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Biological Oceanography Committee

REPORT OF THE WORKING GROUP ON RECRUITMENT PROCESSES

Nantes, France, 26-28 June 1990

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I TERMS OF REFERENCE AND PARTICIPANTS

At the 1989 ICES Statutory Meeting, resolution (C Res 1989/2:40) was adopted as follows:

The Working Group on Larval Fish Ecology will be renamed the Working Group on Recruitment Processes (Chairman: Dr M. Heath) and will meet in Nantes from 26-28 June 1990 at national expense to:

a) Examine and report on a proposal prepared by the Chairman (through correspondence with selected specialists) for a coordinated recruitment study integrating all life stages of two or more species within selected ecosystems.

b) Report on progress on the check list of cod and haddock spawning characteristics.

c) Report on progress on the otolith microstructure intercalibration exercise.

The meeting was attended by the following:

J. Anderson	Canada
O. Astthorsson	Iceland
J. Beyer	Denmark
K. Brander	United Kingdom (England)
S. Campana	Canada
Y. De Lafontaine	Canada
Y. Desaunay	France
B. Ellertsen	Norway
J. Gamble	United Kingdom (Scotland)
A. Garcia	Spain
O. Hagstrom	Sweden
M. Heath	United Kingdom (Scotland) (Chairman)
E. Houde	United States of America
C. Koutsikopoulos	France
N. Lacroix	France
F. Lagardere	France
G. Laurence	United States of America
G. Lough	United States of America
J. Magnusson	Iceland
J.V. Magnusson	Iceland
J. Marchand	France
E. Moksness	Norway
H. Mosegaard	Sweden
L. Motos	Spain
P. Munk	Denmark
W. Nellen	Federal Republic of Germany
J. Nichols	United Kingdom (England)
D. Schnack	Federal Republic of Germany
P. Solemdal	Norway
S. Tilseth	Norway

J. Alheit attended the meeting as an observer from the Intergovernmental Commission of Unesco.

II OVERVIEW OF THE MEETING

1. Introduction

At the start of the meeting the Chairman briefed the participants on two other ICES initiatives relating to fish recruitment which were relevant to the activities of the RPWG (the ICES Study Group on Cod Stock Fluctuations, and the ICES Study Group on Models of Recruitment Processes). The draft report of the Modelling Study Group (CM 1990/A:5 draft) was distributed on the first day of the meeting, and some discussion of its contents took place later. The Meeting heard reports from participants on the development of the Cod and Climate Change programme, and associated initiatives in the USA. The Chairman posed three questions to be borne in mind throughout the Working Group discussions:

a) What stance should the RPWG take in relation to the "Cod and Climate Programme" presently being developed partly under the auspices of the Study Group on Cod Stock Fluctuations?

b) Is the RPWG prepared to organise a coordinated recruitment study programme?

c) What should be the future roles of the RPWG and the Study Group on Models of Recruitment Processes?

2. Review of the Cod and Haddock Checklist

The business of the Working Group commenced with a presentation by K. Brander and discussion of the status of the checklist on cod and haddock spawning characteristics. After a slow start, an encouraging number of responses had now been received, and more were promised. It was stressed that the checklist contained both documented data and observations, as well as the personal ideas and inferences of the contributors. There was agreement that the exercise was valuable and should continue in an interactive way, but remain restricted to cod and haddock for the meantime. There was a general agreement that whilst the full information set should be circulated only amongst the contributors, the well documented information should be collated and receive wider circulation, since this could provide a good starting point for a comparative study. There were obvious links between this aspect of the RPWG activities and the intentions of the Cod and Climate Change (CACC) Programme.

3. Review of the Otolith Microstructure Intercalibration

E. Moksness and S. Campana presented the results of the Otolith Microstructure Intercalibration Exercise. The Exercise had concentrated mainly on readings of larval herring otoliths since herring had been the most convenient to rear in large numbers. However, some comparisons of cod and sole otolith readings had also been carried out. Herring otoliths have particular problems associated with interpretation of their microstructure, in particular the separation of early rings which may be less than the resolution of light microscopy in slow growing larvae. The results indicated that most investigators had some difficulty determining accurate birthdates although there were significant differences among investigators. Age differences between samples were, on average, accurately estimated by most investigators. The results have serious consequences for the conduct of cooperative research programmes in which birthdate distributions are to be determined. There was agreement that the results warranted publication in the primary scientific literature, and that there was now an adequate justification for holding a workshop on otolith microstructure to review methods and procedures.

4. Working Group Discussion Document

The Chairman presented the Discussion Document (see Appendix) to the meeting. The Document had been developed through two earlier draft stages as a result of the Chairmans' participation in the IOC Workshop on SARP and in the ICES Study Group on Models of Recruitment Processes, and comments received from E. Houde (USA). Although the terms of reference called for a proposal for a coordinated recruitment study, the Discussion Document did not specifically outline a plan of research, but summarised and highlighted the important objectives, principles and techniques for recruitment research, and in particular the role of modelling in any future programme. The important topics which should be addressed in a research programme were presented in the form of a dialogue of questions between modellers and practitioners. The meeting was then opened for discussion of the Document.

In the following discussion, participants related experiences from their own field research programmes, many of which are now completed and in a "data digestion" phase. There was strong support for the comparative approach, in particular the comparison of one species in several ecosystems. However, it appeared that there is still an urgent requirement for "synthesizing principles" to form the basis for drawing together the highly detailed information gained as a result of intensive process-orientated studies, such as those carried out in SARP.

It was difficult to see how significant progress towards understanding the regulation of recruitment could be gained from further detailed field investigations, without a new development in basic thinking. In particular, the prospect of incorporating investigations of multispecies processes and ecosystem dynamics into present-day field programmes was viewed with scepticism by some participants, and yet there was general agreement that this would be necessary for a successful ecosystem comparative study. The problems seemed to arise again from the lack of basic synthesizing principles, resulting in a poor capacity to formulate and test meaningful hypotheses concerning highly complex systems.

5. Size-specific Theory

One possible avenue for synthesis was presented by J. Beyer at the previous meeting of the Working Group in Aberdeen (CM 1989/L:22), and subsequently discussed at the IRG, where the need for new developments in basic thinking had also been stressed. This relates to the use of size-specific rates of processes instead of age specific rates. In a recent publication (Beyer, 1989), it was explained how this change in thinking might allow new hypotheses concerning multispecies interactions, ecosytem dynamics, and in particular predation processes to the formulated, synthesizing information across species as well as within species. At the suggestion of the Chairman, J. Beyer presented a summary of the size-specific theory to the meeting. The theory is an attempt to capture the most crucial processes by means of a series of first order generalised principles - simple rules governing growth and survival expressed in terms of the single most important controlling factors.

Considerable time was devoted in the meeting to clarifying the important principles of the theory and discussing their significance for the way in which research programmes might be structured and conducted in the future. Size-specific hypotheses should be based on an understanding of individual variability, whilst classical approaches depend on the processes affecting representative populations. However, many participants had some difficulty accepting that size characteristics could explain a significant proportion of individual variability.

The meeting considered and documented major complications of the theory representing deviations between the first order generalisations and reality. Clearly these should be the focus of future investigations at the cohort/population level as well as at the ecosystem level. Changes in methods or approaches which might be required to furnish the requirements of a size-specific approach to recruitment problems were also discussed. There was no doubt that acceptance of the theory would require new priorities and methods of work in any future field programme.

6. Prospects for a Coordinated Study

There was a consensus view that the RPWG was not ready to plan a coordinated recruitment study since it was not yet possible to design a programme that would "break new ground". There is a clear central role for modelling in any new programme. The models required should synthesize and enlighten, and not attempt to reproduce complex detail. It is too easy to produce a model which is almost as complex and difficult to understand as the processes it seeks to describe. No operational programme devised to date seems to incorporate sufficient synthesizing power to condense detailed knowledge of complex processes into models of the population dynamics in an intelligible manner. Consideration of processes in terms of size-structure appears to be a possible avenue for progress in this respect. The first priority before the next meeting of the Working Group, should therefore be for members to critically examine historical data sets to determine the relationships between growth, mortality and size in the light of the first-order generalisations indicated by size-specific hypotheses.

