Not to be cited without prior reference to the council*

International Council for the
Exploration of the Sea

CM 1989/L:22
Biological Oceanography
Committee

REPORT OF THE WORKING GROUP ON LARVAL FISH ECOLOGY TO THE BIOLOGICAL OCEANOGRAPHY COMMITTEE OF ICES

Aberdeen, Scotland 12-14 July 1989

* General Secretary, ICES, Palægade 2-4, DK 1261 Copenhagen K, Denmark

TABLE OF CONTENTS

I TERMS OF REFERENCE

At the 1988 ICES Statutory Meeting, resolution (C Res 1988/2:40) was adopted as follows:

The Larval Fish Ecology Working Group (Chairman: Dr M Heath, UK) will meet in Aberdeen from 12-14 July 1989 to:

a) review recent research activities on the ecology of early life history stages of fish with special emphasis on interdisciplinary approaches (biology, hydrography, modelling) to the recruitment problem, and on the significance of advection and predation processes.

b) identify potential areas and concepts for international cooperation in the study of recruitment processes.

c) review the results of the efforts to obtain a check list of spawning characteristics in relation to the ecology of early life history stages of cod and haddock from different ecosystems.

d) re-evaluate the need for a workshop on otolith microstructure of young fish.

The meeting was attended by the following:

O Astthorsson	Iceland	F Lagardere	France
J Beyer	Denmark	T Lambert	Canada
S Campana	Canada	J Magnusson	Iceland
G Champalbert	France	J Marchand	France
E Dalley	Canada	E Moksness	Norway
Y de Lafontaine	Canada	P Munk	Denmark
B Ellertsen	Norway	J Nichols	UK (England)
J Gamble	UK (Scotland)	P Rankine	UK (Scotland)
O Hagstrom	Sweden	D Schnack	FRG
M Heath	UK (Scotland)	P Solemdal	Norway
E Houde	USA	S Tilseth	Norway
F Hovenkamp	Netherlands	M Varela	Spain
N Lacroix	France		

J Alheit attended the meeting on 14 July as an observer from the Intergovernmental Commission of UNESCO.

II OVERVIEW OF THE MEETING

The inclusion of item (b) in the terms of reference of the meeting was taken to indicate increased responsibility for providing advice on recruitment matters. Consequently, the format and scope of the Working Group meeting was changed from previous years, becoming more a task oriented interdisciplinary workshop, and less a forum for scientists to meet and compare the results of their studies.

With the increased emphasis on recruitment, the title of the Working Group could now be revised. The need to broaden the scope of early life study to include all stages from egg to adult was repeatedly discussed during the meeting. There was clear recognition that investigations of larval stages alone will not provide a breakthrough in understanding recruitment.

The Working Group was mindful of the criticism that no amount of research will ever produce a deliverable product which can be used for marine resource management, because of the very nature of the variability in the ecosystem. There was little support for this view in the meeting, and discussion of this general problem led to two conclusions.

The first conclusion was that managers and researchers have for too long concentrated on the short term variability in populations, masking the understanding of population stability. Although short term (1-3 years) prediction may be unattainable in the immediate future, the capability to advise on conditions for stable recruitment should be an achievable goal and would be valuable for the development of medium to long term management strategies. An understanding of stable conditions should also provide a better basis for identifying the causes of variability.

The second outcome of the discussion was the recognition of a need to clarify the term "recruitment", which in fisheries science has become synonymous with the abundance of the youngest age group in a Virtual Population Analysis. In reality, this is a most unhelpful definition that may have hindered progress towards understanding recruitment processes. It is hoped that the statement on clarification contained in this report will aid the integration of early life studies into a more general population dynamics approach.

The Working Group was wary of taking on the responsibility for planning and conducting an ICES community programme on recruitment. Nevertheless, it was recognised that advice on this aspect was expected of the group. The participants agreed that there had been considerable progress in recruitment research, but that further major advances would probably require pooling of resources in a well conceived and designed international programme. Accordingly, a tentative set of criteria for a future programme was agreed upon. The Working Group recommended that more in-depth consideration of these criteria should take place, in preparation for the development of a coordinated research programme integrating all life stages of selected species.

III SYNTHESIS OF STUDIES PRESENTED TO THE WORKING GROUP

The participants at the Larval Fish Ecology Working Group meeting presented summaries of individual projects and overviews of ongoing activities in their countries related to the early life history and recruitment of fish (see Appendix). The presentations focused on processes most likely to influence egg and larval dynamics.

Studies on specific questions covering a large variety of ecological aspects of species, locations and methods have been carried out. Particularly rapid progress has occurred in the methods for ageing and estimating growth rates of larvae, and this has led to advances in determining age structure of the youngest stages and in some cases to determination of mortality rates. The success of the otolith-ageing method is largely responsible for this progress. In addition, progress has been made on the nutritional indexing of larvae by biochemical methods, behavioural responses of larvae to environmental physical factors, effects of microturbulence on larval feeding, utility of mesocosms for large scale experimental studies on predation, and the potential use of genetic markers for larval fish. The effects of contaminants of gonads on the viability of spawning products was also brought to the attention of the group as a potential source of recruitment variability.

Some reports restricted their studies to descriptions of ichthyoplankton distribution and abundance. The monitoring of larval abundance as an index of spawning stock abundance (North Sea herring larval surveys, Gulf of St Lawrence mackerel) and of year class size (North Sea plaice, Newfoundland and Barents Sea capelin) were briefly monitored.

A wide range of studies on different topics was discussed by the Working Group, but it was recognised that substantial progress has also been made on other aspects not reviewed during the meeting. Two examples were identified: 1) Immunological methods appear to be promising tools for studies on predation. 2) The application of stable isotope ratios in otoliths has promise as an indicator of past environmental history and could be an important tool for interpreting survival and growth during early life stages.

Recent interdisciplinary projects have attempted to define relationships between interannual variability in recruitment and a variety of environmental factors. These projects have adopted an integrated approach and attempted to cover simultaneously a set of variables believed to be important in the recruitment process. Significant contributions of the projects can be categorised into four major groups:

1. Physical effects: Elements of the Fisheries Ecology Program (FEP) on cod and haddock in south west Nova Scotia and the Autumn Circulation Experiment (ACE) on North Sea herring both address the drift/retention hypothesis and the effect of large scale hydrography and climatic factors on the distribution and transport of spawning products during their development. Both programmes included a large contribution from physical circulation models which served as a starting hypothesis of larval transport.

2. Biological effects: Projects on the trophic interactions between prey availability and larval survival (versions of the match/mismatch theory) are in progress for different stocks (redfish in Newfoundland, cod and herring in coastal Norway). A comparative study of cod stocks (Irish Sea and North Sea) attempted to evaluate the hypothesis that the productivity levels of different regions may influence the recruitment levels in the respective areas. Finally, the field test of the new "strong link/weak link" hypothesis will be evaluated using the Calanus-Redfish interaction in the Gulf of St Lawrence. This hypothesis focuses on the assessment of the production levels and the structure of the food webs and their effect on the transfer of environmental physical signals to the larval fish and recruitment.

3. Physical/biological interaction effects: Studies on the inter-relationships between physical and biological variables on recruitment variability attempt to identify how physical forcing events can influence the more proximal causes of larval mortality and subsequent recruitment. The Gulf of St Lawrence mackerel egg studies, the French sole program, portions of the Canadian FEP, the North Sea ACE program and the North Sea sprat study are examples of such integrated approaches.

4. Multispecies approach: A study on the multispecies interactions between sprat, cod and herring and the influence of abiotic factors on such relationships is in progress in the Baltic Sea.

All of the above projects attempt to consider one or more of the growth/mortality processes in an effort to estimate the relative survival of natural larval populations.

Two reports attempted to further our knowledge of conceptual frameworks by emphasising the importance of the inter-relationship between growth and mortality. First, the idea that episodic events may not necessarily be catastrophic for recruitment was presented to the Working Group. The concept that small and more subtle variabilities in mortality accumulated over time may play a larger role in the resulting recruited population was put forward. In this context, the variability in the duration of the pre-recruit stages is considered to be a determining factor regulating the recruitment levels and variabilities. The second concept focused on the necessity to pay attention to the "stability" of recruitment over a wide range of populations size rather on the interannual variability. It is argued that the general level of recruitment of a given stock may be determined by size specific growth and mortality dynamics.

IV ASPECTS OF RECRUITMENT RESEARCH REQUIRING MORE EMPHASIS

There has been significant progress in research on recruitment of fishes in the past decade. Programmes have evolved from descriptive surveys to more process-oriented studies that attempt to measure vital rates and to understand the causes of recruitment variability. Nevertheless, the Working Group identified a number of deficiencies and needs in recruitment research.

The Working Group recognised that not all of the inadequately-addressed element should be incorporated into every "recruitment study" because of the diverse objectives of programmes and the costs of including all elements. Nevertheless, it is recommended that these elements be considered in the design phase of each programme. Some of the elements are essential if significant advances are to be made in understanding why fish populations vary or in accurately estimating vital rates of early life stages.

IV.i Concepts and Theories

Conceptual and theoretical developments are required before we can understand the causes of population stability and variability. The absence of unifying theory is the major constraint to sustained progress in recruitment research. Generalisations regarding early life relationships and knowledge of the lineage between the early life and adult stages are also required.

A contributory factor to the problem of integrating recruitment research and stock management was identified as the lax and widespread use of the term "recruitment" without an explicit definition in each case. The term has become synonymous with the abundance of a species at the youngest age in a population assessment. In fact, this is rarely the definition which is appropriate to recruitment research programmes, and the confusion may have hindered the focusing of attention by the research community. The concept of "recruitment" is discussed elsewhere in this report, and the Working Group reminds researchers of the need to carefully and explicitly define the term whenever it is used.

IV.ii Methods

Although otolith-ageing has provided the tool to age larvae of many species and to obtain growth rates, methods are still needed to estimate mortality rates of larvae accurately and to estimate the mortality from specific causes. The problems derive from our inability to sample early life stages quantitatively, leading to low confidence in estimates of mortality rates. New samplers and incorporation of analytical and sensing technologies (eg acoustics, optics, image analysis, remote sensing) are required to measure environmental variables with better temporal and spatial resolution simultaneously with early life stages. Methods, including expanded laboratory studies to examine the relationships of physics and biology of eggs/larvae on appropriate scales (including cm-scale microturbulence) must be developed. New biotechnology approaches should be adopted to examine the genetics of early life stages and the adults that produced them.

