compensatory mechanisms such as cannibalism were also discussed and it was noted that this factor is clearly important for some species. Direct estimates of intraspecific predation could be based on stomach content analyses and incorporated directly into recruitment models.

### **2.1.3 Spatial and temporal scales**

The Group recognized the importance of identification of the temporal and spatial scales at which biotic and abiotic environmental factors affect recruitment processes. These considerations help structure the formulation of hypotheses and the definition of types of data to be collected. Clear specification of the mechanisms involved and their spatial and temporal dimensions is necessary.

An example was provided for haddock on Rockall Bank. Recruitment to this population is episodic and it has been hypothesized that successful recruitment to this population is contingent on the establishment of a retention cell over the Bank resulting from Taylor column circulation. A full understanding of the physical conditions resulting in the establishment of this circulation pattern on the appropriate temporal and spatial scales is required to assess the probability of recruitment success for this population.

Subtle but continuously operating factors can also have dramatic effects on recruitment. For example, relatively small changes in growth and mortality rates can effect large-scale changes in recruitment levels.

### **2.1.4 Interspecific interactions**

Predation has been identified as a major source of mortality for fish eggs and larvae. If predators consume fish larvae in proportion to the abundance of the larvae, predation mortality can be stabilizing. However, if predation mortality is density-dependent, a compensatory stock-recruitment relationship can exist which can be destabilizing.

Size-dependent vulnerability to predation is well established for some species and it provides a potentially important mechanism for compensation if growth rates are density-dependent during the early life history.

In contrast to the apparent importance of predation in the recruitment processes of marine fish, much less is known about the role of interspecific competition in guilds of co-occurring species.

### **Research strategies**

Three general categories of models or approaches were defined. These provided the main focus for subsequent deliberations by the Group on Research Strategies for Recruitment Studies. The classifications were:

- Mechanistic models

Models based on specific processes such as cannibalism, density-dependent growth and predation, and linkage of physical oceanographic models with population models, *etc.*

- Practical approaches

Methods which attempt to determine the resilience of the population to exploitation with reference to a time-series of stock and recruitment estimates. These procedures (*e.g.*, determination of  $F_{rep}$ ) are generally based on the slope of the stock-recruitment curve at the origin.

- Comparative approach

This category encompasses hypothesis tests based on comparisons between systems as a way of identifying critical factors in recruitment processes.

The common theme in these approaches is a model-based strategy of hypothesis formulation and data collection. The importance of clear specification of the question to be asked and the data requirements was recognized. Aspects of these general approaches are described in greater detail in the following sections of this report.

## 2.2 Simple Models

Mr T. Jakobsen presented a paper on the use of  $F_{med}$  (Jakobsen, 1989). Using time-series of North-East Arctic cod and haddock,  $F_{med}$  was shown to be a much more robust reference point than  $F_{max}$ . Another advantage of  $F_{med}$  is that it is based on historical data on spawning stock biomass and recruitment and is concerned with a stock's ability to compensate for mortality. The paper suggests that exploitation at  $F_{low}$  might represent a strategy for a relatively quick rebuilding of the stock to a level where  $F_{med}$  can be safely applied. This strategy has, in practice, been implemented for the North-East Arctic cod.

It was agreed that  $F_{med}$  represents a relatively crude approach to the recruitment/spawning stock biomass problem and that more sophisticated methods for finding the most appropriate exploitation level are likely to be developed.

Mr J.G. Pope presented a working paper on generalization of  $F_{med}$ . He argued that having an estimate of the highest fishing mortality which would not lead to stock collapse was a vital component of fisheries management. He described the criteria that an estimate of such an upper limit of fishing mortality should have. This estimator he called  $F_{oph}$  (fishing mortality of prudent harvest) and it was felt that  $F_{med}$  might be a possible candidate. He also generalized the  $F_{med}$  concept by expressing the concept in the form:

$$\ln \left[ \frac{SSB/R \text{ at } F = 0}{SSB/R \text{ at } F_{med}} \right]$$

where SSB/R represents spawning stock biomass per recruit.

This form can be directly calculated from many ICES Working Group reports and was tentatively found to be related to the  $\ln$  (weight at first maturity). This suggests that larger fish can be more heavily exploited (*i.e.*, have their spawning stock driven lower by comparison with the calculated virgin state) than can small fish.

Dr J. Shepherd presented the results of recent work on purely stochastic mechanisms which could make populations resilient to exploitation without involving deterministic density-dependence (Shepherd and Cushing, 1990). He noted that there is abundant evidence of long-term changes in the abundance of fish populations, but the causes are not known. It is almost certain that climatic changes are responsible in part, but the role of population regulatory mechanisms is unclear. The evidence is conflicting. The ability of fish populations to sustain levels of fishing mortality several times the level of natural mortality suggests strong regulatory mechanisms. The persistence of stocks for centuries, with few extinctions or explosions, also implies some regulation, but not necessarily strong regulation. The high levels of fluctuation in recruitment



suggest weak regulation except in the earliest stages of the life history. Under weak regulation, the time taken for effective explosions or extinctions is long, maybe a century for 1,000-fold changes in abundance. There are a few historical records which imply greater stability (persistence) of stocks than this.

Analysis of stock-recruitment diagrams (the fisheries biologists' version of k-factor analysis) rarely yields clear evidence for or against regulation because of high levels of fluctuation, which cannot, therefore, be due to single-species deterministic chaos (though multi-species chaos remains a possibility). Even the exceptions to this rule (North Sea herring, Georges Bank haddock) are not wholly convincing. Conversely, it is credible that these and other long-term declines in recruitment (North-East Arctic cod, North Sea haddock) could be due to regulation, since stock sizes also fell. Regrettably, we cannot distinguish the cause and the effect.

It is indeed quite plausible that the only regulatory process operating for fish populations is a stochastic one: increased (and non-normal) variability at low stock sizes. This would give strong regulation in the mean because of the increasing excess of the mean over the median at low stock sizes, but only because of increasingly large, although increasingly infrequent, outstanding year classes. This sounds like such an accurate description of heavily fished stocks that further exploration of this mechanism seems warranted.

Dr M.J. Fogarty presented a paper on time-series analysis of recruitment series (Fogarty *et al.*, 1990). There was considerable discussion about the utility of this approach, but it was seen as having at least the virtue that it would by-pass the need for estimates of spawning stock size and hence might indicate stock-recruitment effects when these were obscured by poor estimates of spawning stock size. It might also reveal cycles in fish stocks which might point to biotic or abiotic sources of recruitment variation.

### **2.3 Towards Designing a Conceptual Model**

Dr J. Beyer presented his 1989 Dana paper on stock-recruitment models. Features of the population's stock and recruitment characteristics, as can be defined by the ability of that population to be reduced by fishing, may be indicative of that population's characteristic management strategy to prevent collapse. There emerged from the discussion emphasis of the necessity to determine the patterns of absolute variability at different levels of spawning stock size in order to provide an initial assessment of the variability in survival during the key periods.

The conceptual framework to assess the significance of different variables was to be based on simple size-dependent energy flow from "plankton" to larvae (pre-recruits) to "predators". The basic model based largely on the simple model by Beyer (1989) provides an average value of mortality relative to growth rates in relation to size. Deviations from the average relationship, as measured in the field, as functions of space and time frames appropriate to the areas could then be reduced to be related to observed predators and/or prey levels as a preliminary basis for study.

This initial aspect of model building, in order to form a family (zoo) of models, would provide a series of questions about the relative importance of the processes involved in determining cumulative survival as well as the data and sampling requirements needed to assess the proposal, both within and across species. Implicit in this model is that summing the patterns of stage-specific mortality and growth over space will provide an estimate of the stock or cohort under study.

The final note was provided by J. Beyer by expanding the simple framework of all individuals starting at a discrete and identical size to one where the cohort has a distribution of sizes. The purpose is to assess the rate of change in particle size distribution over time in a stochastic framework of vital rates. This approach can be applied to the ecosystem as a whole or to smaller portions.

Note: The focus and methods (*e.g.*, distribution of birth dates *versus* production) of the field experiment designed to test the model(s) were outlined as a series of "micro-questions" through presentation of a draft working document of the Recruitment Processes Working Group. Specific questions were to be rephrased in terms of the characteristics for the design of the basic framework (*i.e.*, variables or factors to be included).

(These questions were considered in detail and are reported on in Section 3.4 and Annex C.)

## 2.4 Inter-Regional Comparative Approaches

Mr I. Somers spoke on aspects of recruitment research in tropical Australia and, in particular, on the banana and tiger prawn species in the Gulf of Carpentaria. The Australian approach has been to monitor as many of the life history stages as possible, looking for factors that affect the links between them. For banana prawns, differential seasonal advection of larvae has explained matches/mismatches in the spawning pattern and immigration to estuarine nursery grounds in the south-eastern Gulf of Carpentaria; rainfall was found to influence the immigration from the nursery grounds to the offshore fishery and further provided the basis for a predictive model of annual recruitment (Rothlisberg *et al.*, 1983, Vanc *et al.*, 1985, Staples, 1985).

In contrast with banana prawns, tiger prawn recruitment appeared to be most influenced by fishing pressure and, until such time that alternative processes could be demonstrated, the fishery administrators have assumed a fitted stock-recruitment relationship (Somers, 1990).

In order to shorten the time frames necessary to study these processes, a Penaeid Recruitment Project (PREP) has been set up throughout the Indo-West Pacific region as a collaborative study under the auspices of IOC/FAO (Staples and Rothlisberg, 1989). It is hoped that this will provide comparisons of recruitment of different life history stages currently, but under very different environmental conditions at the various study sites throughout the region.

Mr C. Roy described a recent analysis of recruitment success, reproductive strategy, and the environment in upwelling areas. The links between recruitment variability, reproductive strategies, and the environment in upwelling areas are investigated. The "Optimal Environment Window" hypothesis for recruitment success is first presented (Cury and Roy, 1989); later results showing the adaptability of clupeoid reproductive strategies to the environment in West Africa are summarized (Roy *et al.*, 1989).

The "Optimal Environment Window" hypothesis suggests a dome-shaped relationship between recruitment success and upwelling intensity to explain small pelagic fish recruitment variability. Two limiting factors are identified: food production and wind mixing. Weak to moderate upwellings have a positive effect on recruitment because larval food availability increases. Strong upwellings have a negative effect because high wind creates strong turbulences that have a negative effect on larval survival. An optimal environmental window exists for moderate upwelling intensity because the effects of the two limiting factors are minimized. The validity of this hypothesis is confirmed by analyzing data from three of the main upwelling areas: Peru, California, and West Africa. In each of these areas, recruitment increases with upwelling intensity until wind speed reaches a value around 5-6 m/s and decreases for higher wind speed values.

The reproductive strategies of West African clupeoids are examined. It is shown that they are long-term adapted to the seasonal environmental signals. In areas like Morocco, where wind speed is greater than 6 m/s during the upwelling season, fish reproduce outside the upwelling season. In areas like Senegal, where wind speed is lower or equal to 6 m/s during the upwelling season, fish reproduce during or at the end of the upwelling season. These results suggest that clupeoid reproductive strategies in West Africa have adapted to reach the optimal environmental window to maximize recruitment success.

Dr A. Bakun described the structure and development of the IOC/FAO Programme of Ocean Science in Relation to Living Resources (OSLR). It is under the auspices of the OSLR Programme that IOC is co-sponsoring this Study Group meeting.

OSLR was initiated for the purpose of bringing the expertise of the international multi-disciplinary ocean science community to bear on living resource issues. Recruitment was identified as a key issue, and an International Recruitment Programme (IREP) was adopted as the primary initial focus. Scientists from ICES Member Countries have had key roles in IREP project development; formal collaboration with ICES on recruitment issues has been continually sought.

The present structure (Anon., 1990) of the OSLR Programme is indicated in Figure 2.4.1.

Dr B. Megrey reported on the Summary and Recommendation from the Fisheries Oceanography Coordinated Investigations (FOCI) Recruitment Modelling Workshop and described the FOCI recruitment project.

The FOCI programme involves a large number of biologists, physical oceanographers, and meteorologists working on trying to understand the processes that affect recruitment variation in walleye pollock in the Gulf of Alaska. FOCI areas of research are comprised of nested space/time scales incorporating time-series and detailed studies of biological (larval and transport) processes. Some of the biological studies currently being conducted include larval patch dynamics, intra- and inter-annual variation in egg, larval, and juvenile distributions, interannual variation in adult maturity and fecundity, invertebrate and cannibalistic predation, larval feeding and nutritional studies, and analysis of larval otolith structures.

The FOCI programme invited recruitment modelling experts from around the United States and Canada to the FOCI Recruitment Modelling Workshop to share their experiences and to discuss the collective state of recruitment modelling. The goal was to investigate methods for combining physical and biological data into integrated models, identification of forcing mechanisms, and model design. Ten papers presented (see Appendix I in the FOCI Recruitment Modelling Workshop report) emphasized inter-regional comparisons of active recruitment research programs.