The ideas on size-structured ecosystem dynamics seemed to have the potential to stimulate significant advances, particularly in relation to predation on larval stages. However, the theory at present has the status of a set of preliminary hypotheses which need further development for the Working Group to be able to formulate rigorously testable hypotheses. In particular, an ecosystem level model may be difficult to interpret in terms of species specific recruitment. A high priority should be placed on convening Modelling Group Meetings to examine and develop the size-structured ecosystem concept and better define the linkage with fish recruitment. This will require a stepwise procedure of hypothesis development and testing, and a continued dialogue between modellers and practitioners.

The collection and collation of information in the cod and haddock checklist was seen as an important task of the Working Group, and one which could help in the development of a coordinated comparative study on these species. The process of preparing a species checklist was considered to be almost an essential precursor for a large scale coordinated multi-ecosystem investigation.

7. Future Role of the RPWG

Some participants expressed concern at the expansion in remit of the Working Group. Previously, the Group had been concerned only with larval fish ecology, but the inclusion of other aspects of recruitment processes required the range of expertise represented on the Group to be widened. Further increases in the number of participants could produce an unmanageably large meeting. Nevertheless, the participation of oceanographic and invertebrate biology experts would be highly desirable.

The vital role of modelling experts in the future activities of the Working Group was clearly recognised. The concept of a dialogue between modellers and practitioners was strongly supported, and it was noted that this appears as a conclusion of the Study Group on Models of Recruitment Processes (SGMRP). However, it was felt that a joint meeting of modellers and practitioners would not be the most productive way forward. It was proposed that the SGMRP should be incorporated into the Recruitment Processes Working Group, but that the two groups should retain separate chairmen, and meet in alternate years with a small number of cross-group participants. The cross-group participants should play a key role by preparing working documents for both groups prior to any meetings. There was some regret that the

1990 meeting of the Modelling Group had been held only shortly before the RPWG with the result that participants did not have adequate opportunity to study and consider the report from the modellers.

III RECOMMENDATIONS

The Working Group recommends the following:

1. a) That the checklists of cod and haddock spawning characteristics should be completed by K. Brander.

   b) That an *ad hoc* subgroup of the RPWG should meet in order to prepare a synthesis manuscript from the cod and haddock checklists for circulation to contributors and Working Group members. Convenor: J. Nichols.

2. That the RPWG should be reconstituted to include the Study Group on Models of Recruitment Processes, and that the following procedure should be adopted:

   a) The RPWG should be composed of two independently chaired components with a small number of cross-group participants.

   b) The future RPWG should incorporate a dialogue between the two components.

   c) The composition of the practitioner part of the RPWG should be expanded to include experts on oceanography and invertebrates.

3. That the next meeting of the Working Group should emphasise the modelling component of recruitment processes, specifically to explore the theoretical aspects of size-specific theory.

4. That the modelling component of the Working Group should meet in 1991. The practitioner component of the Working Group should meet in 1992 in Fuengirola, Malaga, Spain, and the terms of reference should include the following:

   a) Review field and experimental evidence for a relationship between growth and mortality rates in eggs, larvae and juvenile fish.

   b) Consider the statistical basis for determining growth trajectories of individual fish from otolith microstructure.

   c) Review progress on synthesis of information contained in the cod and haddock checklists with a view to identifying underlying principles of recruitment variability.

5. That before the next meeting of practitioners, members of the Working Group should re-examine their existing data bases and research programmes in terms of size-specific theory, emphasising particularly the relationships between growth, mortality and size. The results should be presented at the next Working Group meeting.

6. That the results of the otolith microstructure intercalibration exercise should be further analysed and written up by S. Campana and E. Moksness, with a view to publication in the primary scientific literature.

7. That an otolith microstructure workshop should be convened by S. Campana and E. Moksness within the next two years. The workshop should examine sources of variability in otolith interpretation, and recommend techniques by which accuracy and precision can be improved. Workshop attendance should be restricted to individuals experienced in otolith microstructure techniques who are also members of the Working Group (or their proxies at the same laboratory) and/or participants in the 1990 Otolith Microstructure Intercalibration Exercise.

IV REPORTS ON INDIVIDUAL DISCUSSION TOPICS

1. The Cod and Climate Change Programme

The first of two ICES initiatives in addition to the RPWG involving studies of recruitment was defined by Council Resolution 1989/2:14 which established a Study Group on Cod Stock Fluctuations (chairman S. Sundby) to develop a plan to predict stock fluctuations using climatological indices. The task included:

a) Assembly of time series of oceanographic, meteorological and cod population dynamics data for various regional seas.

b) Development of models relating physical environmental variables to adult and larval cod dynamics.

c) Accounting for population variability in terms of climatological variation on an Atlantic-wide basis.

A meeting to discuss the planning of a study of Cod and Climate Changes in the North Atlantic (CACC) was held in Bergen during 16-18 January 1990. The report of the meeting formed the starting point for the ICES Study Group. Apparently, the CACC is intended to be submitted to ICES as a plan for a study programme, at the Statutory Meeting in 1990.

The CACC also relates to North American initiatives in recruitment research. In particular, the US National Science Foundation Global Ocean Ecosystems Dynamics Program (GLOBEC), the US National Oceanic and Atmospheric Administration Coastal Ocean Program (COP) and Climate and Global Change (CGC) programme, and the Canadian Ocean Production Enhancement Network (OPEN) programme, all have components related to cod population fluctuations in the NW Atlantic. The meeting heard a brief overview of the NOAA plans from G. Laurence. The GLOBEC proposals relating to CACC were discussed at a meeting convened in Nova Scotia during 19-21 June.

No member of the Working Group was able to give a detailed appraisal of the state of development of the CACC in either the NE or NW Atlantic, although some members had participated in the Bergen and Nova Scotia meetings. K. Brander briefly summarised the discussion at the Bergen meeting.

In the absence of any detailed information on the intentions of the CACC programme, the Working Group was unable to evaluate the recruitment component.

2. Report from the Study Group on Models of Recruitment Processes

ICES Council Resolution 2:21 established a Study Group on Models of Recruitment Processes (SGMRP). This was in response to a recommendation from the Intercommittee Recruitment Group (IRG, chairman M. Sissenwine), and the Group met in Paris between 7-11 May 1990. The Chairman and two other members of the RPWG attended the Paris meeting. The draft report of the Modelling Study Group had become available only shortly before the RPWG, so prior circulation had not been possible. However, copies were distributed to participants on the first day of the meeting.

Some participants expressed concern at the emphasis placed in the SGMRP Report on the empirical analysis of stock and recruitment data derived from VPA, and wished it to be noted that this should not be interpreted as an indication that process orientated studies were unnecessary for resource management.

The RPWG had not been asked to consider the application of "conventional" stock-recruitment data. The general task of the Working Group was to derive and quantify information on factors affecting recruitment which in the long term can be applied to develop and improve assessment methods. Nevertheless, in view of the emphasis placed by the Modelling Study Group on the topic, the Working Group discussed the use of stock-recruitment data, and concluded as follows:

a) Stock and recruitment "relationships" are the basis of current management approaches and empirical methods may be a means of obtaining some indication of relatively safe exploitation levels in the immediate term. However, the basis of the empirical S-R methods has no potential for development, nor is it capable of assisting with medium to long-term prognoses, for example the effects of climate change.

b) The empirical S-R approach has no potential for taking into account multispecies interactions, in particular the effects of other species on the stock-density component of the relationship.

c) Existing S-R data may be to a large extent an artefact of Mans influence on marine populations. The present-day biomass of exploited populations is probably very much lower than the pre-exploited levels where density dependent and environmental factors may have an overwhelming influence survival. S-R relationships might be best studied in unexploited species, where it may be possible to determine the so called "slope at the origin" from biological considerations.

d) The empirical approach may be inadequate even for management purposes in situations where there is high uncertainty in the VPA estimates of stock and recruitment, due for instance to high bycatches of juveniles.