Particular aspects of methodology requiring attention were identified as follows:

1. Need for new and better samplers, especially for late larvae and juveniles.

2. Need for more and better methods to obtain estimates of early life mortality.

In addition, the Group identified the need:

3. For methods to link physical and biological measurements at the appropriate scale.

4. For methods to estimate predation on early life stages.

5. To develop better experimental methods to estimate vital rates and variability, eg mesocosm experiments.

6. For methods to evaluate and measure fish larval behaviour, especially with respect to physics.

7. To develop better models of growth and growth rate variability.

8. For studies of genetics and methods to evaluate variability in early life stages eg ability of larvae to feed successfully.

IV.iii <u>Data bases</u>

Synthesised data on vital rates and their variability, associated environmental data and appropriate time series measurements are needed to improve research, develop models and to design experiments. Better and easily accessible data bases would allow faster development of unifying theory and concepts, as well as assist in the design of recruitment research.

Time series data of fish population abundances and recruitment need to be collated and compiled into an internationally accessible data base. This would greatly assist in the planning of programmes and the establishment of comparative studies.

IV.iv <u>Comparative Ecosystem/Species Analyses</u>

Comparing the reproductive biology of stocks may offer a different approach to long term studies for improving our knowledge of mechanisms that operate to control population sizes in marine systems. The approach has seldom been used in recruitment studies but is highly recommended. Individual stocks of one species may have different recruitment patterns or variability in two systems, or several species in a single ecosystem may depend upon different mechanisms to regulate numbers or cause fluctuations. Relatively small and "tractable" ecosystems must be identified in which comparative research can be carried out. The Working Group identified some possible candidate systems, eg parts of the Baltic Sea, the Irish Sea or parts of the Canadian Maritime coastal environment, the Gulf of St Lawrence.

The Working Group identified the need for:

1. Process orientated comparative investigations of one species in two or more "tractable" ecosystems.

2. Process orientated comparative investigations of two or more species in one ecosystem.

3. Comparative studies of ecosystems to identify "tractable" systems which may offer the best opportunity for recruitment studies.

IV.v Approaches

The resources of ICES nations should be pooled to carry out effective multidisciplinary studies on recruitment mechanisms and to link them to international assessment programs. Cooperative research should be planned from the outset and not be dependent upon serendipitous associations, although such efforts have been productive in the past. New efforts can be most effective if carried out after careful planning and design and such studies should be designed to test specific hypotheses. Studies that link egg/larvae research with that on juveniles must be emphasised. Research on physical/biological interactions has also been inadequate in the past. The role of density-dependent regulation in the early life needs to be investigated in the sea and in well-designed experiments. Research on recruitment cannot ignore the dynamics of adult stocks or the differences in egg quality caused, for example, by changes in adult stock age structure. Also, future studies of long term recruitment variability and trends should be planned in the context of global change, particularly the probable effects of long term changes in climate upon recruitment levels and population abundances.

The Working Group especially wished to emphasis the following requirements for new approaches:

1. Need for international cooperative research on recruitment processes, especially multidisciplinary programmes that are defined, designed and carried out to test specific hypotheses.

2. "Global" studies to link long term recruitment trends to climatic change.

In addition, it was considered that programmes need to:

3. Follow rigorous programme design to meet objectives based upon hypotheses to be tested and theory being developed.

4. Address the role of density-dependent regulation in early life, and the concept of regulation vs fluctuations.

5. Link juvenile studies to those on eggs and larvae.

6. Associate process orientated recruitment research with stock assessments.

7. Link adult stage dynamics to early life dynamics, eg the effects of adult age structure on egg quality and the consequences for recruitment.

8. Integrate physical oceanographic studies with recruitment studies.

V THE CONCEPT OF RECRUITMENT

The Working Group discussed the concepts surrounding the term "recruitment". It became apparent that there was some confusion over the best definition of this term, and that it was open to several interpretations, eg the abundance at:

- the age at which a fish reaches sexual maturity
- the age at which a fish enters the fishery
- the age at which a fish arrives in a certain area
- an arbitrary age

- a certain length or weight
- the length or weight of first spawning
- a particular life stage

For stock management purposes, the arbitrary age criterion is generally used. Unfortunately, this has little biological significance. Lack of appreciation of these definitions may have hindered the focusing of early life studies.

The Working Group proposed that "recruitment" can be regarded as the outcome of the complex development of a year class to a particular stage. Our perception of recruitment will be very much influenced by the stage which is specified.

Further interpretation problems may have confused the use of the term "recruitment". The term arises from the perception that year class strength is generally fixed at some early age in the life history, and is not significantly modified by natural causes thereafter. Recruitment is perceived as the transition from the year class strength determinant phase to the fixed strength phase. This perception is compounded by stock management methods. The Virtual Population Analysis (VPA) deals only with the fishable adult and juvenile stages. The early life stages are not considered in the population dynamics analysis. Recruitment has become synonymous with the transition from non-assessed to assessed life stages.

Most VPA techniques use a constant natural mortality of 0.2. This derives from historical studies on plaice and haddock populations. Occasionally, some elevated value may be used for juveniles where these are assessed. The Multi-Species VPA (MSVPA) gives a better estimate of natural mortality, based on predation interactions between fish species. However, the MSVPA is basically an age-based assessment, and it is known that predation mortality rates are mainly related to prey size, rather than to prey age. Hence, survival is an interactive function of mortality and growth rate. The group therefore concluded that the expression of recruitment in terms of abundance-at-age placed a severe constraint on the development of conceptual models of population fluctuation. A more rational approach would be to express recruitment in terms of abundance-at-size (length or weight). Early life studies then become part of the overall investigation of population dynamics, rather than the separable area of research which the conventional recruitment idea implies.

VI RECOMMENDATIONS FOR FUTURE RESEARCH PROGRAMMES ON RECRUITMENT

The Working Group recognised that considerable improvement in the understanding of recruitment has been achieved. However, further significant progress could be made by the development of a well conceived and designed international programme. It was agreed that such a programme would require careful planning and more in-depth discussions on the basic concepts underpinning the role of early life stages in recruitment mechanisms.

The participants agreed that any future programme should focus on process oriented research which will categorise and quantify mechanisms that lead to good and poor recruitment. It should produce predictive models of recruitment levels that will quantify year class strength at significantly earlier ages than is now possible in traditional stock assessments. Such a programme should encompass the following criteria:

Conceptual Framework. Several aspects should be considered before a programme is planned and executed. First, an overall theory must be developed and hypotheses generated to allow explanation of both the short term variability and the long term stability. Secondly, the histories of the stocks to be investigated must be determined.

Comparative Approach. A recruitment programme that compares stocks of a single species in two ecosystems or compares two or more species in a single ecosystem is very desirable. In this way the mechanisms that lead to variable recruitment success or relative stability are likely to be identified. It is critical to select tractable ecosystems and abundant species for the programme.

Experiments. Field, laboratory and enclosure experiments are necessary in the programme that the Working Group foresees. A strong emphasis on the design of experiments to test specific hypotheses is required. The intensity of effort may depend upon the conceptual framework within which the programme is developed.

Physics and Biology. A recruitment programme should focus on the interactions between physics and biology. Fine-scale to mesoscale processes must be emphasised. Mechanisms and models that link biological responses to physical forcing will be produced.

Early Life Stages. A recruitment programme must include research on all stages of development from egg to juvenile because year class strength may be determined or influenced significantly at many stages in early life.

Length of Programme. A multi-year investigation will be necessary. The design of the experiments will be important to define the time frame within which a programme will be carried out.

International Cooperation. Cooperation among ICES nations will allow both intellectual and economic resources to be pooled to ensure the success of a large and complex recruitment programme. Furthermore, the logistics of carrying out comparative studies in two or more ecosystems will be greatly facilitated by a cooperative effort.

VII REVIEW OF PROGRESS ON THE PREPARATION OF A CHECKLIST OF SPAWNING CHARACTERISTICS OF COD AND HADDOCK

At the last Larval Fish Ecology Working Group (ICES CM 1987/L:28) it was decided to instigate the preparation of a checklist of spawning characteristics of cod and haddock in different ecosystems. The purpose of the exercise was to provide background information for each stock and outline the factors that may influence recruitment variability. K Brander (Lowestoft) offered to act as coordinator, and subsequently prepared a questionnaire which was circulated at the ICES Early Life History Symposium and Statutory Meeting in Bergen (1988) (see Appendix).

K Brander reported that there had only been two responses to the questionnaire, and hence he had not been able to prepare a checklist for presentation to the Working Group. The group resolved to continue the gathering of information. The prospect of widening the scope of the exercise to other species was discussed, but rejected until such time as the cod and haddock checklist has been accomplished. The goal of producing a data base of spawning characteristics for different species was considered to be very worthwhile.

VIII RE-EVALUATION OF THE NEED FOR A WORKSHOP ON OTOLITH MICROSTRUCTURE OF YOUNG FISH

The proposal of the previous Larval Fish Ecology Working Group (ICES CM 1987/L:28) that a workshop on otolith microstructure should be convened in Woods Hole during September 1988, was accepted by the Council. However, the workshop was cancelled due to lack of participants. The present Working Group was asked to re-evaluate the need for a workshop.

The large number of studies and significant progress in otolith microstructure examination achieved in the past three years indicated to the Working Group that the lack of participation in the workshop was probably not due to lack of interest from the research community. The use of otolith measurements will be vital for future progress on estimation of mortality, and intercalibration of methods of preparation, mounting and examination used in different laboratories must be a pre-requisite for any international cooperative recruitment programme. The Working Group considered that a workshop on methods would be inappropriate until the results from such an intercalibration were available.

The Working Group therefore decided that the plan to hold a workshop should be suspended and replaced with an intercalibration exercise. The procedure should be to circulate both mounted otoliths and specimens of known age larvae reared in mesocosm to all participating laboratories, to test both preparation and inspection methods. Several species of larvae should be used, but cod and herring were cited as the initial candidates. Erlend Moksness (Norway) offered to organise and run the exercise.

IX CIRCULATION OF A NEWSLETTER AMONGST WORKING GROUP MEMBERS

A proposal was put forward to produce a newsletter for circulation initially within the group. The objective of the proposal was to maintain contact between members of the Working Group and disseminate comment and brief items of information regarding ongoing or planned research.

The suggestion was favourably received, and several possible means of establishing such a document were discussed. It was decided to attempt in the first instance to circulate an informal document, without recourse to expensive printing and editing facilities. M Heath (Scotland) offered to undertake this task.