Three main modelling approaches (single-species life history models, holistic ecosystem models, and correlative recruitment/physical process models) were evaluated in terms of their ability to address recruitment research problems.

Correlative recruitment/physical process models suffer from many problems, but still have potential to identify environmental factors that are likely to affect yield potentials. These empirical/statistical approaches also hold strong potential to refine and validate process studies.

Life history modelling offers the strongest potential to understand processes that control recruitment and affect variability. The individual biological modelling (IBM) approach offers a flexible framework for looking at the stochastic nature of biological processes and a direct way to deal with the fact that recruitment modelling is a multivariable exercise.

Ecosystem approaches force us to consider important linkages in food web components, but data requirements are daunting, defining the boundaries of the system is difficult, and communicating a complex model to resource managers and lay persons is difficult. The Workshop concluded that ecosystem approaches were not viable at the present time.

Prof. B. Rothschild reported on GLOBEC and the CCC project.

GLOBEC is a major initiative in the USA NSF science plan. GLOBEC is intended to increase our understanding of the interaction between ocean physics and the population dynamics of marine organisms. An intended component of GLOBEC is studying the interaction between cod populations of the North Atlantic and climate-related variables. The program is called Cod and Climate Change (CCC). The CCC strategy is to study the linkage between basin-scale and regional-scale physical oceanography models for the White Sea, Baltic, Arcto-Norwegian, Greenland/Iceland, Canadian Atlantic, and Georges Bank regions. The regional models are intended to resolve the spatial and temporal advective fields, frontal regions, and the distribution of turbulence as well as any details that might eventually be determined to be biologically



important. At the same time, first principle models on biological and physical interactions will be developed to account for the physical effects on the growth and mortality of cod. The coupling of the biological/physical models and the physical models is intended to provide a basis for the syntheses of existing information and the collection of new information on the interaction between climate change and the dynamics of cod and other species.

Dr R. Sánchez described a recruitment project in the Southwest Atlantic Ocean.

In 1989, a SARP (Sardine/Anchovy Recruitment Project, IOC/FAO) programme was started in the Southwest Atlantic. At present, the programme involves a large number of scientists working for several laboratories and universities in Argentina, Brazil, Germany, Sweden, Uruguay, and the USA. The main objective is to elucidate processes which are relevant to the understanding of recruitment variability as the basis of a comparative approach.

Field research was started in November 1989 with a cruise aboard the German RV METEOR. During October and November, anchovy spawning takes place off Brazil, Uruguay, and Argentina. Within this wide latitudinal range (24°5'-47°5'S), three particular ecosystems (an upwelling area, an estuary, and a tidal mixing front) were chosen for intensive sampling.

As a starting point it is intended to determine the existence of significant differences between the cumulative mortality (*i.e.*, the ratio of mortality rates/growth rates integrated over two periods of time) between and within ecosystems. As a second step, we shall try to elucidate the causal mechanisms linking growth and mortality to biotic and abiotic factors. Their final stage would imply the formulation of a model relating cumulative mortality during the early development stages to environmental conditions. The set of data obtained include real-time satellite images of temperature fields, salinity, temperature, and current vertical profiles, light penetration, the vertical distribution of phytoplankton, micro-, and macro-zooplankton, and the vertical distribution of anchovy eggs, larvae, and juveniles.

Studies which are at present being carried out include such topics as the coincidence in space and time of anchovy larvae and their potential predators, food items, and size ranges; the interpretation of the influence of physical parameters on vertical migration, transport, and retention; and the analysis of larval age structure, feeding incidence, nutritional condition, and growth rates in each ecosystem.

### **3 GROUP DISCUSSIONS OF ASPECTS OF RECRUITMENT MODELLING**

#### **3.1 Introduction**

The Study Group split into "think tanks" to discuss various aspects of recruitment modelling. The objective of this was to identify problems and approaches to recruitment modelling. The reports of these "think tanks" are important in themselves, but they were also intended to stimulate individual initiatives in Section 4. The groups that met were concerned with:

- 1) simple models;
- 2) box models;
- 3) endogenous models;
- 4) environmental Process models.

### 3.2 Simple Methods for Modelling Recruitment

It is generally recognized that recruitment is a function of many things. One way of expressing this is to assume that recruitment is a function of spawning stock biomass (S) conditional to a number of environmental factors (En) plus a random error term (e):

$$R = f(S | E, E_2, \dots, E_n, \epsilon)$$

The environmental factors may be biotic (*e.g.*, prey, predator, *etc.*) or abiotic (*e.g.*, physical environment). The spawning stock biomass itself is a function of previous recruitment and fishing mortality and is a substitute for the number of eggs spawned.

The simple methods try to reduce this to a dependence on one factor only (though this factor may be complex). There are three types of simple models. These are:

- 1)  $R_i = f(S_i)$  (recruitment is a function of spawning stock size).
  - a) Compensatory models (Ricker, Beverton and Holt).  
Basis for "minimum SSB" management.
  - b) Non-compensatory model (proportionality).  
Basis for the  $F_{med}$  concepts.
- 2)  $R_i = f(R_{j < i})$  (recruitment is a function of previous recruitment).  
Time-series models (auto correlation).
- 3)  $R_i = f(E_i)$  (recruitment is a function of the environment).

The model assumes that recruitment is independent of stock size and therefore on fishing mortality. The model will not be valid for very low levels of spawning stock biomass.

Type 1 represents the most conservative approach for management considerations and should be the null-hypothesis in that context until it can be rejected on the basis of new evidence.

The three types may be characterized by the following limitations and advantages:

Limitations:

- a) Require a large data set (20 data points or more).
- b) Do not in themselves indicate causal relationships.
- c) Vulnerable to sustained environmental changes.
- d) Emphasis on short-term rather than long-term predictions (type 2, 3).
- e) No information on how hard the stocks can be fished (type 2, 3).

Advantages:

- a) May give clues to other processes.
- b) Provide a means of estimating the level of fishing mortality that can be sustained (type 1).
- c) Provide a way of extracting the full information from the data (type 2).
- d) May be useful for short-term predictions (type 2, 3).

These simple models represent attempts to model recruitment without necessarily explaining causal relationships. Although they are, in the absence of more advanced models, necessary tools in management considerations, there is a need to advance beyond this stage, both to improve management advice and to learn more about causal relationships in the recruitment process.

The Study Group focused on the following areas of research and modelling which may help to advance simple models.

- 1) Improve/extend time-series of stock, recruitment, and environmental factors.

It should be noted that valuable information may be contained in existing, but neglected, historic data that are not very precise. Concerning environmental factors, it may be necessary to explore what types of data are available, which ones are likely to be relevant, and how they should be processed to be most useful in modelling. An ICES Theme Session designed to draw out such data might be useful.

- 2) Review stocks where S/R relationships have been demonstrated.

Information about what types of S/R relationships exist may be useful, *e.g.*, in putting constraints on models.

- 3) Compare stocks in the same (or same type of) environment.

The type of environment may affect the recruitment process in a similar way for different species.

- 4) Compare stocks of the same (or related) species in different areas.

The recruitment of a species must have certain characteristics which should be identified.

- 5) Develop models defining critical levels of SSB and fishing mortality.

The underlying assumption is that there is a level of SSB below which compensatory mechanisms are not sufficient to sustain the stock. This level of SSB can also be expressed as long-term fishing mortality.

- 6) Develop S/R models incorporating stochastic processes.

Such models should take account of distribution and variance of recruitment at different levels of SSB.

- 7) Develop models simulating future development of the stock for different levels of fishing mortality.

Simulation models may give information about the likelihood of success of a management strategy. Simulations could also include environmental factors.

- 8) Develop models integrating S/R and E/R (E = environment) relationships.

This is an important step towards more realistic models.

- 9) Develop models taking into account multispecies effects.

This could include multispecies relations at all stages of life.

### 3.3 Box Models

A box model, sometimes referred to as a compartment model (Godfrey, 1983), is a simulation modelling concept in which the "box" or "compartment" corresponds to a quantity that we wish to observe or monitor.

Box models can take several forms: very simple input/output models that represent elementary data transformations (*i.e.*, S/R models); interconnected system components (Figure 3.3.1) represented by a coupled set of differential equations governed by laws of conservation; or a simple probabilistic decision tree. Boxes can occur in space, can represent similar individuals in population, can be moving (a parcel of water) or fixed (a bay), or can develop in time. The connections between the boxes constitute the rules that define how compartments interact. Connections can be deterministic constants, functionally dependent on time or some other quantity (Faddy, 1976), or random variables (Matis and Tolley, 1979; Matis and Wehrly, 1979).

Box models have received some attention in the fisheries literature. An example of a box model for a cohort based on elemental bioenergetic principles was described by E. Cohen (NEFC, pers. comm.). The model includes environmental variables directly in the model formulation. Other examples of box models include ECOPATH (Polovina, 1984), an ecosystem model for a coral reef system, and a population dynamics-based box model of a fishery (Sissenwine, 1977).

By usual convention, connections between boxes represent rates of transfer (flow of energy, material, or individuals) from one compartment to another (Figure 3.3.1). When modelling populations, the box model "currency" will probably be numbers of individuals since this is the most convenient. However, size must be addressed either implicitly or explicitly.

There is a hierarchy of box models. The level of model resolution is determined by the scale at which you have appropriate data or knowledge. The "box" becomes that level (space/time) over which we feel comfortable integrating a process at some finer level of resolution. Box models allow us to break complicated processes down into manageable pieces. Using this approach, we can look in detail at how the separate processes contribute to the overall picture. It also allows us to write down equations or coefficients for manageable space and time intervals for which we have data.

The type of box model used in any specific application should be guided by the objective for modelling and the precise questions being asked or hypotheses being posed. Initially, we suggest that box models are diagnostic. Only when they are completely developed and validated can they be prognostic.

Decision-tree box models are extremely easy to build. For example, each horizontal layer (Figure 3.3.2) could correspond to a day or local food and environmental conditions. Overall, the decision-tree model then represents a template of switches. Transition probabilities could be fixed values or functionally dependent on some internal (density) or external (temperature) value. There is the potential that a decision-tree model could quickly become unmanageable. For example, a model with two transition possibilities per box will have  $2^n$  decision levels, where  $n$  is the number of levels. If we are modelling recruitment, then we will only be interested in one or two pathways out of the many that may exist in a complex decision-tree model. Most pathways will give the frequent result (*i.e.*, poor recruitment), while a very small number of pathways will give the occasional good recruitment result. The decision-tree model allows us to identify the collective suite of conditions necessary for good recruitment to occur.

Simple questions that box models would allow us to ask are:

#### General

- i) Is the range of output consistent with what we observe?
- ii) Are we accounting for all the processes?
- iii) At what level do we need to incorporate things?

#### Management

- i) How many fish will there be next year?

- ii) How many fish should a fishery let free to spawn (escapement)?
- iii) How variable is recruitment in the long term?

The advantages of box model are that:

- they are simple and easy to build; you can start simple and build in more complexity as data and knowledge become available;
- they are flexible and can easily accommodate different scales of space and time;
- they are useful for listing potential effects and quantifying them;
- sensitivity to factors that affect abundance can be examined;
- they can determine the relative importance of different system components and potentially guide field research;

The problems with box models are:

- there is a potential to generate output that is not meaningful or is difficult to comprehend;
- parameterizing the model could be difficult.

We must devise ways to take complicated model output and subject it to analysis procedures that will test, synthesize, and summarize the results.

One interesting topic mentioned in this session concerned fractals. The feature of scale invariant self similarity may make biological systems a fruitful candidate for application of fractal theory. For example, in biological systems there is a consistency in size spectra as you step down through time and space scales (*i.e.*, size of predator and size of prey or logarithmic time steps).

### **3.4 Endogenous Modelling**

This Group had a particularly long discussion and the results of this may be summarized under three items:

#### **3.4.1 Modelling concepts**

Before starting their discussions, the Group agreed that common semantics were very important and the discussion that followed proved that given this, a common basis for talk on model concepts was present. (Where phrases have been given a particular meaning by the Group, they are in inverted commas.)

The level of modelling was seen to be important and the terms "first order", "second order", and "third order" were used.

In principle, it should be possible to describe events at any scale in terms of physical and biological mechanisms at the scale of contact between one individual and its prey or predators. We call these mechanisms "first-order processes", whose rates can be estimated from basic physical and physiological measurements.

In practice, description of events whose effects are integrals of many smaller incidents occurring at a variety of scales and dimensions are likely to be extremely complex and rich in parameters which may be difficult to measure. Such descriptions are subject to high uncertainty as a consequence of interactions between



parameters which may not have been appreciated, and the compound accumulation of variance at high degrees of freedom.