3. Report on the Collection of Information on Cod and Haddock Spawning and Recruitment Characteristics, for Inclusion in a Stock-comparative Checklist

This study was initiated by the Larval Fish Ecology Working Group in 1988, and checklists were circulated at that time, again in 1989 at the ICES Early Life History Symposium, and again in April 1990. The total number of replies at the time of the Working Group was 12 for cod and three for haddock. Half of these were received only four days prior to the meeting, and more were expected.

The areas covered for cod included US waters, part of the Scotian Shelf, Gulf of St Laurence (north and south), Grand Banks and Newfoundland, Iceland, Norway, the North Sea and Irish Sea. The level of detail and quality of data vary greatly, partly due to gaps in knowledge. Nevertheless, the overall result should provide a valuable source of information and ideas to allow comparisons to be made between different areas.

The original proposal for the study stated: "Depending on the level and quality of the response, it may be worthwhile to put all the contributions together in some form of ICES publication, but if it does no more than generate some collective thinking about comparative aspects of recruitment studies it will have served a useful purpose." The latter aim has to some degree been achieved and the possibility of proceeding with publication was discussed.

There are several issues which need to be resolved by contributors to the study and it is proposed to follow these up by correspondence. One of the strengths of the informal approach used so far is that it has encouraged the dissemination of ideas and data sets which might not be sufficiently well formulated to publish. Some data (eg typical densities of eggs) have been supplied in different ways and there may be further scope for trying to standardise the presentation. Bibliographic details need to be collated. Some contributors have offered to supply more information if this is required.

A brief outline and summary of the information in the cod checklists was presented to the meeting. In no area can it be said that the population assessment unit relies on a single distinct spawning group and in some areas a conglomerate of several spawning groups may intermix. The observed fluctuations in year class strength are less than 10-fold (largest year class/smallest year class). Spawning may occur throughout the year at different locations in the north Atlantic. In many cases the timing of cod spawning appeared to be related to the timing of plankton production and particularly to *Calanus*. In some areas the timing of spawning can be shown not to vary with interannual temperature variations. In some areas spawning generally starts in the south and spreads northwards, but in other areas the reverse is true. In several cases a significant proportion of the observed variation in year class size is apparently determined by the time of settlement.

Some editing and completion of the checklists and summary tables and a unified bibliography will be prepared and circulated. Once this has been accomplished the contributors will need to reach a collective decision about what aspects of the study should be published.

4. Review of the Intercalibration Exercise on Otolith Microstructure

The Larval Fish Ecology Working Group (ICES CM 1989/L:22) recommended that an otolith microstructure calibration experiment be conducted to determine both the accuracy and precision of the technique. Given the increasing importance of otolith microstructure examination to early life history and recruitment studies, the experiment was deemed to be an important prelude to any international recruitment programmes that might be conducted. The Working Group also recommended that the results of the intercalibration experiment should be examined before considering the need for an otolith microstructure workshop.

Herring (*Clupea harengus*) and cod (*Gadus morhua*) were selected as the main species for the intercalibration. Known age herring were reared under realistic growth conditions in outdoor mesocosms for up to 57 days, while known age cod were reared in the laboratory under poor and good growth conditions for up to 22 days. E. Moksness (Norway) and S. Campana (Canada) distributed known age larvae to 24 study participants representing 12 countries. Samples were distributed as both unprepared and prepared specimens; ages and sampling frequency were unknown to the participants.

On average, participants were able to determine the relative age of both herring and fast growing cod larvae by counting the daily growth increments. However, absolute ages were underestimated by an average of 8-10 days in herring and slow growing cod. Both accuracy and precision varied substantially among age readers, but most had more difficulty in ageing young (<20 days) herring larvae. Although the analysis had not been completed at the time of presentation at the Working Group, counting accuracy and precision appeared to be the most influenced by reader experience (Tables 1-4; Figs 1-6).

The intercalibration results confirmed the value of otolith microstructure techniques to recruitment studies. However, the Working Group recognised that the observed level of accuracy and precision places some limitation on potential applications; consistent resolution of ± one day is probably not realistic in these species. While cod and herring otoliths are typical of north temperate fishes, inter-specific differences do exist and hence, accuracy and precision may well be greater on other faster growing species. The presence of significant inter-reader differences implies calibration using known-age otoliths is an important prerequisite to collaborative studies.

Inter-sample age differences were reasonably well estimated, implying that growth and mortality could probably be estimated without bias, if imprecisely. Long intervals were more precisely estimated than short intervals. Difficulties in distinguishing increments of young herring larvae imply that birthdate frequencies will probably be somewhat less accurate. The reduced accuracy does not invalidate the approach, but should be acknowledged in interpreting any results.

The Working Group noted that the otolith intercalibration results would be of value to other workers and recommended that the study be published in the primary literature. Such a publication should include recommendations concerning sample preparation and means of examination (eg recommended magnification and the relative utility of SEM and image analysis). The Working Group also recommended other means of standardising and improving techniques, including the conduct of an otolith microstructure workshop and the preparation of an instructional video.

5. Present-day Basic Principles of Population Dynamics, and the Alternative Size Based Theory

The underlying principle of most population dynamics in fisheries science, including VPA, is the age specific mortality relationship:

$$N_{t1} = N_{t0}.\exp(-M.(t1-t0))$$

where N_{t1} is the number of individuals in a cohort at time t1 and M is the age-specific mortality rate over the interval (t1-t0). A consequence of belief in the applicability of this relationship is acceptance that the mean instantaneous mortality rate is constant for any subset of a cohort in which all individuals are exposed to the same predator, prey and environmental conditions. In other words, the individuals in a cohort at time t1 are a randomly selected subset of those present at time t0, or survival is a random process. As an example of this "conditioning" of our thinking, if we wish to measure the mean instantaneous growth rate in a cohort then the most common method is to determine the change in mean length over a period of time, with the inherent assumption that the mortality rate over the same period was independent of length (Fig. 7).

In reality, the case in which the population at time t1 is a random subset of that at t0 may be a comparatively rare occurrence, and may not be a useful generalisation. Indeed, the situation seems completely at odds with even the most basic evolutionary theory which accepts that there is variation between individuals in a cohort, and some individuals will be fitter than others - the survivors must be a non-random subset of the original population.

Beyer (1989) simply asks us to reject the conditioned idea that survival is a random process and accept an alternative generalising principle which may be more fruitful for progress in research. Beyer suggests that as a first order generalisation we take size as the crucial selective characteristic, ie mortality rate is some function of size. In principle, any characteristic could be chosen, but size appears to be the major criterion governing predator-prey interactions. In general, small organisms grow faster, die faster and eat smaller prey than large organisms. Thus, within a cohort we might expect mortality rates to be negatively correlated with size, and positively correlated with the instantaneous growth rate. If we accept this generalisation then we have to recognise that we would have overestimated the mean growth rate in the cohort in our previous example where we measured the change in mean length over a period of time (Fig. 8).

The fundamental change in basic principles suggested by Beyer actually requires only a small change in the way that population dynamics are formulated mathematically. In fact, all that is required in the first instance is to express the decrease in numbers in a cohort as a function of size rather than age:

$$N_{w1} = N_{w0}.l_{(w1,w0)}$$

where $l_{(w1,w0)}$ is the size-specific survivorship for growth from w0 to w1, and in general,

$$l_{(w1,w0)} = \exp\{-\int_{w0}^{w1} (u(x)/g(x)).dx\}$$

where u is the instantaneous mortality rate and g the growth rate. The instantaneous growth rate (G) is given by G=g/w. In the case where the ratio u/G is constant, then the size-specific survivorship is simply:

$$l_{(w1,w0)} = \exp\{-(u/G)(w1-w0)\}$$

and

$$N_{w1} = N_{w0}.\exp\{-(u/g)(w1-w0)\}$$

which is exactly analogous to the form of the age-specific mortality function in common use. The ratio u/g is referred to as the "physiological rate of mortality".