X RECOMMENDATIONS

The Working Group recommends the following:

- that a sub group of the Larval Fish Ecology Working Group should be convened to develop a draft proposal for a coordinated study integrating all life stages of two or more species in a tractable ecosystem. The subgroup to be named the "Recruitment Programme Planning Group (RPPG)", convenor M Heath and to work by correspondence.

- that K Brander should continue with preparation of a checklist of spawning and recruitment characteristics of cod and haddock. The support of the ICES statistician should be sought to solicit information from the various assessment Working Groups.

- that an otolith microstructure intercalibration exercise should be carried out in 1990 (organiser: E Moksness). This should involve the exchange of mounted material and preserved larvae of known age, to test both the preparation and examination expertise in participating laboratories.

- that the Working Group should reconvene during June 1990 in Nantes (France) with the following terms of reference:

  Examine and discuss the draft proposal for a coordinated recruitment study integrating all life stages of two or more species in a tractable ecosystem, to be produced by the RPPG subgroup.

  Review progress on the efforts to prepare a checklist of cod and haddock spawning characteristics

  Review progress on the otolith microstructure intercalibration exercise

XI APPENDIX i. AGENDA OF THE MEETING

Wednesday 12 July 1989: 0900-

Introductions and domestic arrangements.

Brief reviews of research activities by participants.

Report drafting.

1800: Buffet and poster session.

Thursday 13 July 1989: 0900-

Report from Plankton Sampling Study Group.

Presentation of results of efforts to obtain a check list of spawning characteristics in relation to the ecology of early life history stages of cod and haddock from different ecosystems. Document from Keith Brander.

Synthesis of present state of recruitment studies with particular emphasis on the current implementation of multidisciplinary approaches.

Discussion - What is missing from present day recruitment studies?

Report drafting.

Friday 14 July 1989: 0900-

Discussion - How should recruitment studies look in the future? Scope for international cooperation.

Discussion - How can the LFEWG promote the efficient use of resources to study recruitment problems (newsletter, manual of methods, "fact sheet" or things to do and not-to-do, workshops?).

Report drafting.

Discussion - Need for a workshop on otolith microstructure?

Discussion of venue for future meeting and action regarding promotion of recruitment studies.

Concluding comments.

XI APPENDIX ii.i. EARLY LIFE STUDIES IN CANADA

a) Newfoundland Region

Flemish Cap Project

Feeding and Growth of Redfish Larvae in Relation to Survival and Timing of Production

Planning began for these projects in the mid 1970s and initial field sampling began in October 1977, with the final directed studies ending in July 1983. Field sampling was most intensive during 1979-1981. This was a joint project between Canada and the USSR carried out under the auspices of ICNAF/NAFO with preliminary results being reported each year through NAFO. Recent results of the project were discussed during the NAFO Special Session on recruitment (Lilly, 1987) and a major review of the project was summarised by Grosslein and Lilly (1987). Presently, data collected as part of the project are being analysed with completion expected within two years.

The major findings of the project to date centre on the growth and survival of redfish larvae. Larval survival between April and August 1978-1981 varied widely and initially this can be linked directly to growth rate. Modelled estimates of physical dispersal can account for approximately one half of the average estimated larval mortality, but yearly comparisons have not been done. Analyses are presently underway summarising the chlorophyll and nutrient relationships on Flemish Cap, analysing the differences in larval redfish feeding between years. Future work planned includes: analysis of regional differences in feeding, growth and condition of larval redfish in relation to physical and biological factors; analysis of prey availability on the production of the cod stock, analysis of the influence of predation by cod on mortality of juvenile redfish and cod; information on fecundity and the percentages of females which spawned each year; and a more accurate estimate of the cod spawning stock size.

Physical Oceanographic Component of Flemish Cap International Experiment

The Flemish Cap International Experiment was an ICNAF study aimed at identifying the relationships of currents, water temperature and of the environmental factors with the year class strengths of cod and redfish on the Cap. The physical oceanographic component of the study was crippled by the loss of moored equipment. Preliminary analyses of most of the current and hydrographic data have been published and more detailed interpretation of the hydrographic data and their implications for larval dispersion is underway as part of a doctoral thesis (Akenhead, 1988).

Reproductive Ecology of Herring and Capelin

Trinity Bay Recruitment Study

From 1982 to 1986 a series of spring fall surveys, aimed at herring and capelin larvae, were carried out in Trinity Bay. Prey for larvae were evaluated by sampling zooplankton with a fine mesh net, and measures of dry weight biomass of five size fractions were obtained. Temperature and salinity profiles were collected at each station. Correlation analysis is being carried out to examine associations between larval abundance and measures of the biological and physical environment. Preliminary results are quite variable. Some significant associations were identified although trends are not consistent throughout the data sets. Further analysis will focus on aspects of the environmental and meteorological conditions prevalent during the sampling period when significant associations were identified.

The project is also concerned with biases in estimation of larval population parameters for example shrinkage and gear avoidance. In 1987 and 1989 field sampling was aimed at identifying patterns of vertical distribution and also at ascertaining diel variability in standard oblique bongo tows. This information will be used in interpreting data collected during the surveys. No data collections are being made in 1988.

In 1984 a study of Trinity Bay was contracted to described circulation and other aspects of the physical oceanography. This description is intended to aid in the interpretation of larval distribution and abundance data particularly as it relates to dispersal/retention.

b) Early Life History Research at the Bedford Institute of Oceanography, Nova Scotia, Canada

Considerable emphasis has been placed on early life history research in recent years, most of it in association with the Fisheries Ecology Program. The program was designed to focus interdisciplinary research effort on cod and haddock populations spawning on Browns Bank (off south west Nova Scotia) in the years 1983-1985. Associated research included studies of sexual maturation, primary and secondary production, and characterisation of advective and dispersive losses via circulation studies. The results are scheduled to be published as a supplement to Canadian Journal of Fisheries and Aquatic Science at the end of 1989. The following titles reflect the early life history research associated with the project:

1. Seasonal and interannual variability in the physical environment off south west Nova Scotia - P C Smith.

2. Particle dispersion in the surface layer off south west Nova Scotia: description and evaluation of a model - F Page and P C Smith.

3. Structure and interannual variability of the plankton and its environment off south west Nova Scotia in late spring and early summer - J A Koslow, R I Perry, P C F Hurley and R O Fournier.

4. The stage-dependent vertical distribution of haddock eggs in a stratified water column: field evidence and an interpretive model - F Page, K T Frank and K Thompson.

5. Spawning time and egg stage durations in haddock stocks of the north west Atlantic - F Page and K T Frank.

6. Hydrographic effects on the vertical distribution of haddock eggs and larvae on the south western Scotian Shelf - K T Frank, F Page and J McRuer.

7. A drift-retention dichotomy for larval haddock spawned on Browns Bank - S E Campana, S J Smith and P C F Hurley.

8. Distribution and abundance of cod and haddock eggs and larvae in the waters off of south west Nova Scotia - P C F Hurley and S E Campana.

9. Spatial comparison of recent growth in post-larval cod off south west Nova Scotia: inferior growth in a presumed nursery area - I M Suthers, K T Frank and S E Campana.

10. Nutritional status of field-collected haddock larvae from south western Nova Scotia: an assessment based on morphometric and vertical distribution data - K T Frank and J McRuer.

11. Inter-relationships between size distribution, geographical distribution and catch rates of 0-group haddock on the Scotian Shelf - J S Scott.

12. The reproductive biology of south west Scotian Shelf haddock - K G Waiwood.

13. Abundance of young cod and haddock as indicators of year class strength - S Campana, K Frank, P Hurley, P Koeller, F Page and P Smith.

The last mentioned study, which synthesised the results of many of the other studies, used survival curves of each of three cohorts of cod and haddock to identify the life history stages or environmental factors most influential in the determination of year class strength. Estimates of absolute abundance for each of the egg stages, larvae and pelagic juveniles were generated from seasonal production curves. Population egg production and VPA recruits at age one were derived from the most recent stock assessments. The abundance of the egg and larval stages varied substantially between years and could not be used, even qualitatively, to predict year class strength. However, both juvenile abundance and the mortality rate between the larval and juvenile stages could be so used. Interannual differences in the instantaneous mortality rate could not be linked consistently with advective losses, food availability or predation. Analysis of the problem is still continuing, but the results to date clearly indicate the deficiencies of recruitment research focused on a single life history stage or process.

Mackerel Studies in the Gulf of St Lawrence

Mackerel studies in the Gulf of St Lawrence have examined the large and fine scale distribution of eggs both in the horizontal and vertical. Spawning followed closely the pattern of surface warming. Peak spawning occurred at 13°C. Newly laid patches of eggs were mapped and monitored for as long as they remained detectable. Vertical distribution was sensitive to wind action, with eggs being mixed downwards from the surface where they were initially heavily concentrated.

Accumulation of data over several years revealed that mortality of eggs during early developmental stages was a function of initial egg density; high mortalities were associated with high densities. Also, although egg mortality was not related to absolute temperature, high rates of temperature change (rapid surface warming) were correlated with increased mortality. The data thus suggest that during calm weather when eggs are concentrated at the surface, they are very vulnerable to predation, perhaps most likely from mackerel themselves. During unsettled weather the vertical distribution of eggs becomes more homogenous as concentrations at the surface are reduced and eggs are rendered less vulnerable. The hypothesis is supported by evidence from other studies which indicate better recruitment for mackerel in cooler years.

c) Quebec Region

On-going ichthyoplankton research conducted by the Quebec region (Institut Maurice Lamontagne - Mont-Joli) of the Department of Fisheries and Oceans Canada includes a variety of field studies dealing with the dynamics of fish larvae. A new program to evaluate *in situ* the "strong link/weak link" hypothesis which suggests that interannual variability in recruitment is related to the interannual variability in physical environmental signals being transmitted through the food web and depends on the strength of trophic links among the various components. It is suggested that the link between primary and secondary production may be defined as strong or weak depending on reproduction rate of zooplankton in relation to phytoplankton quantity and quality. Therefore, the variability in environmental signals can be filtered either in a weakly (the strong link case) or strongly (weak link situation) manner. A study on the relationship between the copepod *Calanus finmarchicus* and redfish (*Sebastes* sp.) larvae in the

Gulf of St Lawrence has been initiated in 1988 and is presently under progress (Yves de Lafontaine and Jeffrey Runge). Several subhypotheses are being tested in the field: relationship between *Calanus* egg production rate and phytoplankton production, effect of physical structure on phytoplankton and zooplankton community and *Calanus* reproductive rate, co-occurrence of both *Calanus* eggs and nauplii and redfish larvae both horizontally and vertically, feeding activity and selectively of redfish larvae, redfish fecundity studies, determination of redfish larval growth (Yves de Lafontaine and Jeffrey Runge).