One solution to the problem of describing complex events is to reduce the number of parameters taken into consideration. In order that the description should still retain some useful relationship to reality, either the parameters included should be a carefully selected subset of the basic measurements, or a new set of simple analogue parameters which mimic the behaviour of the constituent processes without resorting to full parameterization. One can have more confidence that such "parameter-sparse" models would be capable of providing intelligible insight into the consequences of variation than a model which attempted to reproduce the effects of variation from first principles. We call these "second-order models".

A hypothetical example of this simplification step of moving from first-order to higher-order models would be one in which survival is modelled as functions of "prey availability" and "predation pressure". Such a model might be conceptually simple, and yet neither the "availability" nor the "pressure" parameters are at all simple themselves when considered from first principles. However, if one attempted to model survival directly from first principles with first-order parameters (*e.g.*, swimming speeds, light intensity, turbulent velocities, perception distances), then first of all, some parameters would influence both the feeding and predation mortality aspects of survival, but it would not be possible to evaluate how these aspects operate in their own right, and secondly, the model would be extremely complex to formulate. On the other hand, both prey availability and predation pressure can be relatively easily modelled on their own and the form of their variability visualized in terms of variations in the first-order parameters.

It is recognized that recruitment is the product of processes occurring in very heterogeneous systems. Ultimately, these systems may have to be modelled explicitly: these models would probably be composed of a large number of relatively simple compartments (see above) in which the biological processes can be described by relatively simple governing equations. The results from such a model will be unreliable unless the governing equations are correct, however complicated the description of the physical system is made.

The determination of appropriate forms for governing equations can be addressed by formulating second-order models (*q.v.*) and testing these against field observations. At present, suitable forms are not known, and it is considered that this remains a first priority for research activity, as it has been for many years. Meanwhile, the development of appropriate structures for "third-level modelling" may be worth pursuing using tentative biological governing equations. It must, however, be stressed that the results of any modelling of this type are, and will remain, only illustrative until appropriate forms for the governing equations and the parameters that enter them have been reliably determined.

The descriptions above thus lead us to the following classification models:

#### First-order

These describe real biological processes at the level of individual organisms (*e.g.*, feeding as a function of the density of specific food items, swimming speed). The space-time scales are small (less than one meter/hour). The parameters have direct biological significance.

#### Second-order

These describe processes in a synthesized form, in terms of assemblages of many organisms, using summary variables such as effective food density where this is an aggregate over available species and sizes, weighted by suitability, and perhaps modified by an accessibility factor (maybe depending on turbulence intensity, *etc.*). The definition of these summary variables and the functional form of the equations in which they are used, should preferably be informed by (and ideally be derived from) underlying first-level models even if these are only thought experiments. The summary variables, however, usually have only rather general biological significance.

Second-level models relate to space-time scales over which the relevant variables may be assumed to be constant to a reasonable degree of approximation: of the order of metres in vertical, kilometres in the horizontal, and days in time. These models usually describe single variables (such as predator density) in a uniform environment, and thus fall into the class of box models (q.v.). They may, however, extend to a modest number of compartments, such as a vertical stack of boxes, to allow, for example, for diurnal vertical migration of larvae.

### Third-order

These describe extended regions of space and time within which there are significant heterogeneities of key variables or parameters. Given the non-linearity of the biological processes of interest, such systems cannot usually be modelled holistically, and models incorporating many compartments or elements are generally required. They are, therefore, essentially linked sets of second-level models in which the variation of controlling variables (*e.g.*, temperature, currents, food density) may well be determined by an independent underlying physically-based model of water movements, primary production, *etc.* The relevant scales range from regional (hundreds of kilometres horizontally, hundreds of metres vertically, and weeks or months in time). Indeed, such models as might be used to describe a frontal system or extended to the scale occupied by a fish stock, such as a whole sea or even an ocean basin.

The interaction between these levels of modelling is the most important aspect of having levels. There is a need for a simple definition of a conceptual frame for how to operate this interaction. The property of such a frame should be such that scientists working in this field should feel at home within this frame. Such a simple frame has yet to be formulated, but the discussions of the Group and also this report indicates that such a formulation is feasible.

The sub-division of the environment modelled (*i.e.*, the space of the variables included in the model) was considered important. Two terms were used: "patches" and "stages". The term "patches" was later changed into "micro-environment" in order not to be confused with the previous use of the word "patches".

The definition of "patches" and "stages" may actually provide a way of moving any chosen model operating on, or within, these terms through the system. Such a common "transfer mechanism" may be a tool that would introduce a standard conceptual interface between different models.

The importance of different space and time scaling in different models was stressed in discussions and the introduction of these terms seemed to be a way of choosing the scales on a free basis.

This can be judged from the following consideration of recruitment as a composite process.

From general principles, recruitment to a stock is the end product of an integration over space and an integration over time of spawning of the product of survival through several (possible many) life stages. Thus:

$$R = \int_{\text{space}} \int_{\text{time}} EP(x, t) \prod_i S_i(x, t) d^3x dt$$

where:

$x$  = space,

$t$  = time,

$R$  = recruitment,

$EP$  = egg production (eggs laid per unit volume of sea per unit time),

$S_i$  = the survival through the  $i^{\text{th}}$  life-history stage.

The distribution of  $E$  is itself very patchy (spatially heterogeneous as are the factors (food, predators, physical processes) controlling survival. Replacing the integrations by summations over patches makes it obvious that the end result is the summation over a large number of contributions of very different sizes from different "patches". Such a sum is always dominated by the few largest contributors; thus, most recruits will come from a few patches.

Furthermore, from the stock dynamics (and, therefore, fishery management) perspective, the most important life stage is that at which most density-dependent mortality occurs. Here again, the overall density-dependence (if any) is the summation of that occurring within different stages, which are also likely to be highly heterogeneous. This also will be dominated by that occurring in the stage where the density-dependence is strongest.

We may denote this stage as the "crucial period"; we suspect that this is what Hjort meant by the critical period, but the older term has been given various interpretations by different authors, and we adopt a new term to avoid adding to the confusion.

Specifically, the crucial period may be defined as that for which  $|D|$  is greatest, where

$$D = \frac{d \ln N_s}{d \ln N_0} \quad (A1)$$

Note that if  $D$  is positive, the process is depensatory, whilst for  $D$  negative it is compensatory. ( $N_0$  represents the initial density of animals.) In practice, it is preferable to estimate  $D$  as the average over a wide range of initial number densities. Thus, in terms of survivors ( $N_s$ ), we may in fact use:

$$D = \frac{\Delta \ln N_s}{\Delta \ln N_0} - 2 \quad (A2)$$

Note that it is by no means sure that the crucial period will be the same in different places or at different times. Nevertheless, those stages for which  $|D|$  is often large are those on which our studies should focus. The central point is to concentrate on periods of maximum density-dependence of mortality, not these of maximum mortality *per se*.

Finally, it should be remarked that the variability arising from density-dependent processes occurring before the crucial period will be suppressed. That arising during or after the crucial period will not. This may influence the need to devote resources to the study of density-independent processes in these two classes.

The last model concept that was brought into the discussion was "simulations". It should be the responsibility of everyone to assure themselves that any model being used is simulated through its total variable space. This is because very often a particular model will describe a limited situation quite well, but as it is taken to the outer limits of the variables used in the model, it may prove to perform in ways that are not realistic.

### 3.4.2 Work concepts

An additional tool to models in the practical work is, of course, measurements of variables. A lot of the discussions in the Group concerned aspects of creating a sound and fruitful process of interfacing model aspects with measurement aspects, and also the actual process of moving to and from the different facets of the work.



### The interface between models and experiment

It was noted that there has so far been little contact between available models and the conduct and analysis of field experiments. For example, the second-level model of Shepherd and Cushing (1980) proves a potentially testable prediction for the survival of fish larvae as a function of the abundance of food and predators, but has not so far been so tested. A number of alternative models of somewhat similar complexity are also available (*e.g.*, Beyer, 1989).

The reason for this seems to be essentially a problem of communication. The models are expressed in terms of summary variables which have only indirect biological significance, and it is not immediately clear how these should be estimated from field data. In addition, the time and space scales concerned are not explicit.

Better communication between modellers and experimenters is clearly required and should be encouraged. As a start, experiments should be encouraged to be bold; if presented with a summary variable representing food abundance, for example, they should use their professional judgement to arrive at a definition which in their opinion is appropriate for the estimation of the entity in question. If the concept is so unclear that this is not possible, then appropriate questions should be directed to the model's authors. If the definition adopted is inappropriate and leads to rejection of the model, an educational response from the originators may be expected!

Secondly, it was agreed that existing second-level models are generally based on uniform spatial distributions, and, therefore, only properly applicable to rather small spatial scales on which this approximation is reasonable. This does not prevent attempts to apply and test them on larger scales, but the success of such attempts should probably be considered as fortuitous.

The Group thus agreed that "second principles" models could be a good starting point for work, but it was stressed that this must not be interpreted as advice to stop work on any other approach.

"Testing" and "verification" were seen as very important in this process of development of models. It is very important to be able to formulate why steps have to be taken to move from one point in the process to another.

The methods which need to be used to test second-level models will, of course, depend on the details of the models and the data available. It would, however, be very desirable if the model predictions can be cast in a form which can be fitted and tested using standard statistical techniques, such as linear modelling (regression and analysis of variance).

As a simple example of how this might be done, we may consider the model of Shepherd and Cushing (1980). The result of this may be written:

$$\frac{1}{N_s} = \frac{1}{A} \cdot \frac{1}{N_0} + \frac{1}{K} \left( \frac{1}{A} - 1 \right)$$

where  $A = \exp(-\mu T_0)$  and  $K$  is a measure of food abundance (density). The mortality parameter  $\mu$  should be proportional to predator abundance (density).  $T_0$  (the minimum stage duration) is a constant depending on maximal growth rate and weight change during the life history stage in question.

Considering the application to a hypothetical data set containing a set of observations of initial and final larval numbers ( $N_0$  and  $N_s$ ), at various levels of food and predator abundance, this expression may be recast as:

$$\frac{1}{N_s} = a \exp (Pred) \frac{1}{N_0} + \frac{b}{Food} [a \exp (Pred) - 1]$$

This is a fitable, but slightly non-linear, model for the reciprocal of surviving numbers in terms of the reciprocal of food abundance, and the exponential of predator abundance, with only two parameters (a and b) which one would attempt to determine via the fitting procedure. In fact, it is very likely that A (the maximal survival through the stage) is small, in which case this simplifies to:

$$\frac{1}{N_s} = a \exp (Pred) \left[ \frac{1}{N_0} + \frac{b}{Food} \right]$$

Regrettably, this is still non-linear (it involves the product of a and b), but this is only (!) a technical problem. Note also that it involves the product of  $\exp (Pred)$  and both the food abundance and the initial number terms - thus, as discussed above, it involves the interaction term as well as the main effects (in statistical terminology).

In fact, this model specifically predicts that the reciprocal density of survivors should depend on the second-order interactions of predators and food, and of predators and initial abundance, but not that of initial abundance and food, and that there should be no significant constant or main effects. These are very specific, quite surprisingly, and potentially testable predictions. Falsification of them would be most informative and should guide the development of more refined models, if necessary.

At a very simple level, this just says (not surprisingly) that survival should be positively related to food abundance and inversely related to predator abundance. However, the point is that the model-based approach leads to a much more specific prediction, in terms of appropriate forms for the variables, prior suggestions for parameters (*e.g.*, absence of a constant term), and even probable interactions between variables.

The analysis of this simple model leads to a relatively highly tractable model. With more complicated models and data sets, such a simple result is unlikely to be obtained. Nevertheless, a similar development from the raw model result towards a fitable form is likely to be required in most cases - and further appropriate approximations may be necessary to fit a continuous variable (regression) model, as envisaged above. The same equation can be used to suggest an appropriate categorical ("analysis of variance") model expressed in terms of, for example, high, medium, and low values of food and/or predator abundance, if this seems likely to be more tractable.

The Beverton-Holt form of the relationship between survivors and initial numbers implied by this model is rather interesting because, as originally remarked by Beverton and Holt (1957, p. 57), the result of a sequence of any number of stages each governed by such an equation is a further relationship of the same form, with parameters which are compounded from these of the individual stages. This may be useful because it means that the precise identification of the beginning and end of the crucial period (q.v.) may not be too critical. Indeed, one may try to fit such a relationship using initial numbers measured very early, and survivors very late; the difficulty then would be to know at what stage food and predators should be estimated. One might perhaps try using several potential useful estimates of these variables, and seek those giving the strongest dependence.