6. Fundamental Difficulties Caused by the Use of Age-specific Thinking, and Solutions Provided by Size-specific Principles

It has often been stated that our inability to study predation on larval fish in the field is a major impediment to progress. Occasionally, it is possible to study the interaction between a larval fish species and one predator species. However, the prospect of considering the availability alternative prey for the predator, and alternative, competing predators on the larvae, is one of bewildering complexity. Nevertheless, these issues are of fundamental importance for understanding and interpreting multispecies and ecosystem dynamics. In addition, larvae are themselves predators on smaller prey items.

The origin of this impediment seems to be the conditioning of thinking imposed by age-specific theory. Age is not a characteristic which can be applied across competing species, far less across predator and prey species. As a consequence, every potential interaction between a predator and prey must be dealt with on a species specific level. There is no possibility of synthesizing information based on age alone.

Unlike age, size is a characteristic of an organism which has biological significance both within and across species. Within species, recruitment is better defined as the abundance at size than abundance at age (variance in size at metamorphosis is generally less than variance in age at metamorphosis). Applied across species, then as a first approximation, the ratio of prey size to predator size might be taken as a constant. The use of size-specific rates as the basis for population dynamics does therefore provide an opportunity to synthesize data across species, and presents new and unforeseen possibilities for investigating and expressing multispecies and ecosystem dynamics. Beyer (1989) has presented a first attempt at simple modelling of a pelagic ecosystem in terms of abundance at size for all species combined, and simple food consumption characteristics (Fig. 9). The model contains only the most crucial principles and requires more consideration and development before it could form the basis of a research programme.

7. Possible Complications of Size Based Theory

The size based theory, and size-structured pelagic ecosystem model was presented as an attempt to capture the most essential mechanism as the core of future thinking - the so called "Occam Razor approach". In so doing, it was recognised that in reality there will be many factors which complicate the basic principles. The Working Group divided into subgroups to consider the potential complications arising under various "process headings".

Oceanographic processes

Fish eggs and larvae, their predators and prey are all patchy in the sea. Patches of different species may be advected at different rates, dependent upon behavioural responses. These factors complicate the space/time scales defining the ecosystem surrounding a cohort of larvae. The size-structured ecosystem approach requires the limits of a parcel of water to be defined by the community within it, not just the distribution of one species. Incomplete understanding of the physical oceanography of a system may frustrate attempts to test the size-specific theory.

Physics may interact with biology by disrupting contact between predator and prey at a wide range of encounter scales (ie encounter between one predator and one prey affected by microturbulence, or encounters between km scale patches affected by advective processes. It is not sufficient to assume that all organisms in a parcel of water have equal accessibility to one another.

Finally, an ecosystem is defined as much by energy and nutrients as by the organisms it contains. Yet, many of the aquatic ecosystems with which we are familiar are characterised by significant exchanges with outside systems, eg river flow, currents, storms, which may vary considerably from year-to-year. The influence of these externally derived energy sources on the size distribution of organisms in the ecosystem is undoubtedly substantial, but proved difficult to consider in terms of the size-structured approach. In its present form, the size-structured ecosystem model assumes energy equilibrium.

Growth and mortality

The dependence of mortality on size may vary during the development of a cohort, so size dependence should be tested within life-history stages.

Variation in the instantaneous rate ratio of growth to mortality is a key factor in the theory. An important question is whether this ratio is constant and over what range of sizes for a particular species. Secondly, how does the ratio vary between species of similar size, and between ecosystems for the same species?

The simple size-structured ecosystem concept assumes that predation mortality is the most important source of mortality. It may be necessary to include other causes of size-specific mortality as well.

Predation and food capture processes

The ratio of prey size to predator size is not constant, but follows some distribution about a central value. The range of prey sizes preferred by a predator can increase with predator size.

Within a preferred size range there are preferred prey types ie prey selection is also a function of quality.

Vertical migration

Vertical distribution of organisms is a response to prey searching, temperature preference, or predator avoidance. Any parcel of water defined as an ecosystem for study purposes must have 3-dimensional structure.

Size distributions of organisms at one point may be modified by vertical migration which may vary with ontogeny even within one species.

Predator avoidance and enhanced prey encounter due to vertical migration behaviour must be an important complication of the basic size-structured ecosystem idea.

Spawning population

Recruitment dynamics of a single species may depend on egg size, egg quality and viability, fecundity, age at maturation, and size at maturation, especially at small population sizes. Little is known about how these parameters vary with target, prey and competitor species density.

Egg quality and viability needs to be defined and established in experimental studies and related both to parental condition and larval growth and survival.

Fecundity is related to individual fish size. Hence annual stock fecundity is related to the size composition of the spawner population.

Fecundity is also related to the feeding conditions during maturation. Experiments on cod have shown that under poor feeding conditions the potential fecundity is reduced and in addition some of the eggs are resorbed.

A progressive decrease in egg size during spawning has been demonstrated experimentally and in the field for cod (a batch spawner). Egg size may affect larval size at first feeding, and cohorts produced late in the season may therefore be composed of smaller individuals than those produced at the start.

Low frequency variations in age at first spawning have been observed in several stocks. This effect may be a consequence of variations in growth rate in relation to a relatively fixed size at maturation. There is very little data on variations in the size at maturation.

The abundance and age/size-structure of the spawning population is the only factor affecting recruitment which is influenced by exploitation. In heavily exploited populations the frequency of first-time spawners may reach 80-90%. Reductions in age at maturation have been connected with reductions in spawning biomass for some species.

8. Consequences of the Size-specific Theory for Current Practice in Recruitment Process Studies

Other measures of size will be required, not just length, for example mouth gape, volume, weight.

Prey size:predator size investigations are of key importance, but should be carefully carried out to compare the pre-digestion sizes of prey, with the estimated sizes of organisms actually encountered by the predator.

The shape of the size distribution of individuals in a cohort is vitally important. Sufficient numbers of individuals must be measured to accurately define the tails of the distribution. What factors generate this distribution? If the distribution is found to conform to some recognised statistical form then the variance and some measure of central tendency may be adequate descriptors in the future. These considerations encourage a holistic approach to population dynamics (viewing the population as a whole) rather than a reductionist approach (working only with mean values of population characteristics).

Tagging or other identification of individuals in a cohort is of paramount importance. Techniques for this should include otolith marking, genetic marking, and biochemical techniques.

The time intervals between sampling of populations should be reduced as far as possible to better characterise populations and rates.

In situ mesocosms may have a valuable role in temporarily containing an assemblage of predators and prey.

All life stages of the target species must be studied to achieve a wide size range of measurements on the same cohort.

Knowledge of the growth history of surviving individuals is of vital importance to estimating size selectivity of survival. The most valuable approach is the use of otolith microstructure to back-calculate the survivor length distribution on some earlier date, for comparison with actual distributions measured at the time. However there are serious statistical, methodological and sampling problems associated with this approach which must be solved.

Field sampling must be carried out in such a way as to measure the density not just of the target species, but also of the full range of sizes of potential predators and prey organisms. This will certainly require deployment of several different types of sampling equipment.

Data should be collected and documented in a standardised format at the highest resolution possible to facilitate testing of models. Measurements should be accompanied with an estimate of their precision.