A study on the ontogenetic variation of the feeding diet of plaice (*Hippoglossoides platessoides*) larvae is also under analysis. Data cover a three year sampling period and will allow the evaluation of a predator-prey size relationship (Yves de Lafontaine).

A comparative study on the distribution and survival of cod and mackerel eggs and early larval stages in a large embayment (Baie des Chaleurs) of the Gulf of St Lawrence has been conducted in recent years and results are now analysed (Yves de Lafontaine).

Additional research programmes are being carried out on the effects of red tides (*Protogonyaulax*) on mortality of herring and mackerel larvae (J Gagné) and the mackerel egg annual surveys for spawning stock size biomass (Martin Castonguay).

XI APPENDIX ii.ii. EARLY LIFE STUDIES IN DENMARK. RESEARCH ON LARVAL FISH ECOLOGY AT THE DANISH INSTITUTE FOR FISHERIES AND MARINE RESEARCH

1. Ecology of North Sea Herring Larvae

A number of hypotheses on larval growth and survival have been evaluated through laboratory and field studies. Special focus has been put on the relationship between prey availability and larval growth potential, from first feeding to metamorphosis.

During the last two years the research has been coordinated through ACE (Autumn Circulation Experiments). ACE is an internationally coordinated research programme emphasising a drift and growth of North Sea herring larvae. The programme is described elsewhere in this report.

2. Comparison of Early Life of Herring and Sprat

The changes in population sizes of North Sea herring and sprat show reverse trends. A project has been set up comparing the early life of herring and sprat to evaluate the potential interdependence between the stocks at the larval/juvenile stage. An alternative hypothesis considers reverse influence from environmental parameters. Existing information on herring larvae are compared with information on sprat gained from a series of planned field and laboratory studies. The sprat studies are coordinated to the research on sprat in the international SARP programme described elsewhere in this report.

3. Plankton Dynamics in Hydrographic Transition Zones (Fronts)

Hydrographic transition zones are of potential importance to larval growth and survival. The productivity is often enhanced in the zones, and an unique prey environment to the larvae is created.

An ongoing programme focuses at specific components in the production circle in a transition area. In a two year study period measurements from a fixed buoy system and intensive plankton sampling in the vicinity of a transition area creates the basis for evaluating the importance of the different processes.

4. Synthesis Studies

A former project of theory development for larval fish dynamics has been restarted in July 1988 with the long term purpose of obtaining well-defined starting points for quantifying the combined effect of biological and physical processes on recruitment. Size-dependent predation mortality and turbulence-dependent contact rates between particles in the pelagic ecosystem are considered to be of special importance. Preliminary models are based on particle size distribution theory. However, the intention is to end up with stochastic descriptions of major processes. A by-product of the activity will be an updating of the size-structured multispecies models of exploited fish stocks which did not receive much attention 15 years ago.

In the present start-up phase interest is focused on basic principles in dealing with size instead of age in simple cohort models. Some of the results concerning the impact of density-dependent growth on recruitment stability are mentioned elsewhere in the present report.

XI APPENDIX ii.iii. EARLY LIFE STUDIES IN THE FEDERAL REPUBLIC OF GERMANY

1. Survey work for estimating egg and/or larval production:

   Herring - North Sea and adjacent waters
   Mackerel - West British waters
   Cod - Baltic Sea (Bornholm Basin)

2. Specific aspects of recruitment biology.

2.1 Fecundity of cod and sprat in the Baltic, and sprat in the North Sea. Viability of spawn related to levels of contamination of gonads by pollutants: different species in North Sea and Baltic.

2.2 Horizontal and vertical distribution and migration patterns related to abiotic factors: herring larvae in the North Sea, cod eggs and sprat larvae in the Baltic, eggs and larvae of mackerel compared to other species in west British waters, comparison of taxa in the north Arabian Sea.

2.3 Drift and mortality of eggs and larvae of cod and sprat in the Baltic, cod and redfish in west Greenland waters.

2.4 Characteristics of the biotic environment and feeding ecology of fish larvae in the Arabian Sea, North Sea, Baltic Sea, Elbe estuary; formation of plankton microlayers and its importance for larval fish feeding (Herring in Kiel fjord).

2.5 Histological and biochemical (RNA/DNA, digestive enzymes) analysis on the nutritional status of fish larvae when reared at different food concentrations and caught at ecologically different places at sea; herring and other species; development of methods for measuring individual larvae.

2.6 Comparative studies on the microstructure of larval otoliths (14 species); ageing of larvae; growth rates related to the ecological situation.

2.7 Predation of fish on fish eggs and larvae (North Sea, Baltic).

2.8 Development of high speed underwater video-systems to be combined with plankton samplers for *in situ* determination of small scale distribution of fish eggs and larvae and their prey organisms; improving methods for computer aided quantitative and qualitative analysis of plankton samples and *in situ* video measurements.

3. Integrative programmes related to the early life history of fish.

3.1 Comparative studies on the structure and function of the pelagic ecosystems in different regions of the North Arabian Sea, directing special emphasis to the ecological situation and behaviour of fish eggs and larvae (Meteor-Expedition early 1987).

3.2 Interaction of cod, herring and sprat by predation on early life stages in Bornholm Basin (Baltic Sea) as compared to abiotic factors effecting recruitment success.

3.3 Recruitment studies concentrating on sardines on the South American continental shelf between Brazil and Argentina (Meteor-Expedition late 1989).

XI APPENDIX ii.iv. EARLY LIFE STUDIES IN FRANCE

French Studies on Recruitment Determinism - The Sole Program

A national research program was launched by IFREMER in 1985, focusing on the early life of three species owing to their importance in the French fisheries: the scallop, the oyster and the sole. Field and experimental data of the **Sole Program** have been completed in April 1989. So, all the data are not yet available but preliminary results can be presented.

An other long term program, **CLIMAPECHE**, is concerned by recruitment studies. The aim of this program is to estimate recruitment and its interannual variability and to look for link between climate and recruitment. The interannual variability of 0-group (vertical population analysis) is the main source of data, and this program tries to correlate these results with oceanographical mechanisms or climate forcing.

Conceptual scheme of the sole program

This conceptual scheme includes four levels (Fig. 1), each of them being involved in studies of individuals, subpopulations and populations. This report deals mainly with basic studies conducted by IFREMER, in collaboration with French universities, CNRS and Canadian scientists.

Preliminary results

Relationships between Survival, Growth, Physiology and Environmental Factors

These dealt with observations on individual larvae and juveniles, and were investigated by experimental and field studies.

Survival, larval growth and feeding under experimental conditions

Experiments were carried out during spring 1987, and were designed to test the effects of temperature (12-19°C) and starvation on survival, ontogenetic development and growth rate, as well as the biochemical component contents. Different methods were employed (biometry, histology and histochemistry, protein and lipid content analysis, otolith ageing technique). As far as control larvae were concerned, they provided a sequence of developmental stages and a description of the gut and swimbladder ontogenesis. Similarly, the daily increment deposition for Dover sole larvae was validated. By starvation experiments, the point of no return was determined (19°C experiment only), and stress indexes obtained under the different thermal regimes. They were related to changes in larval measurements, otolith microstructure, histological alteration and biochemical component ratios. The RNA/DNA ratio, the protein and lipid contents changed significantly under starvation, but nucleic acid analysis carried out larvae by larvae indicated important individual variations. Then, the DNA/dry weight ratio and triglycerides/sterols ratio, seemed to represent more sensitive indexes of starvation.

Age and growth of sea caught larvae

In the same time, field-sampled sole larvae were tagged, measured and aged according to the otolith experimental results. As preliminary analysis, growth curves were fitted to these data using simple regression models. They had to be interpreted taking into account both the precision of the age estimates, and of the larval length measurements. Age estimates were obtained from whole mounted otoliths, and experiments showed that deposition of well-defined daily increments started at first-feeding only. One cannot exclude errors in the estimates of days from hatching to first-feeding, and especially when first-feeding was delayed. As a first step and considering the sea water temperatures in the Bay of Biscay, it was assumed that there were no (or few) increments narrower than the thinnest discriminated increment (≈0.50 μm wide). This assumption was supported by the 12°C experimental results, from the sagittal growth curves and from image analysis of the same otoliths. Shrinkage was estimated through experiments, and using standard length vs sagittal diameter relationships. Experiments showed that shrinkage decreased significantly from 20% (reaching 40% after stress during catches) for early larvae, to 2-3% (reaching 10-20% after stress) by the end of the preflexion stages when the skeleton was ossifying. At this stage, the use of sagittal diameters as a shrinkage estimator led to underestimate the size of the oldest larvae.

Relationships Between Distribution, Abundance and Environmental Factors

Distribution and abundance in the northern spawning ground

At the level of the subpopulation, in order to assess the distribution and abundance of plankton stages, 17 ichthyoplankton surveys have been conducted since 1985 in the northern part of the Bay of Biscay (offshore from the Loire estuary), where the most important sole spawning ground is located. Spawning occurs in the open sea (depth of 50-80 m) in February-March and by April metamorphosing larvae of 8-13 mm reach the coastal nursery areas. The preliminary results suggest a low interannual variability in the distribution of pelagic stages of which the maximum density occurred between 1 and 15 April, the oldest larvae being caught principally towards the coast. The spatial distribution of the pelagic stages of sole reveals the existence of a common structure of both eggs and larvae, showing a low variability and surrounded by an area of high variability, mainly towards the coast, ie with a sector showing high hydrological variability.

From age estimates, it appeared that larval sole can be sampled on the spawning grounds at least until they were 30-35 d old. Back-calculated birth dates gave information from one cruise to the other. However, metamorphosis induced a change in the larval behaviour and, by this way, a lack in the estimates of true abundance of the oldest stages in these areas.

Then the question was to elucidate how the larvae reach the coast about one month after the spawning. Do they access to the coast thanks to a passive drifting process, or through active movement, or both? These were important questions, since this may be a critical period for sole larvae.

Behaviour and environmental factors under laboratory conditions

Experimental project consists in a study of the effects of internal factors (age, endogenous rhythms) and external factors (light, gravity, temperature, salinity, pressure, currents) on the swimming activity and the orientation of larvae (from hatching to metamorphosis) and juveniles (from post-metamorphic stages to juveniles a few months old). Experiments were carried out with special actography devices adapted in the laboratory for such studies: actographs and actotaxigraphs using infra-red barriers to detect animals in different kinds of tanks (horizontal tanks, vertical tanks, U shape tanks) during experiments over several days. In some actographs and actotaxigraphs, special systems induce cyclic or non-cyclic variations of light, temperature, salinity, pressure, currents.