### 3.4.3 Field studies and experimental studies

Under the discussion of model concepts, two basic groups of field studies were stated as necessary. The first group of field studies was simultaneous measurements of "food", "animals", and "predators". A possible reformulation of these terms into the "total size spectrum" of the part of the ecosystem involved in the model was described. It was argued that any such investigation should not necessarily be limited to the part of the ecosystem described by any particular model being tested at the time of the investigation. If it were possible

to include a larger part of the ecosystem in the particular field study, it may well ultimately prove profitable to do so.

The second group of field studies encourages the study of the actual life history of individuals.

This is because models for understanding the essential mechanisms underlying recruitment stability (*i.e.*, stages with the highest density-dependent regulation of survival) and variability must be derived from stage-specific quantifications of the vital rates (based on first principles). The vital rates refer to the individual level and it is necessary to adopt individually-based approaches. We do not know the extent to which it becomes necessary to specify the individual fish (in terms of number of characteristics or attributes). However, the starting point consists of selecting the single most important ecological attribute of an organism (which was identified as body size already in the 1920s).

A basic requirement for data collecting is to obtain precise (better than 10%) and well-defined measurements (*i.e.*, standardized) of body length. (Simultaneous measurements of body shapes and weights are, of course, also of importance, in particular, for the development of suitable measures of larval fish condition, standardized weight-length relationships, growth models, *etc.*.) The typical size of a representative sample of larvae for characterizing the larval population in a specific "micro environment" far exceeds the standard number of 10-20 for estimating the mean. For the purpose of identifying and estimating the form of the size-distribution of larvae, a minimum in the order of 1,000 measured larvae per cohort is required. Once a general class of distributions (such as the log-normal type) has been identified (if possible), then a couple of hundred larvae will be sufficient to estimate the parameters or the characteristics of the distribution (*e.g.*, mean, variance, skewness). In practice, it is necessary to make sure that the tails of (compound) larval size distributions are covered well (*e.g.*, down to the 1% level) to ensure the likelihood of success in identifying individual cohorts (*i.e.*, survivors from the same batch of eggs).

An important possibility for studying the growth and mortality (*i.e.*, the vital rates) of larval fish is provided by the information on the past life history stored in the otolith. Individual growth trajectories are needed as an important element in the development of satisfactory growth models of larval fish. The individual growth trajectories represent a prerequisite to begin distinguishing between genetic and environmental (food consumption) causes of variability in growth rates. This type of information (from future, detailed otolith readings) is expected to form an essential basis for the development of stochastic growth models.

Information on the past history is also important in other respects. The feeding behaviour of larvae may very well depend on their past experience and it may thus become necessary to incorporate part of this information (*i.e.*, "memory") in the state-variable description of the larvae. Furthermore, it is important to obtain all possible information on (past) periods of starvation, recovery, *etc.* with the purpose of understanding characteristics of life histories that have lead to survival. Appendix A describes these techniques in more detail while Appendix B describes some fitting problems.

Besides precise age readings and quantifications of daily growth increments, tagging could provide a valuable means of identifying cohorts and hence, the correct estimation of (size-specific) mortalities. The tagging should also be easily detectable in the digestive tract of the predators.

The switch from classical population dynamics (perceiving the cohort as comprising identical fish) to individually-based approaches makes it necessary to deal directly with the concept of competition (*e.g.*, the distribution of available food between small and big larvae). Information on individual feeding behaviour (including an understanding of the physical-biological factors determining encounter rates at sea) in the dynamics of the larvae's prey organisms - competitors - predators environment may, therefore, be crucial to our ability of understanding the essential mechanisms determining actual food availability and prey ingestion for the individual member of the cohort.

### 3.5 Environmental Processes and Characteristics

Environmental processes and characteristics acting over a broad range of time and space scales can potentially affect the level of recruitment. The choice of primary issues to be addressed will depend on the system of interest. The discussants recognized that there may be no direct "brute force" approach to the overall recruitment problem, but that a variety of approaches may contribute to an accumulation of useful insight on key issues.

Several categories of processes were of general interest. These included:

- Advective processes (the potential interaction of vertical behaviour with vertically structured flow fields was emphasized).
- Diffusive processes (effects of turbulence on feeding (efficiency, dispersion of path structure, *etc.*).
- Processes regulating primary production (stability, mixing, upwelling, nutrient supply, illumination, *etc.*).
- Dynamics of ocean fronts (surface convergence, tidal-mixing fronts, *etc.*).
- Physiological effects (temperature, salinity, dissolved oxygen, toxins, *etc.*).

Many of these processes (or effects) would tend to act in a density-independent manner. In such a case, the question as to whether they might act prior to, or subsequent to, life-cycle periods where density dependence (of growth or mortality) might occur has special relevance. When environmental processes act prior to density-dependent controls, they directly interact with density-dependent population regulation. When they act subsequent to such controls, they may merely modify the "regulated" population level. Effective density-dependent population regulation may occur in rather limited space/time "parcels" where special conditions may generate anomalously high growth and/or low mortality, and correspondingly high local densities. Thus, environmental processes that control patterns in the habitat are of major interest. Newly-available measurement systems such as Doppler current profilers may offer new information on topographically-trapped hydrodynamic structures, *etc.* that could rapidly broaden our insight into such issues.

The question of interaction among variables was emphasized. Response to one variable could be conditioned by the magnitude of another variable. For example, suppose that larval growth is affected by temperature and salinity, but in an interactive way such that the response to temperature is substantially different at different salinity levels. Not including salinity in such a model, even though salinity variation itself may produce no significant independent response, could result in a model that may exhibit substantial skill for a while, but then suddenly fail in some crucial situation. Thus, it is important to study the action of each potential variable at its most fundamental level, and to test each important variable for interactions with other variables.

It is likely, in coming years, that fisheries scientists will become increasingly concerned with potential effects of global climate change on exploitable marine populations. While the details of the changes are presently uncertain, substantial effects on the dynamic processes in the upper ocean environment are expected. Discussants emphasized that the changes may be reflected, not only in mean state, but also in variability. Credible models of processes affecting recruitment would serve to transfer insight and information, that may become available on the very large "global" scales, to the regional and smaller scales on which fish population dynamics are affected.

Participants noted that regional-scale dynamic circulation models, presently under development in the physical oceanographic community, may be a source of information on many of the processes needed for modelling recruitment. It was noted that intensified development of this class of models is required if they are to be available for meeting the near-term needs of recruitment research in regions of interest. It was also considered extremely important that fishery scientists be active collaborators in the formulation and



development of these models. For example, discussants stressed the need for adequately representing variability in frequency bands where non-linear interactions with biological processes or behaviour occur. The importance of appropriate vertical structure for specifying interactions with vertical behaviour was cited as one example. The capability for regional models to drive "nested" sub-scale models of much smaller scale processes having biological importance was also cited as an important aspect to be incorporated in model development.

There was agreement that much might be done by appropriate exploratory analysis of available data and experience. A search for generalizations within and among populations and regions was considered a useful focus for activity. The comparative method of science is the appropriate alternative to the experimental method in situations where experimental controls are impractical. This applies to nearly all the important scales of ocean processes relevant to recruitment. Many examples of application of the comparative method to generating insight into physical factors affecting recruitment were cited during the meeting. The need for appropriate physical models to provide a comparative context for investigating biological processes was also elaborated. For example, the proper use of different water parcels as replicates for investigating interactions of larvae with food particle distributions would be facilitated by physical models capable of specifying similar physical history and character of the parcels.

#### **4 INDIVIDUAL APPROACHES**

The preliminary conception of models is usually the work of individuals or very small groups of co-workers. Their subsequent development and validation, however, can often profitably be carried on by study and Working Groups. This pattern of individual conception and group development and testing can be observed in the work of the ICES Multispecies Assessment Working Group. (See IRG report, Anon., 1989a.) In the Multispecies Assessment Working Group, individual efforts are encouraged by allowing a report section (Section 8) where the Group exerts little control over what individuals have to say (Anon., 1989b). It seemed appropriate to adopt a similar approach for this Study Group and encourage members to outline personal perspectives and ideas for future work. These are necessarily provisional and all views expressed in this section are those of individuals and not necessarily the Group's and thus should not be quoted. It is hoped that, as in the Multispecies Assessment Working Group, some of these contributions will form the seed corn for future work. At a more practical level, they provide a basis for some contributions to the ICES 1991 Mini-Symposium on "Models of Recruitment Processes Relevant to the Formulation of Research Strategies" convened by Dr M. Sissenwine (USA).

##### **4.1 Density-Dependent Processes, Density-Independent Factors, and Fishery Management**

As has been discussed in Section 3.2, a crucial parameter for fishery management is the slope at the origin of the stock-recruitment curve, since this is directly related to the maximum fishing mortality which the stock may be able to withstand.

The division proposed in Section 3.4 of processes occurring before, during, and after the crucial period is useful in this context because it makes it clear that this slope is determined primarily by the density-independent processes (typical maximum mortality and loss rates of various sorts). Studies of these processes may, therefore, lead to an improved understanding of the perturbations of this vital parameter, though the estimation of its average value may perhaps be more safely done through empirical studies of stock-recruit data with appropriate co-varieties. The study of the density-dependent processes themselves may not be very helpful to this particular goal, even though their existence is crucial to the abundance of the stock under less heavy exploitation.

Furthermore, it may well be that almost all of the variance of survival is due to stock-independent variables, and that very little is due to variation of the stock itself. Nevertheless, this does not mean that conventional population dynamics are irrelevant and that the stock-recruit relationship may be ignored. The slope at the origin remains the key parameter, and the only really relevant information in deciding fishery management strategy. Allowance for, and possibly even control of, the exogenous factors may be useful in predicting

stock and yield, but does nothing to solve the perennial problem of estimating the maximum tolerable rate of exploitation. This is demonstrated rather nicely even in the rather bizarre simulations of Shepherd and Cushing (1990) where there is almost no density-dependence and very high variability. Nevertheless, the average level of recruitment (and therefore stock and yield) is strongly dependent on the level of fishing mortality imposed.

Only in cases of extreme density dependence (*e.g.*, constant recruitment down to very low stock sizes) might one argue that stock-recruit studies are irrelevant, and even here one might equally maintain that finding the limiting stock size for this special behaviour is the most important goal.

Paradoxically, the emphasis in most studies has had the opposite emphasis. Most attention has been paid to stock-recruit relationships where recruitment is least variable and they are least necessary. Conversely, where recruitment is highly variable, presumably because of density-independent processes, the perturbations have been studied, whilst the effect of stock size has sometimes been ignored. Whilst understandable, this is undesirable, and the balance needs to be redressed. The determination of  $F_{oph}$  should, therefore, be a higher priority for, say, North Sea haddock, rather than for North Sea plaice.

## 4.2 Some Approaches Based Upon the Null Hypothesis of Linear S/R Relationships

Some approaches are considered based upon the null model that recruits are proportional to spawning biomass. *i.e.*,

$$R(y) = a * SSB(i)$$

where  $a$  is a constant, at least at low stock size. These are:

- We might estimate  $a$  from the weighted geometric mean  $\ln\{R(i)/SSB(i)\}$  where  $R(i)$  is the recruitment and  $SSB$  the spawning stock biomass in year  $y$ . There would be a common sense argument for making this a weighted mean using  $1/SSB$  as the weighting. Such a weighted estimate (possibly with some additional censoring of outliers) could lead to an alternative to  $F_{med}$ . These weighted estimates would be based more upon the slope near the origin. It might accord more closely to the  $F_{oph}$  concept outside prudent harvest.
- We might improve the estimate of  $a$  by considering it a function of environmental or predation effects using weighted regressions (or by other means).
- We might see if it is possible to generalize estimates of  $\alpha$  across stocks. This might be done by first converting  $a$  into the form in  $\alpha/(SSB/R \text{ at } F = 0)$ . A working paper to the meeting found a relationship between the  $F_{med}$  derived equivalent of  $a$ .

$$\ln\{(SSB/R \text{ at } F_{med}) / (SSB/R \text{ at } F = 0)\}$$

and the weight for each stock of fish at the age of first maturity (Figure 4.2.1).

The implication of this (if true) is that bigger fish can stand a greater reduction in spawning stock than smaller fish. This is an idea that could be easily tested on a wider range of stocks using available assessment reports and might lead to "safety net" rules for new fisheries.

## 4.3 Including Multispecies Predation Effects in Regressions of Recruitment on Exogenous Variables

This relates to the objective of understanding external factors which may perturb recruitment. Analyses which use lagged regressions of predators on recruits to explain some variations in recruitment have already been reported for North Sea gadoids (Pope and Woolner, 1981) and by Cook and Armstrong (1984). The problem is that of restricting the choice of predictors to a few for which an *a priori* hypothesis exists.

Two existing ideas may assist with this choice:

- 1) The Multispecies Assessment Working Group (Anon., 1989b) provides a matrix of predation monitoring coefficients  $M2$  (pred age, prey age) per unit predator biomass for some North Sea stocks.
- 2) It is usually possible to explain much of the variation in population-at-age data by an ANOVA of  $\ln$  (year class),  $\ln$  (year), and  $\ln$  (age) effect (cf. Shepherd and Nicholson, 1986).