9. Priority Topics for Examination in the Light of Size-specific Theory

a) The importance of tracking the growth trajectories of individuals is greatly enhanced by acceptance of the size-specific theory. Techniques for interpreting otolith microstructure should be critically examined, in particular the statistical aspects of estimating individual length at some time previous to sampling from increment measurements and otolith radius vs fish size data. This specific problem was highlighted both in the Study Group on Models of Recruitment Processes, and in the present Working Group.

b) The feasibility of alternative measures of size in addition to standard length should be examined. In particular, the feasibility of automation of size measurements (eg by image analysis) should be critically considered, in order to enhance the number of individuals measured each sample collected.

c) The statistical aspects of estimating the physiological rate of mortality (u/g), from for example size distribution data, should be carefully considered.

d) All members of the Working Group should critically re-examine existing data sets on larval and juvenile fish, to determine whether:

   i) acceptance of size-selective mortality could seriously undermine the conclusions of previous analyses.

   ii) the existing data can provide any insight into the dynamics of population size distributions and in particular into the relationship between growth rate and mortality rate.

   iii) the resolution of the existing data is adequate in view of the requirement of size-specific theory, and if not, how it could be improved.

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Beyer, J. 1989. Recruitment stability and survival - simple size-specific theory with examples from the early life dynamics of marine fishes. *Dana* 7, 45-147.

Table 1. Summary statistics of the readings from the different participants.

Partici-pant No.	Sample ID	True Age (days)	Estimated No. increments						Age conver
			Averag	Diff	SD	Min	Max	N	
3	H-9	9	9	0		8	9		-
	H-11	29	18	-11		17	18		
	H-12	40	24	-16		23	24		
4	H-13	3	3	0	0.9	2	5	18	+3
	H-14	18	8	-10	2.7	3	12	8	
	H-15	27	18	-9	3.8	11	22	8	
	H-16	43	30	-13	4.4	21	37	20	
5	H-17	12	0	-12	-	-	-	10	+3
	H-18	21	12	-9	4.7	4	17	9	
	H-19	32	33	+1	2.2	29	36	10	
	H-20	37	43	+6	2.1	39	46	9	
6	H-21	6	2	-4	-	-	-	12	0
	H-22	15	3	-12	0.8	2	4	5	
	H-23	29	16	-13	3.1	11	22	11	
	H-24	47	37	-10	6.5	24	46	12	
7	H-25	9	9	0	1.1	8	11	5	
	H-26	18	13	-5	2.2	10	15	5	
8	H-29	12	3	-9	1.2	2	5	5	
	H-30	21	9	-11	2.2	5	10	5	
	H-31	32	17	-15	5.6	10	22	5	
	H-32	43	39	-4	3.7	34	44	5	
9	H-33	6	0	-6	-	-	-	10	-
	H-34	18	3	-15	0.4	2	3.5	8	
	H-35	37	30	-7	0.6	29	31	10	
	H-36	54	42	-12	0.8	41	43	4	
10	H-38	15	9	-6	-	-	-	1	0
	H-39	24	31	+6	1.7	29	33	4	
	H-40	57	61	+4	1.5	59	64	9	
12	H-46	27	17	-10	1.0	16	18	3	+9
	H-47	35	30	-5	0.9	29	31	4	
	H-48	47	43	-4	2.4	40	46	4	
14	H-53	12	3	-9	1.9	0	6	9	+10
	H-54	21	10	-11	4.1	2	14	13	
	H-55	32	18	-14	4.8	8	25	16	
	H-56	54	40	-14	6.6	28	51	16	
15	H-57	9	3	-6	0	3	3	3	+7
	H-58	15	8	-7	5.9	0	14	5	
	H-60	40	35	-5	4.7	27	40	5	
16	H-61	12	5	-7	1.7	3	8	11	+3
	H-62	27	17	-10	4.1	10	24	10	
	H-63	37	27	-10	4.4	18	32	19	
	H-64	47	37	-10	4.3	31	45	11	
17		16	5	-11	0.5	4	5	5	+10
		29	21	-8	2.0	18	25	13	
		36	26	-10	3.8	16	32	21	
20	H-78	5	4	-1	0.5	3	5	10	+8
	H-79	12	5	-7	0.6	4	6	10	
	H-80	21	12	-9	3.9	12	21	9	
	H-81	29	20	-9	2.9	12	21	10	
21	H-82	9	3	-6	0.4	2	3	5	0
	H-83	18	8	-10	0.7	7	9	5	
	H-84	33	25	-8	2.9	21	29	5	
23	H-89	29	19	-10	1.5	18	20	7	-
	H-90	43	30	-13	3.7	27	36	5	
24	H-91	21	7	-14	2.8	1	11	15	-
	H-92	35	20	-15	2.5	16	24	10	
	H-93	47	34	-13	2.2	31	37	9	

Cod

Table 2. Summary statistics of the readings of C-123 (age 12 days) from the different participants (data from lapillus).

Partici-pant No.	Estimated No. increments					
	Averag	Diff	SD	Min	Max	N
5	15	+3	0.6	14	15	5
6	9	-3	1.8	7	11	4
8	10	-2	0.6	9	10	4
9	8	-4	3.8	4	11	3
12	12	0	0.6	12	13	3
15	14	+2	3.1	11	17	3
16	11	-1	1.2	10	12	3
23	7	-5	1.0	5	8	8
24	6	-6	1.2	5	7	3
25	8	-2	2.0	7	11	4

Table 3. Summary statistics of the readings of C-150 (age 22 days) from the different participants.

Partici-pant No.	Estimated No. increments					
	Averag	Diff	SD	Min	Max	N
5	15	-7		15	15	1
6	6	-16		6	6	1
8	9	-13		9	9	1
9	7	-15		7	7	1
12	21	-1		20	22	2
15	16	-6		16	16	1
16	10	-12		10	10	1
23	13	-9		12	13	2
25	8	-14		8	8	1

Table 4. Summary statistics of the readings of C-189 (age 22 days) from the different participants (mounted and polished prior to distribution).

Partici-pant No.	Estimated No. increments					
	Averag	Diff	SD	Min	Max	N
5	24	+2		23	24	2
6	15	-7		15	15	1
8	14	-8		14	14	2
9	6	-16		6	6	2
12	15	-7	3.6	12	19	3
15	29	+7		29	29	2
16	13	-9		13	13	1
20	-					
23	15	-7		15	15	1
24	6	-16		6	6	2
25	10	-12		12	12	1

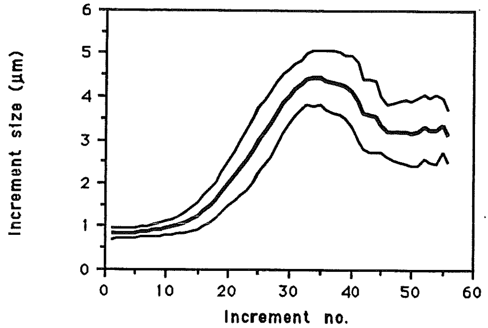


Figure 1 . The average increment size (µm) with standard deviation of the examined herring otoliths. Data from the reading on herring otoliths at Research Station Flødevigen.