All the experiments tend to show that the transport of old larvae and juveniles from the nursery to the coast and the estuaries is not passive. Actually, animals exhibit active horizontal and vertical migrations in which variations of external factors (especially light intensity, pressure variations generated by waves and tides, currents) can synchronise the endogenous rhythm of swimming activity.

Relationships between distribution and environmental factors in the field

1. Larval stages

Lagrangian drifters, ie sea surface Argos buoys equipped with drogues, have been used. These devices permit the correlation of larval movements with the ocean currents, according to vertical migrations of these small organisms. Such a study was conducted in 1986 and 1987 (CIRESOL), using three and nine Argos buoys respectively, moored at different depths in the centre of the northern spawning ground (Fig. 2). The preliminary results showed that the Argos buoys remained more or less in the same area for three weeks. The upper layer buoys were more influenced by marked wind-driven deplacement. These experiments can be linked to the stability of the distribution of early stages and they suggest that the spatial stability of pelagic larvae could be explained by a passive behaviour of eggs and post-hatched larvae and the appearance of preferences concerning the vertical distribution with increasing age.

In parallel, the microscale horizontal and vertical distribution of the larval stages was in relation to environmental measurements as tidal currents, light, temperature and salinity. The preliminary results gave informations on periodic variations of the larvae, according to their size: early stages (length $\leq$ 3.5 mm) were mainly sampled all the 24 h cycle round between 20 m under the surface down to the bottom, while older larvae came to the surface every night.

2. Metamorphosing larvae and juveniles

The study of the settlement conditions of the metamorphosing larvae and newly transformed juveniles have been conducted since 1986 in an estuarine area (Vilaine estuary) depending of the Bay of Biscay. Moreover, the further distribution and abundance of juveniles on the nursery grounds have been surveyed for nearly 10 years.

About the estuarine migration of the sole early stages, four main objectives have been considered:

- to determine in which environmental conditions the sole immigration starts and if interannual variabilities of the pattern occur. The first results indicate that environmental factors like the river flow, the wind regime and the tidal cycle have a strong effect on the hydrological structure of the estuarine ecosystem, and consequently on the onset of the sole inshore migration; the occurrence of a hydrological front may delay their settlement;

- to examine the size and characteristics of the young cohort which enter in early spring; this cohort may include: (1) metamorphosing larvae and newly transformed juveniles which may migrate either in one or in several pulses according to the environmental conditions and (2) juveniles of which development occurred out of the nurseries areas;

- to follow the spatio-temporal distribution of these young stages in the bay and estuary ecosystems and to compare their location with those of other Pleuronectiforms or their potential predators (Cnidaria and Ctenophor);

- to determine if the newly settled soles have any particular rhythm or behaviour in the nursery areas. An endogeneous activity rhythm linked to the photoperiod was observed in metamorphosing larvae and newly transformed juveniles, with the progressive development of a tidal rhythm linked to their feeding activity.

Relationships Between Sole Subpopulations of the Bay of Biscay

Since 1988, the area prospected during the ichthyoplankton survey has been extended to the southern part of the Bay of Biscay (offshore from the Gironde estuary) in order to observe a possible diffusion between the different spawning grounds.

However, a genetic study has been carried out on juveniles from two separated coastal nurseries, and the results showed no significant differences. So, it must be the same population, even if a slight heterogeneity occurs.

Tagging experiments have been also performed on juveniles from these nursery areas. They tend to show a wide dispatchment of young soles (at the Bay of Biscay level); so, the level of recruitment on the fisheries may result from several nursery grounds, inducing compensatory mechanisms.

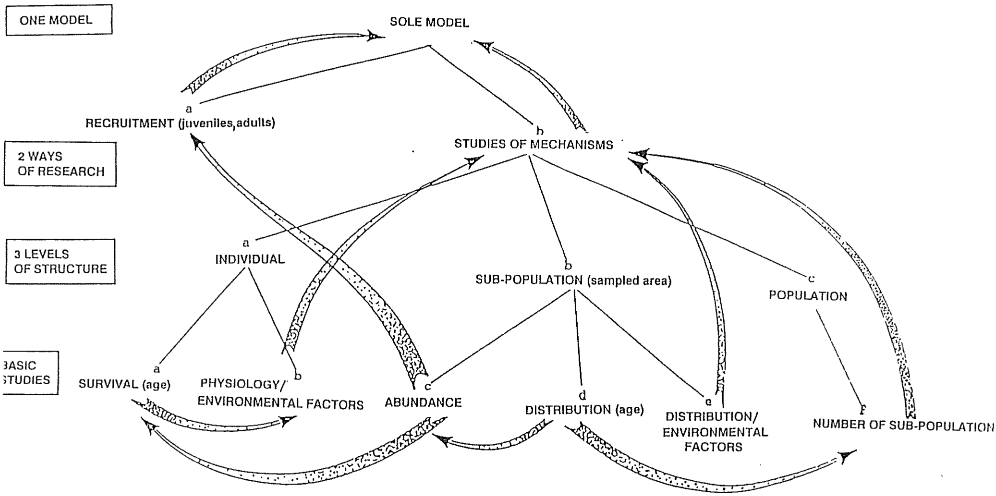

Fig. 1 : RECRUITMENT STUDY : Conceptual scheme for Sole Program

1 - Satellite
2 - Oceanic waters
3 - Separation between freshwaters and marine waters
4 - Cold and freswaters of the Loire/Gironde
5 - Coast
6 - Thalassa (research vessel)
7 - Bioness sampler
8 - Mooring with current meters and tide recorder
9 - Young larvae
10 - Long depth drogue (>30 m)
11 - Argos buoys
12 - Upper layer drogue (< 15 m)
13 - Long moving
14 - Little moving
15 - Vertical migrations of larvae
16 - Spawners
17 - Eggs
18 - Bottom
19 - Estuary
20 - Oldest larvae
21 - Juveniles/nurserie

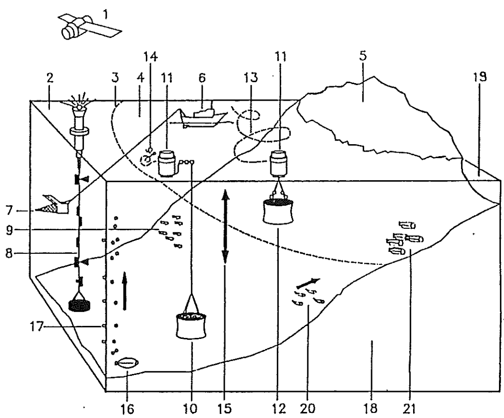

Fig. 2 : RECRUITMENT OF THE SOLE (CIRESOL, 1987)

XI APPENDIX ii.v. EARLY LIFE STUDIES IN ICELAND

In recent years only limited studies have been undertaken in Icelandic waters on fish larval biology and ecology. However, some studies which are of relevance are briefly mentioned below.

In order to obtain initial information on the recruitment of the most important commercial fish stocks (cod, haddock, capelin and redfish) 0-group surveys are conducted in August each year in the shelf area all around Iceland and between Iceland and Greenland.

In 1985 a stomach sampling program was carried out on the east Greenland shelf in order to look particularly at the predation of cod and adult redfish on 0-group redfish. The results demonstrated that both species prey heavily on 0-group redfish in this area.

Studies have been undertaken on the food of the larvae of cod, haddock, capelin and sandeel on spawning grounds at the south west coast of Iceland. Similarly studies on the food of juvenile cod off the south and south west coasts are in progress.

There were plans to initiate in the spring of 1989 multidisciplinary ecological studies on the main spawning grounds of Icelandic commercial fish stocks of the south west coast of the country. These, however, had to be postponed but it is hoped that such studies will start in the spring of 1990.

XI APPENDIX ii.vi. EARLY LIFE STUDIES IN THE NETHERLANDS

Field Studies on Plaice Recruitment

Netherlands Institute for Sea Research

Purpose: To identify factors influencing year class strength operating during egg and larval stages.

This four year project will reach its end in October 1989, and has focused mainly on growth and immigration. Plaice larvae and juveniles have been sampled at open sea, during immigration and after settlement in 1987-1989. Preliminary results indicate that in different years the larvae may have originated from different spawning grounds, ie the English Channel and the Southern Bight vs the Southern Bight and the German Bight, and that the relative importance of the spawning grounds can differ strongly within and between years. In 1987 growth has been studied only with the otolith increments, and a large variation in otolith growth rate was observed, which could largely be explained by differences in sea water temperature. In 1988 a start has been made with the analysis of RNA/DNA ratios, and now both methods are being combined. RNA/DNA ratios supported the results found with the otolith increment technique.

Future results will probably involve a re-assessment of plaice larvae mortality data with new data on stage durations based on increment counts and work on growth dependent mortality.

Literature:

Hovenkamp, F. 1988. Within-season variation in growth of larval plaice. ICES CM/ELHS No 70.

Hovenkamp, F. 198?. Growth differences in larval plaice in the Southern Bight of the North Sea as indicated by otolith increments and RNA/DNA ratios. Mar. Ecol. Prog. Ser., in press.

Publication of the results will continue in 1990.

XI APPENDIX ii.vii. EARLY LIFE STUDIES IN NORWAY

Cod

1. Mortality

The instantaneous natural mortality coefficient, m, decreases much from the period egg/hatching larvae - post-larvae stage (m = 42 $year^{-1}$, or 10.9% per day) to the period post-larvae - 0-group (average m = 8 $year^{-1}$, or 2.2% per day). Also the variation of mortality between years is considerably larger for the period before the time of the post-larvae stage than for the period between the post-larvae and the 0-group stage. In addition the larger part of the mortality variation in the period from post-larvae to 0-group stage is correlated with the abundance at the post-larval stage (density-dependent mortality) (Sundby *et al.*, 1988).