If we put these ideas together, we could develop an aggregate  $M2$  generated by one year class of predator on one year class of prey. The effect would be (where  $S, A, Y$  are predator species, age, and year, and  $s, a, y$  are prey species, age, and year):

$$M2(S, Y-A, S, y-a) = \sum_{\text{all } A} \hat{M2}(S, A, s, a) \times \text{age}(A) \times \text{year class}(Y-A)$$

where age is the age effect and year class the year-class effect.

Thus we might expect:

$$\ln \text{ year class}(y-a, s) = \alpha - \sum_{\text{all predators}} \beta \times \hat{M2}(S, A, s, a) \times \text{year class}(Y-A)$$

Thus, regression of  $\ln$  (prey year-class strength) on lagged predator year-class strength would be worth considering for predators where

$$\sum_A M2(S, A, s, a) \times \text{age}(A)$$

is relatively large, but best avoided where these effects are small.

For stocks outside the North Sea where  $\hat{M2}$  estimates are not available, stomach content data should help to identify which predators at which time lags might be most important to include in regressions of  $\ln$  (recruits).

This idea would mostly be developed using existing data. It has little implication for field programmes except those conducted for multispecies purposes.

#### 4.4 The Influence of Perturbations on Noise at Various Stages

The model of Shepherd and Cushing (1980) leads to a Beverton-Holt type relationship for the crucial period (CP). It is a second-order model, strictly applicable only to a homogeneous (and, therefore, fairly small) system. Nevertheless, it leads to some specific conclusions regarding the effects of perturbations at various stages, which may be illuminating and possibly even of more general validity. The model has two parameters:  $A$  (describing density-independent mortality due to predation) and  $K$  (representing food abundance and affecting density-dependent growth). Both of these are likely to be variable, from year to year, for example. In addition, there may, of course, be fluctuations in density-independent mortality before the crucial period, leading to fluctuations of initial numbers, and also after the crucial period, leading to multiplicative noise affecting the survivors.

Noise arising before the density-dependent processes in the crucial period will be (at least in part) suppressed by them, whereas that arising after will not. The fate of noise generated during the crucial period depends on its source.

It then follows from this model that:

- a) fluctuations of mortality rates during or after the crucial period will lead to fluctuations of recruitment at all stock sizes;
- b) fluctuations of food abundance during the crucial period will lead to fluctuations of recruitment only at high stock sizes;
- c) fluctuations of mortality rates before the crucial period will lead to fluctuations of recruitment only at low stock sizes.

Different results apply to R/SSB; the overall picture is summarized in the table below:

Effects of perturbations on R and R/SSB ratios

Source of perturbation	Stock size	
	Low	High
Mortality during CP	Both	Both
Mortality before CP	R only	Neither
Food availability during CP	Neither	Both

These results may not be general, but similar results should be derivable for other models. Investigation of the nature and incidence of fluctuations may, therefore, yield useful clues as to the source of the noise, and perhaps also to the identification of the crucial period.

#### 4.5 Can We Detect a Signal From the Noise?

An essential aspect of models required by field programmes is a recommendation on methods to integrate the data obtained from several samples into parameter-sparse representations of environmental conditions within a study region assumed to be reasonably homogeneous. Even if we can assume that we know (or that we can estimate realistically) how processes (*e.g.*, feeding rates) are related to basic state variables (*e.g.*, size and abundance of organisms), any field experiment/study will be faced with two essential sources of noise. One source is a realization of sampling variability and the other comes from the stochastic nature of interactions between organisms. Models of different processes (*e.g.*, the interaction between microplankton, larvae, and predators) can be used to ask:

How much of the variability is due to main effects and how much can be due to "random" (stochastic) factors that we do not understand at this point in time or that we can never essentially measure?

For example, it is simple to ascertain that the survival of a cohort of larvae is measured by the stage-specific mortality and growth rates which are themselves determined by the abundance of predators and prey, respectively. We can ask whether sampling a series of "patches" will provide a representation of mortality/growth in relation to the abundance of predator and prey which is sufficiently accurate to assess cumulative losses over several stages given sampling variability and that random (stochastic) interactions are taking place. A simple scenario for simulation can be to represent the simple food chain as a complex of size classes, the interaction of which is represented by size-dependent relationships, over a range of abundances. There is sufficient information on sampling variability (in relation to abundance and sample volume) available to model the significance of different sampling schemes. Incorporating random encounters/interactions into the simulations will produce a basic level of noise that can define the signal-to-noise ratio (percentage of variance related to the explanatory variables) which we can hope to achieve. Data requirements for such an exercise can be represented from a synthesis of published information on vital rates, sampling variability, and models of encounter patterns (frequency distributions). The difficulty is in determining the time/space



scale for the simulations. However, the results may provide insight into our ability to produce general and repeatable studies of simple biological interactions in the field.

#### 4.6 Decision-Tree Models

The FOCI programme of NOAA/NMFS has shown that the recruitment of walleye pollock in the Shelikof Strait is affected by biological processes in conjunction with the physical variability. Recruitment of cod around Iceland is strongly affected by water-mass variation and frontal location. Both of these systems are tempting candidates for simple models (using PC-type spreadsheet software) that consists of a simple decision tree. Input data would consist of data about biological rates, and the time development of physical events.

For the former example, beginning with the eggs, reduced at a regular rate (dependent on temperature) due to mortality and advected to favourable or unfavourable environment, the first stages might look as follows:

Stage A	Spawn			
Effects:	1. Depths of spawn	2. Temperature	3. Flow-up strait	
Stage B	Eggs			
Effects:	1. Decay due to temperature-dependent mortality	2. Beneficial effect of surface eddy	3. Storm-wind effect	4. Swept offshore
Stage C	Larvae			
Effects:	1. Advection rate to nursery	2. Food supply (density-dependent effect?)	3. Temperature	

Each effect can be associated with a coefficient so that the final recruitment would be:

$$N_{\text{recruit}} = N_{\text{eggs}} \cdot \alpha_1 \cdot \alpha_2 \cdot \alpha_3 \cdot \beta_1 \cdot \beta_2 \cdot \beta_3 \cdot \beta_4 \cdot \gamma_1 \dots\dots\dots$$

where  $\alpha_i$  corresponds to effects  $A_i$ ,  $\beta_i$  corresponds to  $B_i$ , *etc.* A zero anywhere along here, or a very small coefficient, causes year-class failure. Inputs would consist of values (or functions) to set the values of  $\alpha_i$ ,  $\beta_i$ ,  $\gamma_i$  ....

Such a simple model could include density-dependent effects. Making the food supply to the larval stage, *i.e.*, making  $\gamma_2$  depend on:

$$(\prod_i \alpha_i \beta_j) \gamma_i$$

would lead to non-linearity.

These models would allow an easy assessment of the relative effects of different contributions to the recruitment variations associated with the variation in the parameters. The process will also serve to list the processes affecting recruitment and hence focus discussion on the question of completeness of the list.

## 4.7 Fractal Backgrounds of Marine Ecosystems

Marine ecosystems have features which suggest they might be described by fractals. Most obvious suggestions come from the self similarity of feeding relationships, the regular log numbers, log size spectrum noted by Sheldon *et al.* (1977), and the varying space and time scales noted by Steele (1965).

Fractal descriptions of natural objects such as trees, rivers, mountains, and blood vessels have led to useful insights and it seems possible that some insights might be gained from their applications to marine ecosystems. It seems much less likely that they would be capable of providing a satisfactory description of the dynamic properties of such systems, but they might provide a description of the stage scenery against which the players act out their lives.

As an illustration of the use of fractal geometry as a descriptor of an imaginary ecosystem, we might consider the simple fractal construction of the Sierpinski gasket. This is constructed by dividing an isosceles triangle into four parts by connecting the mid-points of the sides and then removing the centre triangle. The remaining triangles are then treated in the same fashion, and so on (Figure 4.7.1).

If we think of the resulting holes as animals of mass equal to their linear size, then we obtain an ecosystem whose numbers-to-weight spectrum has the form:

$$\ln N_0 = -1.58 \ln Wt$$

Of course, this is not quite the same form as found by Sheldon *et al.*, but not so far off.

If we think of one side of the triangles as a mouth about to eat the smaller triangles it touches, then we see that the big triangle will have a diet of the smaller triangles as in the text table.

	Weight				
	1/2	1/4	1/8	1/16	1/32
Stomach content	1	2	4	8	16

And hence food is given by the suitability of the different triangles as:

$$\frac{W(pred)}{W(pre)} \frac{\exp}{2} + 1.58 \ln W[(prey)/W(pred)]$$

which is not Eric Ursin's log normal model prey preference model, but has some similarity.

This simple example thus serves to illustrate that even a very simple fractal form can be interpreted to give results that have some features in common with marine ecosystems and thus should encourage us to explore more realistic models. These in turn may indicate questions to be asked of scientists involved in field programme designs. These might, for example, be questions about the autocorrelation in functions that describe within and between size-group distributions.

## 4.8 Pluralism in Recruitment Research

Despite an extensive history of research into the background and physical processes affecting recruitment of marine fish, relatively few recent conceptual advances have been made. Two possible explanations for this apparent impass can be identified:

- 1) We have been unable to identify and estimate the relevant variables on the appropriate spatial and temporal scales.
- 2) We have asked the wrong question.

Implicit in the first issue is the view that the recruitment problem is amenable to a reductionist approach in which the stabilizing (compensatory) factors can be isolated and the determinants of variability can be identified and quantified. Clearly, this is the preferred outcome because it would allow both a mechanistic understanding of recruitment processes and presumably some predictive capability. An alternative view is that little progress has been made because we have not identified the correct mechanisms and/or the processes are inherently stochastic and will not be amenable to conventional approaches. Shepherd (this meeting) provides an example of both elements:

- a) a new mechanism has been proposed to explain the resilience of a population to exploitation (or other disturbances) based on a density-dependent mechanism,
- b) stochasticity is an essential component of the mechanisms.

There can be little doubt that process-oriented research should be pursued in an attempt to partition the variance in recruitment into its individual components. Here, it is argued that attention should also be devoted to a pluralistic approach in which radically different mechanisms are explored. We should keep in mind that the most significant advances in science occur not just with the accumulation of facts, but with new ways of looking at the problem.

## 5 CONCLUSIONS

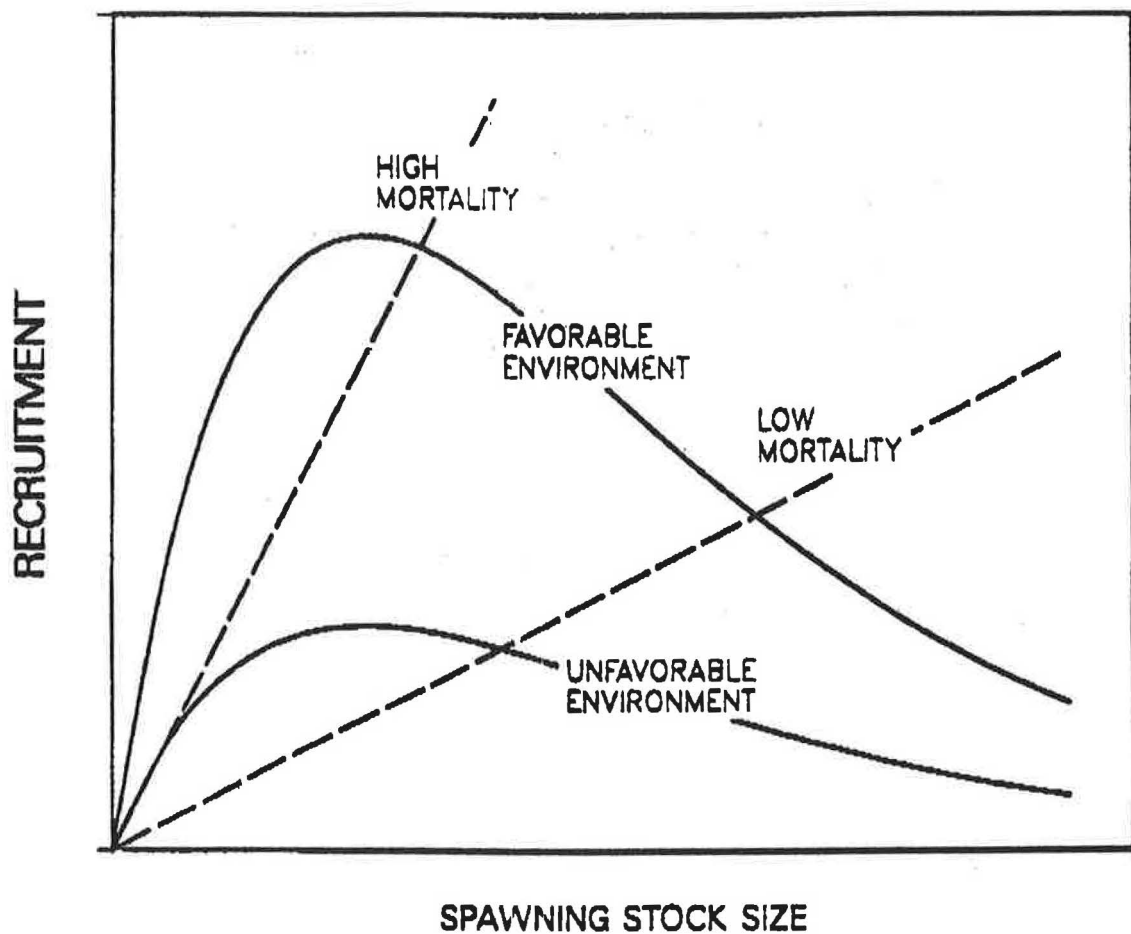
- 1) Simple models of stock-recruitment should firstly address the question of the slope of the stock-recruitment curve at the origin.
- 2) Extensions of time-series to earlier years using existing, but cruder, data sets than virtual population analysis would be very useful. ICES should refer this problem to the Working Group on Methods of Fish Stock Assessment and consider convening a Theme Session or meeting to encourage the availability and production of such time-series.
- 3) At present, validated models for larval growth and mortality are not available for use in large-scale models. The development and testing of second-level models, therefore, remains of very high priority among the possible lines of research.
- 4) Data collection and modelling activities must develop in close collaboration. ICES should consider convening multidisciplinary meetings when more progress has been achieved on specific problems.
- 5) The inter-regional comparative approach is a powerful tool for examining environmental effects on recruitment and is an alternative to the experimental approach.
- 6) Interactions within and between biotic and abiotic variables are possibly as important as the main effects (in statistical terms) in determining recruitment. This might explain why repetitive statistical interpretations of recruitment series seldom give clear answers and indicate that more detailed models and field data collection will often be needed to elucidate these interactions.
- 7) The comments on field research given in Section 3.4 and Appendix C provide a very useful communication between modellers and field scientists.