FIG. 2 FREQUENCY HISTOGRAM OF HERRING

AGE-COUNT DISCREPANCIES

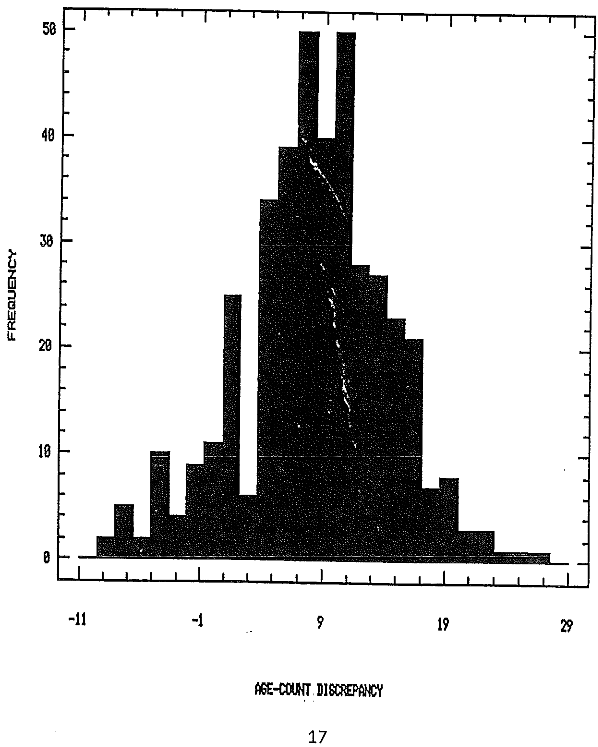
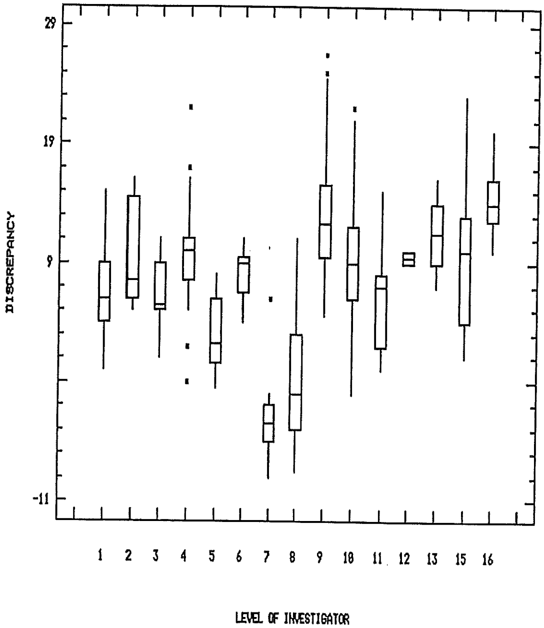


FIG. 3. BOX AND WHISKER PLOTS

FOR FACTOR LEVEL DATA



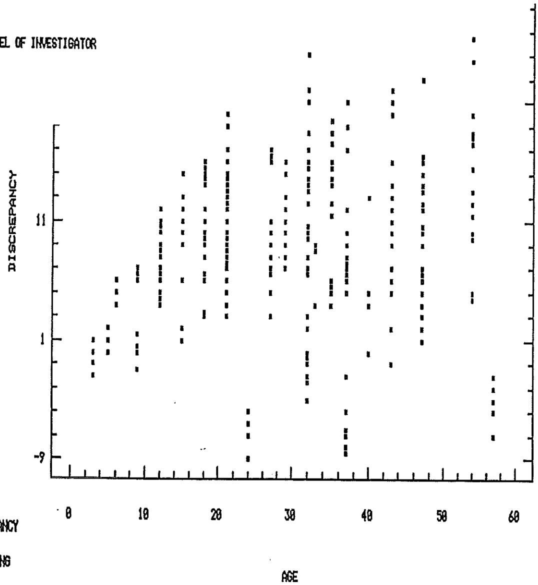


FIG. 4. AGE-INCREMENT DISCREPANCY

AS A FUNCTION OF AGE IN HERRING

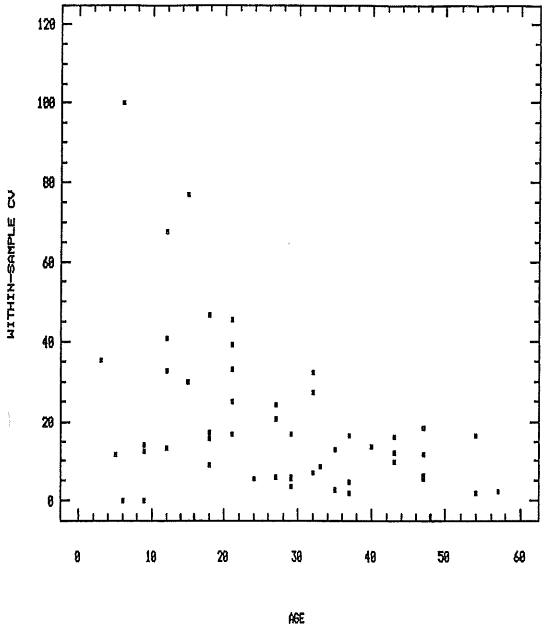


FIG. 5. WITHIN-SAMPLE PRECISION (CV) BY AGE FOR HERRING

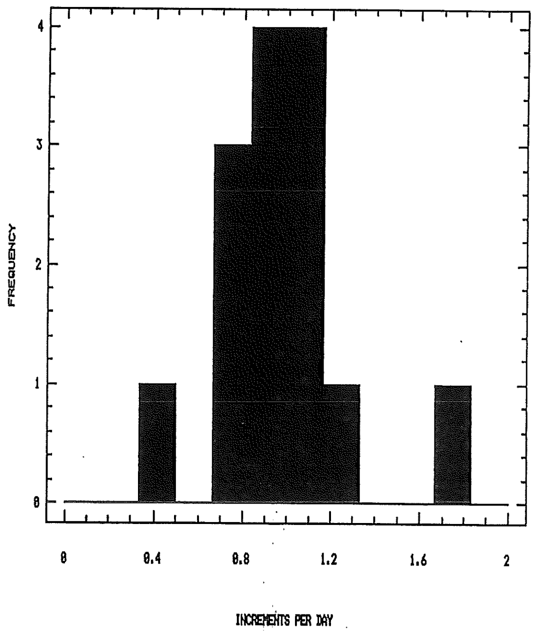


FIG. 6 FREQUENCY OF APPARENT INCREMENT FORMATION RATES ACROSS INVESTIGATORS

Figure 7

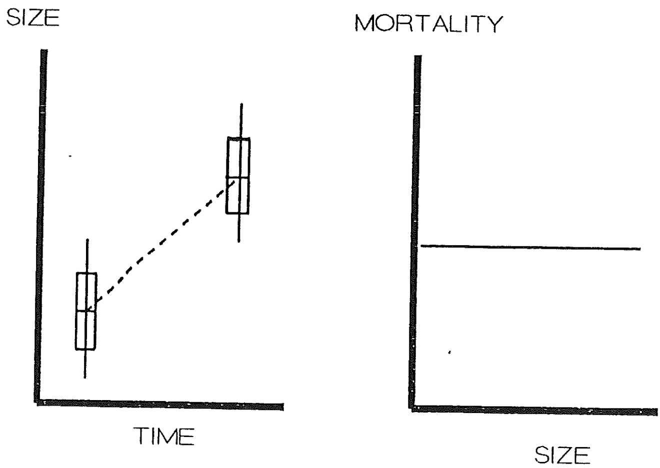


Figure 8

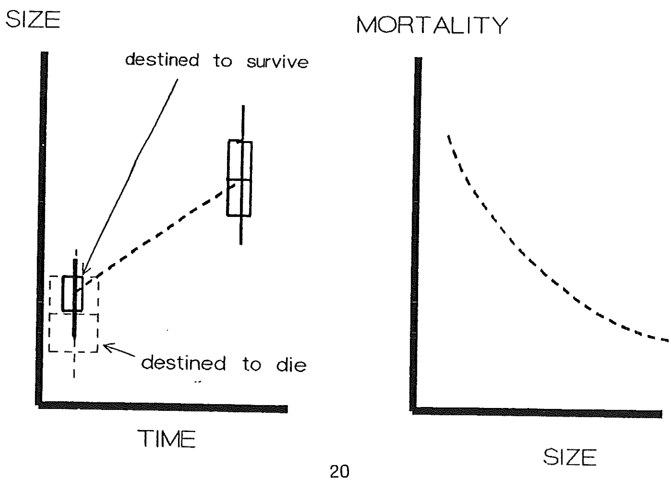
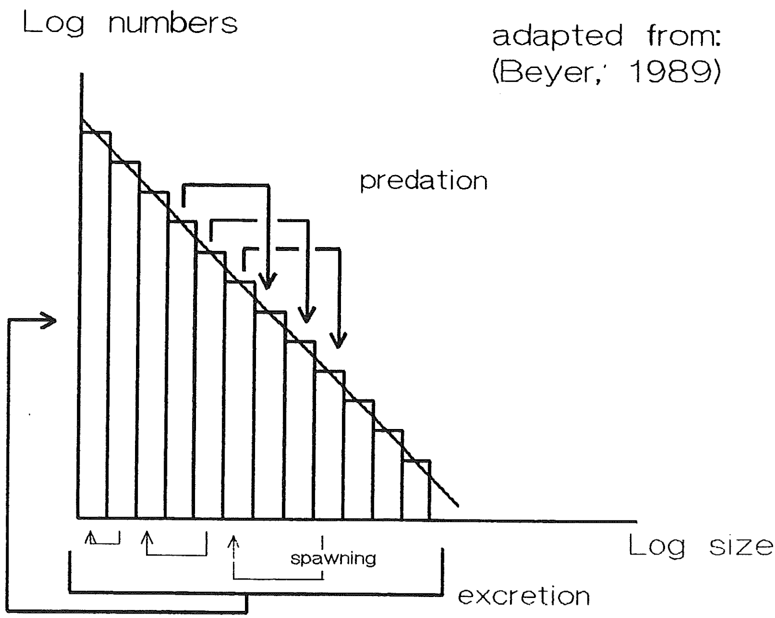