2. Recruitment mechanisms

a) Match/mismatch

During a series of years the production curves of nauplii and of first feeding cod larvae were monitored. The critical concentration of nauplii for larval survival is estimated to 5-10 nauplii per litre. The best overlap in time occurred in years with water temperatures above mean, resulting in good year classes. Extreme low or high temperatures are connected with low year classes. The peak spawning of *Calanus finmarchicus* is very temperature sensitive, varying 1½ month over a temperature range of only 3°C (Ellertsen *et al.*, 1988).

b) Microturbulence

The Rothshild-Osborn theory of the effect of microturbulence to increase the contact rate between fish larvae and its prey, has been demonstrated on cod larvae from Lofoten (Sundby and Fossum, 1989). During a cruise to Lofoten in April-May 1989 a special constructed ultrasound current meter was used to measure the microturbulence directly. Discrete samples of cod larvae were obtained with a large pump (Solemdal and Ellertsen, 1984).

c) The condition of the cod female

Cod females with different feeding background were spawning individually in tanks. Egg mortality during incubation was significantly low for the heavily fed, old fish and the fecundity was higher than for the starved cod females. All egg batches from a low-ration first-time spawner had very high egg mortality (Kjesbu, Klungsøyr and Solemdal, unpublished).

3. Larvae surveys

Surveys for early juveniles (2-3 months of age) and 0-group (5-6 months) are carried out since 1979 and 1965, respectively. The indices of early juveniles in 1987 and 1988 were 10.7 and 6.0, compared to 74.7 for the large year class 1983. The same indices for the 0-group investigations were 0.17 and 0.33 compared to 1.69 for the large year class 1983 (Sundby *et al.*, 1988).

Collecting wild juvenile cod, rearing and release of 0-group cod to improve local stocks.

a) Large concentrations of early bottom stage juvenile cod are found in very shallow water along the Finnmark coast. Experiments to catch large numbers (600,000 in 1988) for aquaculture purposes have been successful (Olsen and Soldal, 1988).

b) Cod enhancement project in northern Norway

In connection with the mass-production of juvenile cod in a pond to be released in a small fjord to improve the local stock, experiments to design an optimal production system were carried out in plastic bags.

For tagging tetracycline in combination with Floy tags were used. (Pedersen *et al.*, 1988; Pedersen and Jobling, in press).

Similar experiments are carried out in western Norway (Blom *et al.*, 1989). A model for estimating cod's consumption rates were compared to zooplankton biomass and production.

c) Genetic markers

In spring 1988, 1.5 million yolk sac larvae were released into a small landlocked fjord in western Norway. The larvae used were offspring from a cod broodstock which was homozygote for a rare allele at the PGI-1 locus. The release were followed by a sampling programme, and larvae carrying this allele were distinguished from wild larvae by starch gel electrophoresis. This pilot experiment was the first step into a study aiming to evaluate the effects of mass releases of yolk sac larvae on local recruitment, and the potential in using a genetic marker for estimation of survival and growth of early life stages of cod under natural conditions (Svåsand *et al.*, 1989).

Other Species

Capelin

Since the collapse of the Barents Sea capeline population in 1986, an increase in larvae production is observed during the last years. The 1989 survey is just finished and shows an index about 28 times larger than in 1988.

Saithe

0-group surveys for saithe has been carried out since 1985 during the pelagic period in April and May. The results indicate that the end of April is too late to get a good measure of the pelagic 0-group in the North Sea, before the saithe enter the littoral area (Nederaas and Smestad, 1987). The index (x 10^6) from the different years are as follows: 828 (1985), 545 (1986), 280 (1987), 165 (1988) and 242 (1989).

Herring larvae in Skagerrak area

To map the inflow and distribution of herring larvae in the Skagerrak by sampling along three transects once per month in the period October to April. The larvae are aged by reading daily increments in the otoliths and daily length increments of larvae are back-calculated.

Norwegian spring-spawning herring

The herring larvae investigations started in 1985, and was from 1986 on included in the Norwegian HELP program. The objectives are to study the recruitment mechanisms of the Norwegian spring spawning herring, to obtain detailed knowledge of the distribution in space and time of the larvae and their food organisms, and to study the physical factors affecting both the transport-dispersion and the living conditions of the early life stages. Predation studies will be included at a later stage. The HELP program will be concluded in 1990 and replaced by a program on coastal ecology which will concentrate on recruitment studies of cod and herring.

References

Blom, G., Kristiansen, T.S., Otterå, H. and Svåsand, T. 1989. Relationship between production of zooplankton and production of cod fry (*Gadus morhua* L.) - Modelled from studies in a marine semi enclosed ecosystem. ICES 1989 EMEM paper No. 1.

Ellertsen, B., Fossum, P., Solemdal, P. and Sundby, A. 1988. Relations between temperature and survival of eggs and first feeding larvae of the Arcto-Norwegian cod (*Gadus morhua* L.). ICES ELH Symp./Paper No. 26: 1-29.

Nederaas, K. and Smestad, O. 1987. Abundance and distribution of post-larvae in the 0-group saithe survey in the North Sea and the north east Arctic in 1986 and 1987. ICES CM/G: 31.

Olsen, S. and Soldal, A.V. In press. Observations on inshore distribution and behaviour of 0-group NE Arctic cod. Rapp. P.-v. Rèun. Cons. int. Explor. Mer, 1989.

Pedersen, T., Eliassen, J.E., Eilertsen, H.C., Tande, K.S. and Olsen, R.E. 1988. Feeding, growth, lipid composition related to environmental conditions in an enclosure at 70°N in northern Norway. ICES ELH Symp./Paper No. 114.

Pedersen, T. and Jobling, M. In press. Growth rates of large sexually mature cod *Gadus morhua*, in relation to condition and temperature during an annual cycle. Aquaculture.

Solemdal, P. and Ellertsen, B. 1984. Sampling fish larvae with large pumps, quantitative and qualitative comparisons with traditional gear. In: Dahl, E., Danielessen, D.S., Moksness, E. and Solemdal P. (eds). The propagation of cod *Gadus morhua* L., Flødevigen Rapportser, 1: 335-363.

Sundby, S., Bjørke, H., Soldal, A.V. and Olsen, S. In press. Mortality rates during the early stages and year class strength of the Arcto-Norwegian cod (*Gadus morhua*). Rapp. P.-v. Rèun. Cons. int. Explor. Mer, 1989.

Sundby, S. and Fossum, P. 1989. Feeding conditions of north east Arctic cod larvae compared to the Rothshild-Osborn theory on small scale turbulence and plankton contact rates. ICES CM 1989/G: 19.

Svåsand, T., Jørstad, K.E., Kristiansen, T.S. and Blom, G. 1989. Application of genetic markers for early life history investigations on cod (*Gadus morhua* L.). ICES EMEM paper No. 76.

XI APPENDIX ii.viii. EARLY LIFE STUDIES IN SWEDEN

Recruitment surveys are carried out yearly in Skagerrak-Kattegat and in the Baltic within the framework of ICES.

Analysis of lipid components are used for determining the condition of fish larvae and to estimate mortality due to starvation. The work has so far been concentrated on anchovy larvae from the Californian stock but plans are to apply the method to herring larvae in the water surrounding Sweden.

Micro structure analysis of otoliths from larvae to adult fish are ongoing to study life history and daily growth. Pilot studies have also started to look at the possibility of stock characteristics in the micro structure of otolith.

XI APPENDIX ii.ix. EARLY LIFE STUDIES IN THE UK (ENGLAND, LOWESTOFT)

The plankton ecology group are involved in two main areas of work outside the routine "stock assessment" surveys for herring larvae and mackerel eggs. The first of these is a joint project with the Plymouth Marine Laboratory under contract to MAFF to examine production processes in the Irish Sea in relation to fish larvae growth and survival. The second is an ongoing programme of herring larvae studies off the north east coast of England and in the autumn and in the southern North Sea and eastern Channel in winter. In addition a pilot study of field enclosure systems has been carried out based on the spring herring spawning in the Blackwater estuary (Essex).

The Irish Sea project was conceived in order to examine what is considered to be the low productivity of fish in that area compared with the North Sea. Fish yield per unit area in the Irish Sea is about one third of the North Sea and has persisted at that level since the 1920's. This difference is thought to be the result of lower recruitment due to higher egg and larvae mortality which is in turn related to differences in the production cycle. This is the principal hypothesis which is being tested with particular emphasis on the timing and magnitude of primary production in the two areas.

The field work has since 1987 been concentrated in the Irish Sea but there is a move to the North Sea for 1989 and 1990. To date differences in primary production have been observed between 1987 (0.6 $gCm^{-2}\,d^{-1}$) and 1988 (1 $gCm^{-2}\,d^{-1}$). Compared with the North Sea, production over most of the Irish Sea is late, with the exception of the Irish coastal area where many fish congregate to spawn. The study is beginning to focus in on there being fewer areas in the Irish Sea which provide a suitable larval habitat. These have been categorised by examination of particle size and species throughout the water column. In many parts of the Irish Sea there is a high detritus load with detritivores dominant amongst the zooplankton. Their production does not, however, appear to be limited by the primary production cycle. The copepod *Calanus* which does provide a strong potential link with primary production has not been abundant in the study years.

The herring larvae ecology programme in the North Sea has been linked to standard stock assessment surveys. This has proved a serious limitation with the major effort and priority devoted to the latter. Nevertheless, the period of study since 1985 has been a fascinating one covering the recovery of the central North Sea stock following a complete ban on fishing from 1977-1983. There has been a re-occupation of spawning sites on the Dogger Bank abandoned over 20 years ago and thought by some to have represented the extinction of a genetically determined local stock.

Some larval mortality estimates have been made from patch studies over short periods. Observations have ranged from 5 to 35% per day. Using satellite tracked marker buoys some inter-annual differences in the speed and direction of larval drift have been observed. Some tentative conclusions can be drawn from the abundance of under-yearlings in the nursery areas in the following February. The slow drift and short term retention observed in 1985 appears to be more favourable for survival than the early and rapid easterly movement of larvae observed in the autumn of 1987. Such observations still beg the question why, and specific studies on the nutritional status, growth rates and sources of mortality are needed to support this study. Observations of the vertical distribution of herring larvae and their food organisms have also been made. These have been done in thermally stratified water, mixed water and in boundary regimes between those two. These data, collected with an LHPR system, have been used as part of the Autumn Circulation Experiment (ACE) data base.

The field trials of a system for mesocosm studies were carried out in 1987 and 1988 and the first experiment will be conducted in 1990. The system uses 10 6 m^3 mesh bags to enclose a natural population of herring larvae and their predators. In the trials to date up to 150 larvae have been taken in one enclosure and held for 4-5 hours. In the confined waters of the Blackwater estuary it may be difficult to operate the system for longer periods than 12 hours at a time.