- 8) Modelling is a job for individuals and small teams. The ideas in Section 4 provide some starting points for further work and it is hoped that individuals will take up the challenge to extend these and the other ideas in the report.
- 9) Modelling recruitment processes requires scientists who are equally at home with the biotic and abiotic variables involved. Such scientists are in short supply and it is suggested that a suitable educational (or breeding programme) be established, perhaps by IOC.

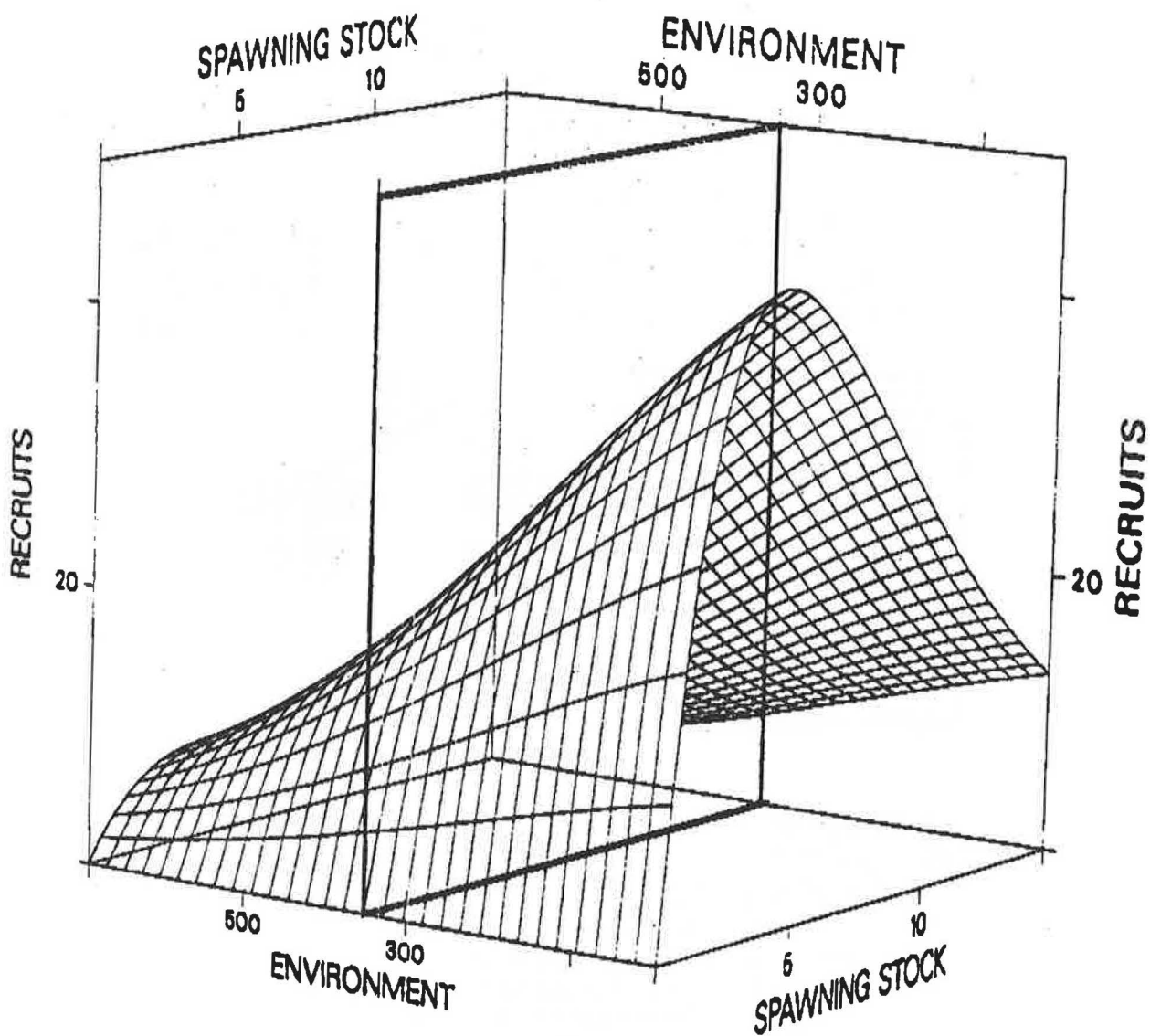
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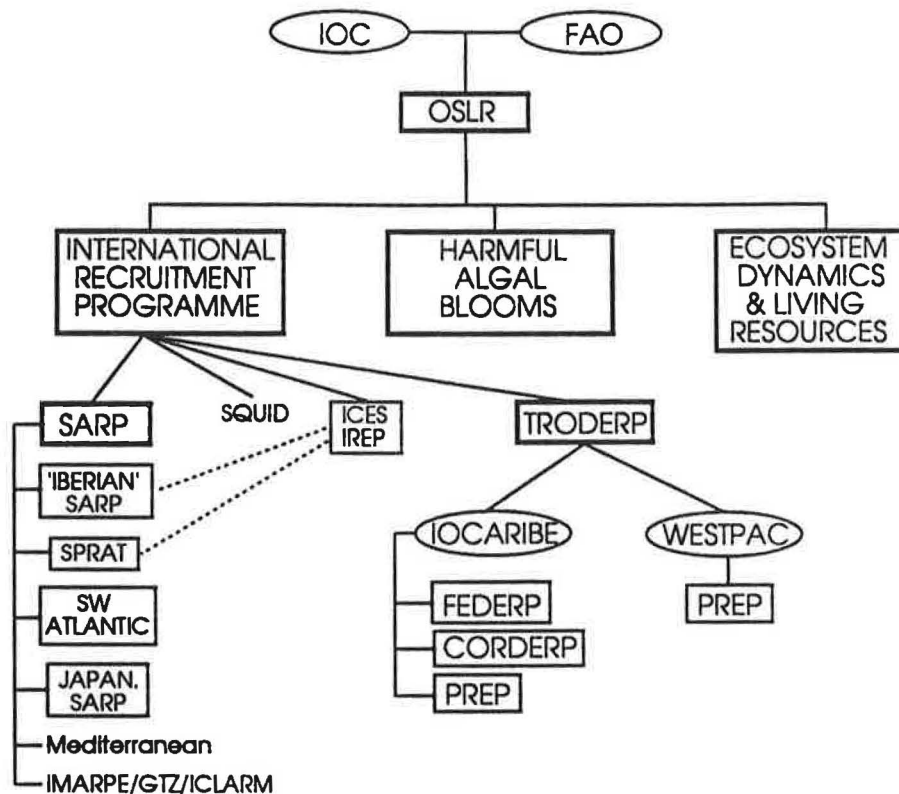


**Figure 2.1.1** Hypothetical recruitment curves under two environmental regimes. The straight lines represent density-independent relationships relating spawning stock size to recruitment under two harvesting levels. The intersection between the stock-recruitment and the recruitment-stock curves represent equilibrium points. Note that for the combination of high fishing mortality rates and "unfavorable" environmental conditions, a stock collapse is predicted.



**Figure 2.1.2** Hypothetical relationship between spawning stock, recruitment and an index of biotic and/or abiotic environmental variables. The vertical plane represents a slice through the surface for a particular set of environmental conditions.

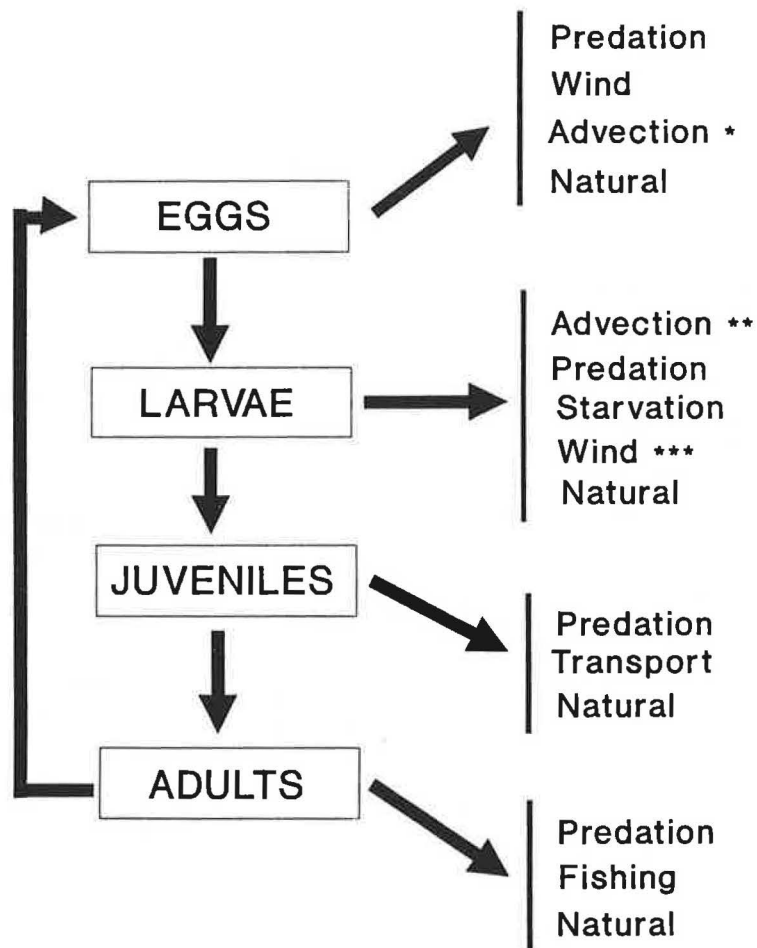




IOC: Intergovernmental Oceanographic Commission  
 FAO: Food and Agriculture Organization of the U.N.  
 OSLR: IOC-FAO Programme of Ocean Science in Relation to Living Resources  
 IREP: International Recruitment Programme  
 SARP: Sardine/Anchovy Recruitment Project  
 TRODERP: Tropical Demersal Recruitment Project  
 FEDERP: Fish Estuarine-Deltaic Recruitment Project  
 PREP: Penaeid Recruitment Project  
 CORDERP: Coral Reef Demersal Recruitment Project  
 IOCARIBE: IOC Sub-Commission for Caribbean and Adjacent Regions  
 WESTPAC: IOC Regional Committee for the Western Pacific

**Figure 2.4.1** Present structure (Anon., 1990) of the OSLR Programme.





- \* - *fxn (current, salinity and lipid content)*
- \*\* - *vertical migration*
- \*\*\* - *successful hatching*