Figure 9

Pelagic ecosystem model

adapted from: (Beyer, 1989)



VI APPENDICES

APPENDIX 1. Agenda for the Meeting

Tuesday 26/6 - Introduction

Cod and Haddock Checklist Report and Discussion
Otolith Intercalibration Report and Discussion
Report on GLOBEC and CCAP Activities
Discussion Document Presentation
Open Discussion on Study Document

Wednesday 27/6 - Subgroups Consider Aspects of Study Proposal

Plenary Presentations from Subgroups
Open Discussion of Study Proposals
Report Drafting in Subgroups

Thursday 28/6 - Report Drafting in Subgroups

Plenary Session and Approval of Documents
Approval of Recommendations and Terms of Reference for Future Work

APPENDIX 2. ICES Recruitment Processes Working Group - Working Document

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Members of the IOC *ad hoc* expert consultation on SARP, La Jolla, California, USA 30 Oct-1 Nov 1989

Members of ICES/IOC Study Group on Models of Recruitment Processes, Paris, France 7-11 May 1990.

Objectives of recruitment research

A frequently stated objective of recruitment research is to enable prediction of annual recruitment to fish populations. In practice, this is probably not a realistic objective, or of great value since in most cases the abundance of the recruiting year class can be measured by field sampling. Of much greater importance are the objectives of assessing the consequences of long-term change in the environment (due for instance to global climate change), and of determining the likely consequences of various exploitation patterns under different environmental conditions.

The relationship between recruitment and adult population dynamics

The link (if any) between adult population density and recruitment has generally been made via a supposed stock-recruitment relationship. Early life stages are assumed to be tied to the parent population by unspecified density dependent relationships. It is certainly true that egg production must be a major factor contributing to the determination of recruitment, but many other biological and physical environmental factors could potentially be involved. It has been common practice to represent these other factors as the variability about some unique stock-recruitment relationship fitted to a series of historical data for a stock. This method of presentation has encouraged many attempts to "explain" the variance in recruitment by means of multiple linear regression techniques taking stock size and a number of environmental parameters as independent variables. In fact, this approach may be invalid if as seems likely, there are interactions between any non-stock related factors contributing to the overall variability, or if the effect of any environmental signal on recruitment is non-linear. For these reasons, the practice of fitting any single stock-recruitment relationship to a historical time series is considered to be most misleading. It seems preferable to regard each annual data point as lying on a multidimensional non-linear surface, of which stock size is just one component.

There can be no doubt that compensatory mechanisms are present which tend to reduce the variability in recruitment, since the variance in recruitment is substantially less than might be expected from the variance in spawning populations and even modest expectations of variance in mortality rates (Anon, 1989; Beyer, 1989). The loci of density dependent-dependent periods in the lifecycles of fish species are not clearly understood, but are of crucial importance for the understanding of recruitment. In general, density dependence may act at the adult stage to regulate fecundity, and age or size at maturity (affecting the number of eggs produced per unit biomass of adults), through predation on eggs, larvae or juveniles, and through the growth rate of larvae. Identification of density dependent life stages should be a high priority of future research programmes.

The lack of any unifying theory linking early life stages and adults has been identified as a major factor limiting the development of understanding of recruitment (Anon, 1989). Beyer (1989) has considered this problem and identified the use of age-specific mortality models for both adult and early life stages as being a major hinderance to progress, and suggested instead the reformulation of survival models in terms of size-specific processes. In addition, factors in the adult stages which influence the number and quality of spawning products are rarely considered in the context of recruitment. Development of theory which integrates life stages is considered to have a high priority.

Outline of research options for recruitment studies

The experimental and comparative approaches have been called the two great methods of science (Mayr, 1982). The experimental method is chosen when variable parameters can be readily controlled. The comparative method offers an alternative in cases where intervention or control may be impractical. Mayr credits "nearly all the revolutionary advances in evolutionary biology" to the comparative method.

The ocean-atmosphere system is uncontrollable. Moreover, the range of scales of motion in the ocean makes it very difficult to define the boundary conditions for an experimental volume of water, unless it is artificially contained. However, artificial containment restricts the scales of crucial dynamic processes and also presents anomalous interfaces and substrates which can alter essential mechanisms.

The numerical reduction in population size that occurs between spawning and recruitment of a fish species is generally very large. Individual survival to the age or size of recruitment is a very rare event compared to the fates of the overwhelming majority of hatchlings. We do not know whether survivors represent lucky average larvae, or individuals with characteristics which differ markedly from the average. If the latter is the case, then observations of the average state larvae in the field may be quite irrelevant to eventual recruitment at the population level. Experiments should, therefore, ideally be performed at the population level but interpreted in terms of processes operative at the individual level.

Mortality during early life can be due to many causes. Both episodic and subtle long term variability in mortality and growth can significantly affect recruitment (Houde, 1989). However, large episodic losses from the egg or larval population need not be catastrophic due to the high fecundity of fish species. On the other hand, relatively minor changes in average daily instantaneous mortality or growth rates can have major consequences. Density dependent processes, if they occur, most likely operate through regulation of growth rates. Thus, there is scope for both multispecies interactions and environmental episodes to regulate recruitment.

The comparative method would seem a natural approach to understanding the problem of recruitment variability in marine populations. In fact, it seems surprising that the comparative method has not been more widely employed in fishery-environmental science, which appears to have been more preoccupied with diversity than with synthesis, and prone to view each local situation as unique (Bakun, 1985). The comparative approach is a generic method which can be operated at any scale. For example, comparisons of populations in neighbouring patches on length scales of metres may be as informative as comparisons of ecosystems in different oceans, but in relation to quite different processes.

Some recent applications of the comparative approach have been informative. On the large scale, comparisons of geographical and seasonal aspects of spawning habits of sardines and anchovies in eastern boundary upwelling areas with the seasonal variations of environmental characteristics, have indicated a pattern of simultaneous avoidance of offshore transport and wind-induced turbulent mixing in several ecosystems. These observation have been interpreted as implying that upwelling and certain levels of turbulence are detrimental to reproductive success (Parrish *et al.*, 1983; Cury and Roy, 1989). Time series analysis of reproductive success of the Peruvian anchoveta (Mendelssohn and Mendo, 1987) and of larval mortality of the northern anchovy off California (Peterman and Bradford, 1987) tend to corroborate this result. Comparison of time series models of a number of eastern boundary sardine and anchovy populations indicates that an "optimal environmental window" for reproductive success may exist between wind speeds too low for sufficient upwelling to enrich the trophic pyramid and wind speeds so high that turbulent mixing may destroy fine-scale food concentrations essential to successful larval feeding and offshore transport may sweep surviving larvae away from the favourable coastal habitat.

The comparative approach has been applied on the small scale to interpret growth variability of larval cod and haddock on Georges Bank (NW Atlantic) (Buckley and Lough, 1987). In this case, growth rates of larvae were estimated from RNA/DNA ratios at three locations covering a distance of approximately 40km. Differences and similarities were interpreted in terms of the prey availability and hydrographic characteristics. In addition, the comparison of the two species over the three sites indicated that cod were better adapted to grow at low prey availability than haddock.