XI APPENDIX ii.x. EARLY LIFE STUDIES IN THE UK (SCOTLAND)

Larval Fish and Recruitment Related Research in Aberdeen

Egg development and mortality

Studies on herring egg deposition and survival on Ballantrae Bank (Firth of Clyde) were carried out in 1988 and 1989 using both shipboard and *in situ* (SCUBA and ROV) techniques. In 1988 mortality was found to be due to predation by benthic organisms and sandeels in general and also to blanketing by ophiuroids in certain areas. In 1989 a storm disrupted the egg bed shortly after deposition and resulted in mass mortality of many of the eggs.

Larval mortality due to predation

Predation by herring, sprat and sandeels on herring larvae was studied in mesocosms. The predation was not necessarily related merely to size of the predator but varied between each species. The developmental state of the larvae had a large effect on predation mortality and could implicate the visibility of the larvae to the predators as a major factor.

Predation on large larvae/newly metamorphosed O-group herring by whiting

Field investigations were carried out in the North Sea in April 1989 to investigate the vulnerability of herring to predation by whiting at around the time of metamorphosis. The hypothesis was that larvae, prior to the development of scales and pigmentation, were less vulnerable to predation than metamorphosed fish due to their relative transparency. Circumstantial support for this hypothesis was provided by data from the ICES Stomach Sampling Programme. Sampling of the larvae/0-group population was carried out in the western, central and eastern North Sea using the IYGPT and midwater frame trawls. Whiting were sampled with a demersal trawl, and the stomachs collected for analysis. In the Skagerrak, samples collected with the midwater gears contained both late larvae and recently metamorphosed fish. A variety of organisms were found in the whiting stomachs, including herring. Initial analysis indicates that only metamorphosed herring were being consumed by the whiting.

Larval growth and vertical distribution, and interactions with oceanography

Field data on the vertical distributions of herring larvae were analysed and a simple model developed. Larvae were found to move towards the surface during daylight and become more diffuse at night. Wind mixing events caused a deepening of the distribution. The vertical distribution model was linked to a prey grazing model to produce a time-depth structured model of food intake by the larvae.

Field data collected adjacent to a drifting buoy located in the centre of a patch of larvae were compared with the results from the grazing model. The model indicated that the passage of a storm during the study should have resulted in a significant reduction in prey consumption. Daily data on condition indices and otolith ring counts also indicated the presence of a signal on the corresponding day.

ACE participation

A major part of early life research effort was devoted to the Autumn Circulation Experiment (ACE) which is described elsewhere in this report.

Larval Fish and Recruitment Related Research in the Dunstaffnage Marine Laboratory, Oban

Predator-prey relationships: a laboratory and field study

Work has recently started on this project which involves integrated field and laboratory studies to investigate the survival of larval and juvenile flat fishes in relation to their predators and prey. The project will range from investigation of sensory systems in the laboratory, through trophic studies in mesocosms to *in situ* analysis of predator-prey interactions on sandy beaches. The results will help to explain the massive mortalities in the early stages of fishes that determine recruitment to the adult stock.

The project consists of a study of two inter-related phenomena applicable to both fish and invertebrates. (1) vulnerability as prey and (2) effectiveness as predators.

Specific objectives will include:

1. To determine, in the laboratory, the role of sensory and locomotor systems in escape from predation, with particular reference to larval and juvenile fishes.

2. To determine the changes in sensory and motor performance of flat fishes that take place during development, especially related to feeding and predation, at metamorphosis and settlement.

3. To determine from field and laboratory studies the relative importance of factors such as substratum type, food availability and predation in affecting habitat selection and survival of flat fishes during and after settlement on sandy beaches.

4. To determine whether temporal patterning of activity of predator and prey influence survival.

5. To develop models of interaction between prey and predators with a view to predicting vulnerability and survival.

XI APPENDIX ii.xi. EARLY LIFE STUDIES IN THE USA

1. Federal Activities

The NOAA recruitment research program will focus on the mechanisms that control the survival of larval and juvenile fish with the goal of understanding the recruitment process in order to achieve the capability of predicting fish productivity in the context of abiotic and biotic change. The research program will focus on comparative recruitment processes of a limited number of species in a limited number of target marine ecosystems. Various NOAA researchers and agencies (NMFS, OAR, ERL, Sea Grant and NURP) have been involved in recruitment research.

One of the major ongoing NOAA efforts in recruitment fisheries oceanography is the Fisheries Oceanography Coordinated Investigations (FOCI). This is a joint ERL/NMFS project to study larval recruitment into the walleye pollock fishery of the western Gulf of Alaska. Critical aspects of the physical environment under investigation are the temporal and spatial behaviour of wind driven currents, the Alaska Coastal Current and slope/shelf exchange. Biological research focuses on the major sources of mortality of eggs, larvae and juveniles and how these are influenced by oceanographic conditions, egg quality, larval and juvenile food resources and predator interactions. The study employs advanced technology in conducting detailed biological and physical field sampling as well as historical satellite imagery to relate physical environmental variation to recruitment success.

An earlier ERL/NMFS cooperative project, conducted between 1978 and 1982 was an investigation of the relation between the physical features of the Mississippi River plume and the feeding growth and survival of larvae of several economically important species. This project focused on the biological importance of the Mississippi River front rather than larval transport and currents.

The NMFS Georges Bank Ecosystem Study contains a recruitment research program. The primary focus has been on the interaction of food supply, temperature, growth and starvation and predation from the egg to juvenile stage of cod and haddock. The effects of advective loss of eggs and larvae from the Bank due to entrainment by storms or Warm Core Rings has also been considered. A particular emphasis has been on the predation on juveniles by other fish because of its direct implications for management. A good deal of effort has been directed into developing quantitative sampling devices and techniques for all early life stages. In addition, biochemical methods for assessing condition of the fish have been developed. In recent years the NEFC has used manned submersibles to supplement bottom trawl surveys in order to study recently settled juvenile cod and haddock. The results indicate that juvenile cod and haddock primarily inhabit an extensive pebble-gravel deposit located on the north eastern edge of Georges Bank at 70-100 m water depth. This past year, 1988, a redirected effort has been made towards herring to provide an index of adult spawning biomass based on larval production during the autumn spawning season and, thereby, allow the centre to address rebuilding of herring stocks in the Nantucket Shoals-Georges Bank area. Also a retrospective analysis of the decadal changes in the recruitment of sandeels, herring and mackerel is underway. This study is focused on the competitive and predatory interactions between the three species that appear to affect their recruitment.

A long term joint state and NMFS research project on the California Current Upwelling System (CalCOFI) has led to a proposed comparative project on the four major eastern boundary current systems - Peru, Canary, Benguela and California - and the analogous Brazil-Falkland/Malvinas current system. This is the Sardine Anchovy Recruitment Project (SARP) promoted under the Program of Ocean Science and Living Resources (OSLR) which is cosponsored by the Food and Agriculture Organisation of the United Nations and the Intergovernmental Oceanographic

Commission. The project seeks to develop important linkages between the physical features of these systems and recruitment dynamics. The project uses the most advanced techniques to examine the details of intra-annual recruitment mechanisms. One of the strengths of this and other NOAA programs (eg the Georges Bank ecosystem) is the combination of field sampling, laboratory experimentation and mathematical modelling employed.

The ecosystems dynamics initiative also moved forward over the past year (GLOBEC). It had started out as an effort to make a concerted attack on the problems of recruitment ecology, and had broadened into the more general goals of understanding and predicting the variability of ocean ecosystems and populations on an interannual to decadal time scale. Following a large workshop last year (Wintergreen, VA, 1988), sponsored by federal agencies, a substantial report was produced by the academic community participants. The essence of the report was the conviction that the time was right to embark on a large new program of ecosystems dynamics, taking advantage of advances in physical oceanography and technology, and the development of models which incorporated biology and the physical and chemical "climate" of the ocean. Nominations were called for from the community at large to form a steering committee to start planning these activities, with particular reference to cooperative studies with international efforts already under way, such as the ICES activities. Most academic recruitment related studies presently funded by NSF, ONR, NOAA, NASA and DOE probably will be subsumed under GLOBEC.

2. Some non-federal Early Life History Research Programs on the United States East Coast and Gulf of Mexico

Listed below, with brief notes, are some programs and principal scientists who are carrying out ichthyoplankton studies, larval ecology research, or recruitment programs. The list is not complete. For example, it does not include programs funded by industry and does not include many studies carried out by individuals States.

a) University of Maine. Herring larval ecology and recruitment studies in the Gulf of Maine. D Stevenson.

b) University of Maine. American and European eel spawning, larval ecology, oceanography, transport, etc. J McCleave.

c) Bigelow Laboratory. Herring larval ecology and oceanography, Gulf of Maine. D Townsend.

d) Connecticut Department of Environmental Protection. American shad recruitment, larval ecology, density-dependent factors, stock and recruitment relationships. V Crecco.

e) State University of New York, Stony Brook. Bluefish larvae ecology and oceanography. Larval transport, recruitment stock identification. R Cowen and D Conover.

f) State University of New York, Stony Brook. Silverside (*Menidia*) larval ecology, dynamics, stock-specific attributes, latitudinal effects hypotheses. D Conover.

g) University of Rhode Island. Winter flounder larvae ecology and factors affecting egg/larval survival, growth, condition. A Durbin, E Klein and G MacPhee.

h) University of Delaware. Early life studies on the sciaenid *Cynoscion regalis* (weakfish). Ecology, oceanography; includes studies in mesocosms. C Epifanio.

i) University of Maryland. Growth and survival of anadromous fish larvae, especially striped bass and white perch. Growth rate variability, events, subtleties. E Houde.

j) University of Maryland. Bay anchovy early life ecology and oceanography. Factors affecting variability in survival, growth, condition. Field and mesocosm studies. E D Houde.

k) Philadelphia Academy of Natural Sciences. Low oxygen and larval fish survival, growth, behaviour. D Breitburg and E Houde.

l) Virginia Institute of Marine Sciences. Development of a camera-net egg/larval sampler and development of automated data analysis from silhouette photographs. J Olney and E Houde.

m) Virginia Institute of Marine Sciences. Striped bass egg and larvae ecology, dynamics, including predation effects. J Olney.

n) Virginia Institute of Marine Sciences. Ichthyoplankton ecology and oceanography in the Chesapeake Bay plume front. J Olney.

o) East Carolina University. Striped bass spawning, larval survival and growth, foods and feeding. R Rulifson.

p) Old Dominion University and Virginia Institute of Marine Sciences. Croaker and spot (Sciaenidae) larvae transport, ecology, oceanography and recruitment. Includes age and growth, etc. B Norcross and C Jones.

q) North Carolina State University. Transport of sciaenid larvae and recruitment mechanisms. J Miller and L Pietrafasa.

r) North Carolina State University. Storms, spawning and survival, growth, condition of menhaden eggs/larvae. D Checkley.

s) North Carolina State University. Larval relationships, size-related phenomena, size-dependent dynamics, individual based models, etc. J Rice, L Crowder and T Miller.

t) University of South Carolina. Otolith-ageing, microstructure of otoliths, methods and applications, especially to striped bass. J Dean.

u) Gulf Coast Research Laboratory. Sciaenid larvae ecology and recruitment mechanisms, especially red drum (*Sciaenops ocellatus*). J Schultz.

v) Louisiana State University. Ichthyoplankton and oceanography transport studies, frontal zone influence, Mississippi plume, etc. R Shaw.

w) University of Texas. Sciaenid larvae ecology and oceanography; recruitment mechanisms. J Holt and S Holt.