Figure 3.3.1

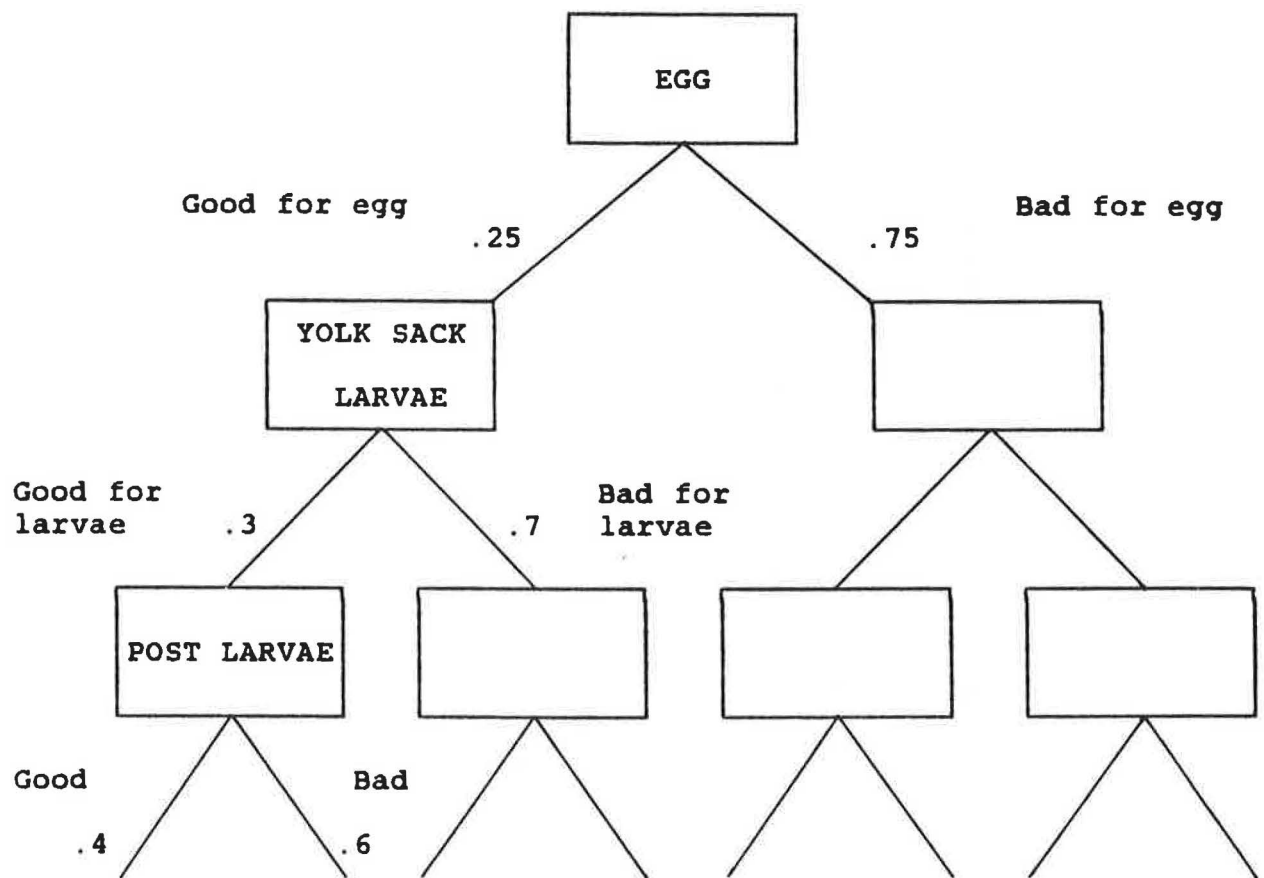


Figure 3.3.2 Simple decision tree model.

SSB reduction  $\{ \ln(SSB/rIF=0/ssb/rIFmed) \}$   
 Versus  $\ln(\text{Weight at 50\% maturity})$

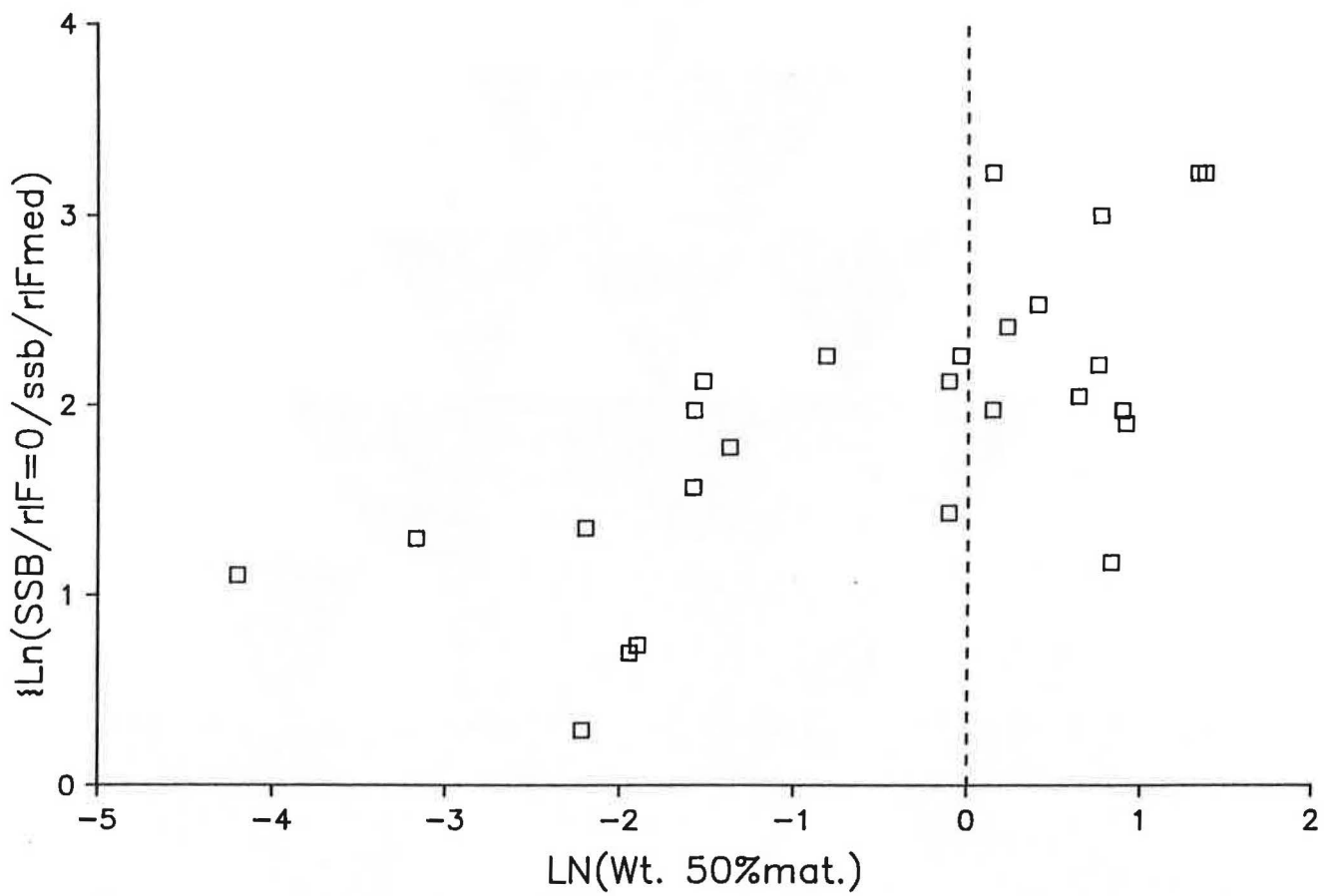


Figure 4.2.1

## Sierpiński gasket

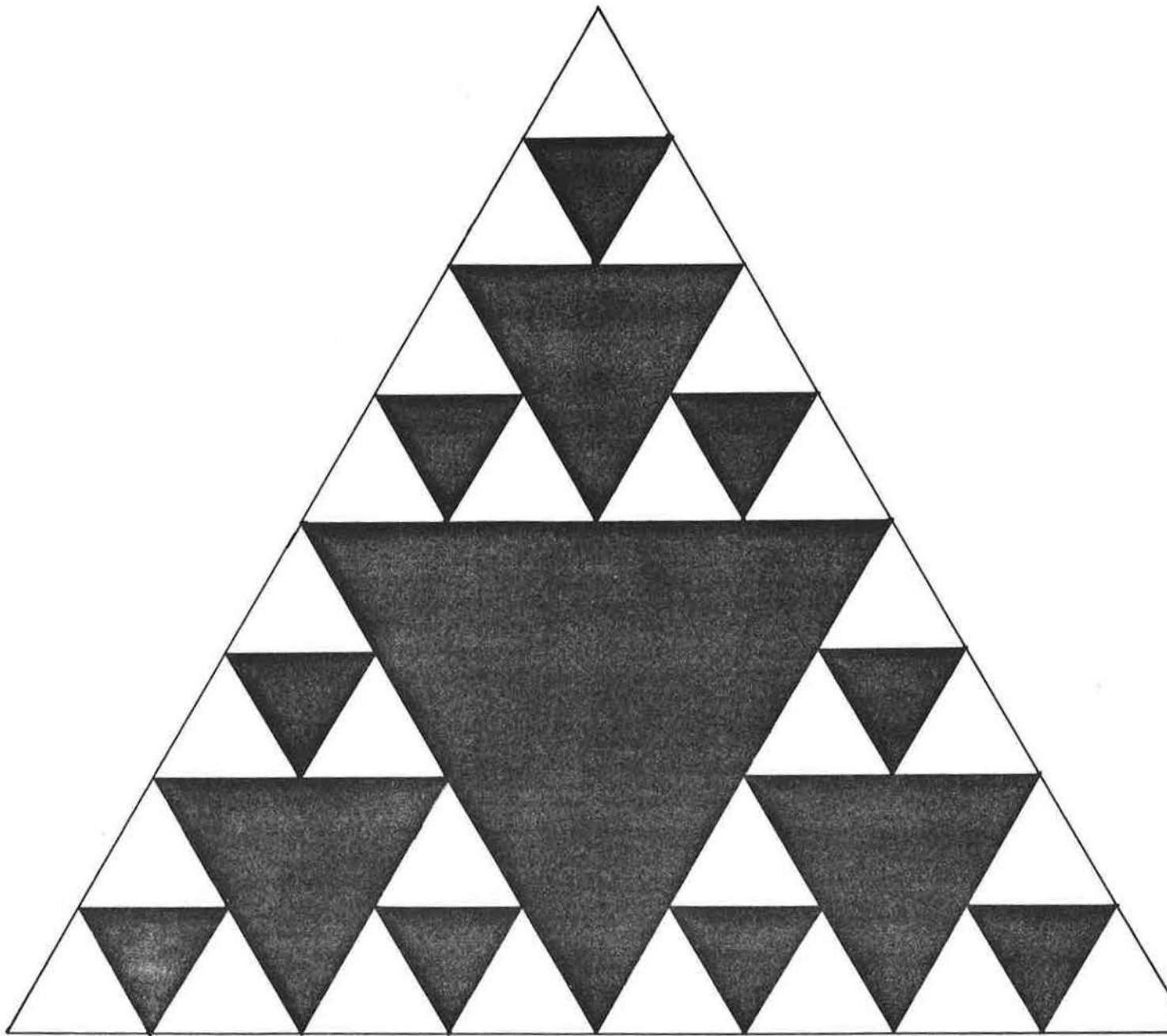


Figure 4.2.2

## APPENDIX A

### LARVAL OTOLITH MICROSTRUCTURE and THE GROWTH TRAJECTORIES OF INDIVIDUAL LARVAE IN THE SEA

It is well known that the microstructure of larval fish otoliths may be interpreted in terms of the age of individuals with a resolution of 1 day. In general, after some early stage corresponding approximately to the time of first feeding, ring increments are deposited on the otolith with diel frequency, and are visible by light microscopy. The number of rings in an individual otolith, therefore, indicates the age since hatching, minus the age at first ring deposition (Panella, 1971; Campana and Nielsen, 1985).

In principle, considerably more information on the past history of the individual larvae may be obtained from otolith microstructure. The width of the otolith is lineally related to the standard length of the larvae for most species. Hence, the radial distance of each ring from the otolith centre is a direct record of the growth trajectory of that individual. This realization has given rise to two approaches which have the potential to give great insight into early life survival processes, and provide vital data for modelling studies.

The first approach is designed to estimate the temporal variations in relative mortality within an annual spawning season for a population. The principle is to sample the surviving recruit population (metamorphosed individuals), and to estimate the proportion of the survivor population originating from each hatching date during the season from the otolith microstructure. The difference between the proportion of survivors derived from each hatching date, and the actual contribution of that hatch date to the total annual production of larvae (estimated from ichthyoplankton sampling) is then a measure of the relative mortality of those hatchlings relative to larvae hatched on other days during the season. The survivor-birthdate approach was developed to study the seasonal pattern of survival of northern anchovy (*Engraulis mordax*) in relation to mesoscale oceanographic features. Periods of strong upwelling were found to be correlated with low relative survival of larvae (Methot, 1983). The approach has subsequently been successfully employed in a number of regions to establish the important mesoscale processes having most significant influence on survival.