Important functions of the comparative method may be to provide both inspiration and ultimate validation of models. The history of recruitment research has been that correlations between straightforward measurements of the physical environment and recruitment ultimately break down. The process is probably far too complex for simple correlations to hold and success will most likely be realized through the development of models which synthesise the behaviour of the environment. The most effective means of validating these models would be their successful application in different regions of the world. In fact, such a comparative approach may be the only way that such models can be validated over the short term.

Modelling concepts in recruitment studies

In principle, it should be possible to describe events at any scale in the early life history from first principles, in terms of physical and biological mechanisms at the scale of encounter 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. Most observable events or processes in the sea occur at scales many orders of magnitude greater than individual encounters, and represent the integral of many encounter incidents. We refer to these as "higher order processes".

In practice, attempts at describing from first principles the effects of higher order processes 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. In addition, the method of integration of first order processes over space and time is critically important.

One solution to the problem of describing high order 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 parameterisation. One can have more confidence that such "parameter-sparce" 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.

A hypothetical example of the simplification step in moving from first order to higher order models would be one in which survival was modelled as functions of "prey availability" and "predation pressure". Such a model might be conceptually simple, and yet neither the "availability" or the "pressure" parameters would be at all simple in themselves, when considered from first principles. However, if one attempted to model survival directly from first principles with first-order parameters (eg swimming speeds, light intensity, turbulent velocities, perception distances etc), 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 relatively easily be modelled from first principles on their own and the form of their variability visualised in terms of variations in the first order parameters.

Very often, higher order models describing survival, such as that outlined above, are developed without reference to first principle considerations. Some functionally convenient relationship between for instance food availability and growth is chosen which enables modelling the the survival process in a relatively simple fashion. It is sometimes difficult to attach biological or physical significance to parameters such as "food availability" which represent a condensed analogue of many first order processes. An important part of model development should therefore be to indicate the relationship between such condensed terms and measurable physical and biological parameters. Only then can higher order models be tested on field measurements.

One of the biggest difficulties in studying the survival of a year class is to account for the losses in terms of predation. Investigations of specific predator-prey interactions are unlikely to assist in the overall task, since each predator species probably acts episodically on a population of growing larvae (ie predation is fundamentally stage or size specific), and there is a large range of potential predators. It is not easy to see how data on mortality inflicted by one predator can be extrapolated to give information relevant to year class survival.

Part of the difficulty in dealing with predation and mortality in general may relate to the previous use of age-specific mortality models, rather than size-specific rates (Anon, 1989; Beyer, 1989). The previous habit of considering predation mortality only from the view of the larval fish may also have blinkered the progress of research. Beyer (1989) has pointed out that the if predation is governed only by size selective criteria and there is a constant ratio of prey size to predator size (but see Longhurst, 1989), then the predation pressure on all organisms of the same size is equal. Larval fish are both prey and predator in the same system, but the crucial factors determining their final population abundance at recruitment is their growth rate and whether the predator field discriminates for or against the larvae in relation to alternative prey of an equivalent size. For example, Pepin *et al.* (1987) have investigated predation mortality on larval fish by mackerel in the presence of alternative prey in experimental systems and found that predation on larvae was 20-30% less that on prey of equivalent size.

This approach to investigating the early life survival of larval fish has an essential requirement for high order, population level modelling in order to gain an understanding of the consequences of size-species-selective predation in a multispecies system. There are difficulties in integration over space and time dimensions to obtain estimates of the ecosystem wide size distribution of organisms, but an important feature of the idea is that it provides a framework for condensing the first order interactions between predators and prey, into a high order description of the ecosystem. The approach therefore represents a much needed bridge between species specific laboratory investigations of physiology, and field measurements of predation mortality. In addition, the approach seems suited to the comparison of the survival of one species in several ecosystems, or of the survival of several species in one ecosystem.

Techniques for future recruitment studies

From the above discussion it is clear that recruitment issues cannot be adequately answered by studying either the processes involved, or the gross population effects alone. Both levels of interest must be integrated. There are few techniques which can link processes to population effects in the field. However, two methods for utilising information from larval otolith microstructure have great promise in this respect.

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 one 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 (Pannella, 1971; Campana and Nielsen, 1985).

In principle, considerably more information on the past history of the individual larva may be obtained from otolith microstructure. The width of the otolith is lineally related to the standard length of the larva 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 realisation 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 (Anon, 1983, 1984, 1987).

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 the 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, eg 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 estimated from measurements of ring radius measurements. Any discrepency 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 (ie the mean back-calculated length of the survivors is shifted towards larger sizes relative to the original length) (Post and Prankevicius, 1987; Tsukamoto *et al.*, 1989).

Both of these approaches rely critically upon unbiassed 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 realised.

Implicit in the concept of "survivor-population" studies is a loss of spatial resolution. The surviving recruits represent the natural integral over spatial dimensions of all the dispersal, migration, growth and mortality processes operating during the early life. In some respects this may not be a crucial drawback because the most energetic sources of short-term environmental variability (atmospheric storms, etc) have large spatial scales. On the other hand, biological interactions may be highly stage specific and develop over short spatial and temporal scales, giving rise to density dependent interactions and the potential for stabilisation of recruitment. It may be difficult to observe the consequences of the small scale processes in a population scale survivor experiment.

The within-year relative survival approach may be well suited to investigating the gross consequences of environmental variations. Nevertheless, detailed process studies at the individual scale are still required to understand the fundamental basis of survival. Techniques for investigating short-term and small scale variability in growth and survival rates are becoming available, for example biochemical and otolith increment measures of growth rates.

Process orientated topics for future recruitment studies

The shape of future recruitment studies should be determined by two factors. First, the need for focussed 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 important issues have been presented in the form of a dialogue between modellers and field practicioners. 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.

a) Variation in Large Scale Physical Oceanographic Features, Larval Retention and Dispersal

Questions from modellers to practicioners

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?

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Questions from practicioners 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 measurements are likely to be necessary to enable the effects of small scale processes to be integrated over larger spatial and temporal scales?

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Methods: Interactive multidisciplinary ichthyoplankton and hydrographic surveys using drifting buoys, satellites and acoustic current profilers and models to track water currents. 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.

b) Growth and Mortality and Their Interaction

Questions from modellers to practicioners

Is it possible to define a "parcel" of water in 3-dimesions (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, ie 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 recognised in the otoliths?

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Questions from practicioners 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 distinguishing 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 (eg Shepherd and Cushing, 1980)?

How can we recognise 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?

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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: 1) comparison of temporal production pattern of larvae with survivor birthdate frequencies, to determine within season variations in relative mortality at a function of birthdate; 2) 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. Indirect, 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.

c) Predation on, and Food Capture by Larval Fish

Questions from modellers to practicioners

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-prey 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 (ie is behaviour purely deterministic or are learning and adaptation important)?

Is predation mortality density-dependent? Note: the incidence of between or within cohort cannibalism would be of considerable interest since this would represent a potential density dependent regulating mechanism, even if predation mortality was density independent.

What characteristics of prey need to be taken into account when considering prey quality?

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Questions from practicioners 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?

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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. Focussed 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 immunoassay where a applicable. Incidence of starvation can be estimated from histological methods (eg 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 immunoassay 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.

d) Vertical Migration and Distribution Larvae

Questions from modellers to practicioners

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

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Questions from practicioners 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?

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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 (eg using acoustic doppler current profiler and CTD systems). Accurate measurements of subsurface 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.

e) Structure and Physiological Condition of the Spawning Population and Reproductive Output

Question from modellers to practicioners

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?

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Methods: Trawl sampling of adults for fecundity vs age measurements and age composition of adult stock. Fat content measurements 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 utilised 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 General 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 (eg 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 laboratory evaluation of consequences for survival.

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

Feasibility: Highly feasible if the situation arises.

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