The second valuable application of otolith microstructure involves the evaluation of size-dependent mortality in a population. As before, otoliths are collected from samples of the surviving metamorphosed population, but in this case the objective is to determine what the length distribution of the survivors was on some date prior to sampling, *e.g.*, when the population was still in the larval phase. Instead of back-calculating the age at a particular size (hatching) from individual otoliths, the size at a particular age is determined from measurements of ring radius measurements. Any discrepancy between the back-calculated length distribution of the population and that measured at the time in the field is then a measure of the relative size-specific mortality. In general, where this approach has been applied, the data indicate higher mortality of the smaller individuals in the population relative to the larger individuals (*i.e.*, the mean back-calculated length of the survivors is shifted towards larger sizes relative to the original length) (Post and Prankevicius, 1987).

Both of these approaches rely critically upon unbiased sampling of the survivor population to obtain otoliths. Nevertheless, if carefully performed, the methods provide unique and powerful opportunities to study the interactions of growth and mortality at the population level in the field, and their full potential for evaluating models of survival processes has yet to be realized.



## APPENDIX B

### ESTIMATION PROBLEMS OF LARVAL FISH GROWTH

Fish larvae vary in their date of egg release and their growth rate. They are subject to size-selective fishing mortality and are sampled with size-selective gear. The mean and variability of growth and size-selective mortality cannot be simultaneously estimated using samples of the length distribution at age alone (Myers, 1989). Therefore, it is necessary to use individual growth trajectories calculated from growth increments from otoliths. In order to obtain the full information from such data, the parameters describing the variability of growth and egg release, size selective mortality, and the size selectivity of the sampling gear must be estimated using a likelihood which is a function of the growth trajectories of individual larvae, as opposed to simply the length at age distributions. Such estimation methods have not been developed.

## APPENDIX C

### PROCESS-ORIENTATED TOPICS FOR FURTHER RECRUITMENT STUDIES

The shape of future recruitment studies should be determined by two factors. Firstly, the need for focused data gathering to support objectives specific to model formulation or testing, and secondly, the need for more general observational information on the biology of early life stages of species under investigation. To illustrate the types of process-orientated issues which might be addressed, a list has been prepared. It should not be regarded as exhaustive, but represents those aspects which may be considered to be important for future recruitment studies from both a modelling perspective and to improve basic understanding. In each case, the appropriate methods have been indicated, and the feasibility of carrying out such measurements is assessed, taking into account both scientific and financial considerations. It is important to note that none of the topics listed could stand alone as a "recruitment programme", but would need to be linked together.

#### **1 Variation in Large-Scale Physical Oceanographic Features, Larval Retention and Dispersal**

##### Questions from modellers to practitioners:

- What is the variability in physical oceanographic conditions over the spatial range occupied by the spawning products of a stock?
- How does the spatial range occupied by a stock vary with stock density?
- At what stage do larvae become capable of significant horizontal migration behaviour?

##### Questions from practitioners to modellers:

- Can the large-scale temporal and spatial variability in the volume and distribution of suitable habitats for larval fish be related to climatic and basin-scale oceanographic characteristics?
- What types of measurement are likely to be necessary to enable the effects of small-scale processes to be integrated over larger spatial and temporal scales?

##### Methods:

Interactive multidisciplinary ichthyoplankton and hydrographic surveys using drifting buoys, satellites, acoustic current profilers, and models to track water current. Laboratory investigations of swimming behaviour and schooling in relation to organogenesis development to determine when horizontal migration may become active, rather than through interaction with vertically structured horizontal advection.

##### Comments:

The objective is to investigate the co-distributions of larvae and oceanographic features such as fronts, eddies, filaments, and coastal currents which may be characteristic features of shelf ecosystems, and evaluate the effects of these features. The approach is, therefore, very valuable for ecosystem comparisons. The information is essential for determining the scales required for integration of basic biological and physical parameters.

### Feasibility:

Highly feasible at many levels of sophistication.

## **2 Growth and Mortality and Their Interaction**

### Questions from modellers to practitioners:

- Is it possible to define a "parcel" of water in three dimensions (horizontal and vertical) which can be regarded as behaving like a homogeneous Lagrangian "box" over some specified time period?
- Can growth and mortality be measured separately or together at the spatial and temporal scales used to define the box?
- Do growth and mortality vary with space and time, *i.e.*, between parallel or sequential Lagrangian boxes? If so, by how much?
- Is the ratio of mortality to growth constant over any interval in the spatial, temporal, or larval size dimensions?
- How do the increments in larval fish otoliths relate to growth in length, particularly during periods of food limitation? In particular, if growth in length ceases for a period of days, how is this recognized in the otoliths?

### Questions from practitioners to modellers:

- How do growth and mortality rates (and the variability in these rates) interact to control survival?
- Is it important from a population dynamics point of view to devote effort to distinguish between larvae which die as a result of starvation at first feeding, and those which suffer high daily mortality as an indirect consequence of reduced (food-limited) growth?
- What are the appropriate spatial and temporal sampling resolutions required to provide data for evaluating the functional parameters in various models of survival (*e.g.*, Shepherd and Cushing, 1980)?
- How can we recognize the occurrence of density dependence of growth or mortality during the early life history?
- How can we take account of possible density dependence as well as environmental factors in measurements of the temporal variation in relative survival of larvae hatched at different times during the annual spawning season, as estimated from otolith microstructure data?

### Methods:

Direct estimation of growth and absolute mortality by sequential surveys of eggs and larvae abundance, and subsequent tracking and sampling of cohorts. Indirect estimation of relative mortality by sampling of late larvae and/or early juveniles, and examination of otolith microstructure to determine birthdates and individual growth trajectories over time of survivors. Two possibilities for estimating relative mortality:

- a) Comparison of temporal production pattern of larvae with survivor birthdate frequencies, to determine within season variations in relative mortality at a function of birthdate.

- b) Comparison of length distribution of survivors at some time previous to sampling calculated from individual growth histories, with the actual length distribution observed at that time, to determine relative mortality in relation to size. Indirect estimation of growth rate possible by RNA/DNA, TAG/sterol ratios, and other biochemical correlates of growth.

#### Comments:

Estimation of absolute mortality is difficult due to problems of accounting for dispersal. Indirectly, otolith approaches have not yet been widely practiced. Both approaches are very labour intensive both in terms of field sampling and laboratory analysis. Valuable approaches for ecosystem comparisons, and of fundamental importance for evaluation of models.

#### Feasibility:

The cohort tracking approach is not very feasible on the large scale, and depends on finding a suitable situation of easily identifiable patches. The otolith approach is feasible but requires careful consideration of sampling implications and methods to avoid bias in the analysis.

### **3 Predation on and Food Capture by Larval Fish**

#### Questions from modellers to practitioners:

- Can the abundance of actual food and predator organisms be estimated at the scale of the Lagrangian box?
- How much of the variance (if any) in growth and mortality can be explained in terms of variations between boxes in predators, food, and physical factors affecting predator encounter rate?
- How variable is the ratio of prey size to predator size, and are there any consistent trends in the variability?
- How important is past experience in determining the prey selection behaviour of fish and larvae (*i.e.*, is behaviour purely deterministic or are learning and adaptation important)?
- Is predation mortality density dependent? If so, in what way would cannibalism be of considerable interest?
- What characteristics of prey need to be taken into account when considering prey quality?

#### Questions from practitioners to modellers:

- We can observe a general decreasing trend in abundance of organisms with increasing size in the sea. How does the rate of decrease relate to predation mortality?
- How does the temporal and spatial variability in size-structuring of organisms relate to the mortality losses of larval fish that we actually observe?

#### Methods:

Field sampling of a wide size range of organisms in the sea, aiming to sample as many size classes in the ecosystem as possible, with equal precision. Enumeration and identification of larvae and other organisms. Concurrent sampling of larvae for stomach contents analysis to measure size, shape, and species composition of prey. Focused studies on potential predators to detect eggs or larvae in stomachs where feasible and evaluate size, shape, and species composition of alternative prey. Gut evacuation rate data required for

predators and larvae. Study should be carried out in conjunction with investigations of total or relative larval mortality rates.

Prey identification in stomachs by microscopic analysis, or immuno-assay where applicable. Incidence of starvation can be estimated from historical methods (*e.g.*, height of gut epithelial cells).

#### Comments:

Very difficult sampling problems since several gears required to cover the range of species required in the analysis. Extremely time-consuming analytical task. Identification of eggs and juveniles in vertebrate stomachs is relatively easy in some cases, but larvae are very hard to detect. In cases where both predator and prey are captured with the same gear, codend feeding may be a problem. Eggs and yolk-sac larvae can be identified in some invertebrate stomachs from immuno-assay techniques. The approach is very valuable for ecosystem comparative studies. Profitable interface with ecosystem modelling approaches.

#### Feasibility:

Difficult, expensive, and time-consuming, but potentially very rewarding. Identification of predators is very difficult.

### **4 Vertical Migration and Distribution of Larvae**

#### Questions from modellers to practitioners:

- What are the time and space scales of vertical migration in larval fish in relation to the dimensions of the Lagrangian box previously defined as the unit of sampling volume?

#### Questions from practitioners to modellers:

- What consequences do the temporal and ontogenetic variations in vertical distribution and migration that we observe in larval fish have for their horizontal dispersal?
- How do the vertical migrations and distributions of prey and predators interact to affect the growth and survival of the larvae?

#### Methods:

Vertical distribution sampling of larvae, prey, and potential predators with high time resolution using opening and closing nets or acoustics. Concurrent measurements of vertical distributions of horizontal velocities and hydrographic parameters (*e.g.*, using acoustic doppler current profiler and CTD systems). Accurate measurements of sub-surface light intensity.

#### Comments:

This question represents a key interface between biology and physics and should be a high priority project. The consequences of spatial interactions of larvae, prey, and predators in the vertical dimension require evaluation in a model framework to estimate the encounter rates and probability of capture. The approach is especially valuable for the comparative ecosystem approach.

#### Feasibility:

Highly feasible.



## 5 Structure and Physiological Condition of the Spawning Population and Reproductive Output

### Questions from modellers to practitioners:

- What is the range of variation in egg quality and annual egg production (eggs/g mature fish), age at maturity, and size at maturity in relation to the abundance of the target and competitor species?

### Methods:

Trawl sampling of adults for fecundity vs age measurements and age composition of adult stock. Fat content measurement on adults to assess condition. Measurements of egg size, yolk content, and hatching success to assess egg quality.

### Comments:

Annual fecundity of migratory species may be determined during the feeding migration. Fat accumulated during the feeding phase may be related to total fecundity and/or egg quality. It is possible that industry records of fat content could be utilized for time-series studies of condition once the detailed interrelations had been worked out.

### Feasibility:

Moderately feasible - diverse sampling and analysis methods required. Annual fecundity difficult to determine for batch spawners. May be difficult to obtain samples of adult fish at the appropriate time of year for some species. Attractive, but not an essential element of a comparative ecosystem study.

### Supplementary questions:

- Do toxic algal blooms have a significant effect on survival?

### Methods:

Laboratory assays of toxicity and opportunistic field sampling of bloom organisms and larvae, aided by satellites.

### Comments:

Laboratory assays are not well understood or readily available. Targeted sampling is difficult to achieve. Of local significance, but little value for ecosystem comparisons.

### Feasibility:

The approach is being carried out in some areas and is very feasible.

- Does pollution affect the survival of eggs and larvae?

### Methods:

Considerable controversy over methods (*e.g.*, embryo development as an index of pollution stress). Few methods available.

Comments:

Principle problem is to distinguish variability due to pollution from natural variability. There are few convincing studies where this has been achieved. The approach is of little value for ecosystem comparisons.

Feasibility:

Very low feasibility with present technology.

- What is the role of genetics in determining growth and survival?

Methods:

No well-established methods.

Comments:

The question is very challenging and is an important area of fundamental supporting research with many sub-questions. We do not have many geneticists involved in our science, so it is difficult to gain an assessment of the potential of this area.

Feasibility:

Not generally feasible with present technology.

- Is disease and/or parasitism a significant cause of mortality or growth impairment?

Methods:

Opportunistic observations of parasite incidence, followed up with a laboratory evaluation of consequences for survival.

Comments:

Has been demonstrated to be a significant factor in some circumstances. Not generally of high value for ecosystem comparisons, but potentially a powerful density-dependent regulation process.

Feasibility:

Highly feasible if the situation arises.

## ANNEX A

### ICES-IOC STUDY GROUP MEETING ON MODELS FOR RECRUITMENT PROCESSES

Paris, 7-11 May 1990

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