XI APPENDIX iii.i. SUMMARY OF RESULTS FROM THE AUTUMN CIRCULATION EXPERIMENT (ACE)

ACE was both an oceanographic and biological study. The collection and analysis of biological data was coordinated by the Marine Laboratory, Aberdeen and carried out with the participation of the Danish Institute for Fisheries and Marine Research, Fisheries Laboratory, Lowestoft, Institut für Meereskunde, Hamburg, and Flodevigen Marine Station, Norway. Approximately monthly field observations of the distribution and biological characteristics of herring larvae in the North Sea between September 1987 and March 1988 were collated and compared with distributions predicted by a three dimensional transport model developed at the University of Hamburg.

The transport of herring larvae is controlled by the vertical distribution of the larvae and the horizontal water currents. A model of vertical distribution patterns was developed from field observations. The vertical distribution model then dictated the computer simulated behaviour of tracer particles in a transport model. The horizontal flow data for the model were provided by a three dimensional water circulation model of the North Sea run at Hamburg University. The transport model was used with some success to predict the changes in the horizontal distribution of larvae in the North Sea between September 1987 and March 1988.

Circulation in the North Sea is wind driven during the winter, and during ACE anomalous atmospheric conditions caused a reduction in water transport relative to the long term climatological mean. As a result, the model predicted that larvae from northern North Sea and west of Scotland spawning areas failed to reach the juvenile nursery areas off the Danish coast. This result was confirmed by the results of the monthly field survey data collected during ACE. It is likely that these larvae were carried out of the North Sea by the north flowing Norwegian coastal current, and would therefore be unavailable to recruit to the North Sea stocks in future years.

The investigations of vertical migrations of herring larvae in the North Sea during ACE indicated a complex interaction with the light and turbulent mixing environment. The underlying relationship was diurnal - larvae ascend towards the surface during daylight and descend at night - but this may be modified by the effects of tidal shear. The field investigations combined state-of-the-art biological and physical sampling techniques in the form of opening and closing nets, and an acoustic doppler current profiler. The results suggest that the simple model of vertical migrations used in the advection modelling part of ACE, was not fully adequate to account for the vertical distributions of larvae over the whole North Sea.

Regional and temporal differences in growth potential of herring larvae were studies using comparisons between otolith microstructure and larval length. During each cruise, samples were collected in four regions and analysed for ring-count/length relationships. Significant differences between areas were found indicating an increase in growth potential from northerly to southerly regions, and a decrease in growth rate over time (September-February) throughout the North Sea.

Field studies of phytoplankton and zooplankton productivity (the latter measured by copepod egg production) were combined with investigations of the diet assessed from stomach contents, and prey capture modelling to study the regional variations in the growth potential of herring larvae in the North Sea. Significant primary and secondary production continued throughout the winter in the central North Sea, and this was reflected in higher growth rates of larvae than in the northern North Sea. The diversity of prey items was substantially lower during the overwintering period than in the autumn, but this was not entirely reflected in the zooplankton populations.

The collapse of North Sea herring populations during the mid 1970s is believed to have been due to a period of several years of low recruitment coupled with high fishing activity. Predicting variations in recruitment in advance of fishery legislation will be essential for future management of fish stocks. However, such predictions are extremely difficult. The results from ACE suggest that a better understanding can be achieved with the aid of environmental modelling methods.

XI APPENDIX iii.ii. SARP STUDIES ON SPRAT RECRUITMENT IN SE NORTH SEA

The south eastern North Sea, particularly the German Bight, is a very hydrographically complex region characterised by several frontal systems such as tidal mixing fronts and river plume fronts confronting sprat larvae with a number of different "types" of physical environments. The working hypothesis is: the survival of sprat larvae depends crucially on their physical environment (temperature, salinity, turbulence etc) which determines via the trophic links condition and growth rates of sprat larvae. Analyses in the different "types" of water includes interalia the following:

- vertical distribution of chlorophyll concentration.
- particle size analysis determined by Coulter Counting analysis to define potentially suitable in feeding conditions for larval feeding.
- vertical distribution sampling for eggs and larvae.
- collection of sprat larvae for condition and gut contents analyses (RNA/DNA ratio, enzymatic studies, vitamin C analysis, histological analysis).
- collection of sprat larvae for growth/mortality assessments from otolith studies.
- co-occurrence with potential predators.

The synthesis of these analyses will show which set of physical factors gives the best survival of sprat larvae.

This project is a cooperative effort of the UK, Denmark and the FRG involving three research vessels. Two cruises of the RV *Victor Hensen* and the RV *Challenger* have been carried out successfully in May and June 1989. The sampling will be completed by a cruise of the RV *Dana* in August 1989.

XI APPENDIX iii.iii. SARP PROJECT ON IBERIAN PILCHARD

This project started in 1986 through a Spanish-American Joint Scientific Cooperation with the IEO (Institute Español de Oceanografia) and the Southwest Fisheries Centre of La Jolla, California. This initial project mainly funded some scientific equipment and the training of SARP techniques in La Jolla. This led to the creation of an IEO funded program in order to carry out the SARP objectives.

Objectives of SARP and Realisations

The principal aim of the project is to study the environmental processes which affect the recruitment of the North Atlantic Iberic pilchard (*Sardina pilchardus*). These processes were classified under two main categories: physical oceanography and biological oceanography.

Also, within the framework of this SARP project on sardine recruitment variability, new stock estimation procedures were also approached in our objectives, such as the Egg Production Method. EPM is the actual method used for fisheries assessment purposes and for the respective year class spawning biomass estimates of northern anchovy, *Engraulis mordax*, from the Pacific coasts of the USA. ICES at the moment is also recommending fishery independent estimates.

The physical oceanography aims to analyse the influence of upwelling occurring in the north western Galician Shelf on recruitment success/failure of pilchard. Another objective which is under development is a larval transport study.

Biological oceanography has focused its attention on the study of pilchard seasonality (monthly sampling) in three locations of the Spanish North Atlantic coastline (Vigo, La Coruña and Santander), the delimitation of the spawning grounds in the continental shelf and slope of the Cantabrian Sea, complemented with the zooplankton and phytoplankton analysis and physical parameters (CTD casts).

Under this category, there is another important line of laboratory investigation which is underway, investigating larval condition (inanition) through an histological technique (Theilacker), larval growth and birthdate data analysis through computerised image analysis, fecundity studies, artificial induction of spawning in order to validate field data on these investigations.

Under this project, several cruises have been realised since field work began in 1986. Although classified under one of the two categories mentioned, these cruises were multidisciplinary. For example, a survey in 1987 was carried out in the Galician and Cantabrian areas of the North Atlantic which had as a main objective the delimitation of the extension seaward of sardine spawning grounds. In this cruise, investigations on phytoplankton, zooplankton and physical oceanography were carried out.

Physical oceanography, as well carried out, cruises during the upwelling season with the cooperation of other field work in this same year.

A monthly sampling scheme based on the main objective of studying pilchard seasonality in three different situations of this northern Spanish coastline began since 1987 to this date.

During 1988, another cruise was carried out to realise the first attempt in European waters of EPM on pilchard. This cruise was coordinated with Portugal, which realised this cruise in

Portuguese waters approximately during the same dates. Both cruises were simultaneous with the acoustical tracking and evaluation of this resource. Physical oceanography was also carried out.

At this moment, the data collected is under the final process of analysis. In October, a SARP joint American-Spanish symposium is being prepared with the purpose of presenting a summary of all the investigational work carried out under the project.

Since this project led to an important cooperation with Portugal, most of the mentioned activities have been carried out by the INIP.

XI APPENDIX iv. QUESTIONNAIRE ON COMPARATIVE STUDIES OF COD AND HADDOCK RECRUITMENT

Comparative Studies of Cod and Haddock Recruitment

A number of authors have argued for a comparative approach to studies of larval fish ecology and the recruitment problem (eg Bakun, 1985. Comparative Studies and the Recruitment Problem: Searching for Generalisations. CalCOFI Rep. Vol. XXVI). At the ICES Working Group on Larval Ecology in 1987 there was a discussion about comparative studies within the ICES area and the group endorsed a proposal to bring together existing data on early life history stages of cod and haddock in a systematic way, in order to provide a background of information for stocks of these two species. This would provide a basis for exploring hypotheses concerning recruitment variability. For example, most cod stocks spawn early in the year, often in coastal water masses where primary production starts early. A comparison of the various stocks may help to refine hypotheses and models which seek to link larval survival with primary and secondary production.

The proposal to compile a checklist of biological and environmental data for comparing spawning strategies of stocks in different areas was discussed at the Biological Oceanography Committee of ICES in 1987 and supported by them. K Brander agreed to coordinate a checklist for cod and haddock and the committee considered that it would be useful to extend the initiative to other species in the ICES area, such as stock of flatfish in the North Sea and Bay of Biscay.

You are invited to fill out a checklist for any cod or haddock stock and since this is the first use of the checklist you are also invited to suggest additions and alterations to the checklist. Where possible the information should come from published sources, which should be referred to, but unpublished material can also be included. The present intention is that all those contributing a checklist will receive copies of all other checklists from the coordinator, on condition that unpublished information cannot be used without expressed permission of the person supplying it. Depending on the level and quality of 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.

Complete checklist should be sent to:

Dr K Brander
Marine Fish Division
Bedford Institute of Oceanography
PO Box 1006, Dartmouth
Nova Scotia, B2Y 4A2
Canada

by the end of 1988, so that they can be circulated early in 1989. Checklists received after that date may be circulated in later mailings. If the ICES Larval Ecology Working Group meets in 1989, that would be an opportunity to discuss the outcome of the exercise and to take it further if it seems useful to do so.

Checklist of Biological and Environmental Data for Comparing Reproductive Strategies

1. Species, stock and area of distribution

- evidence of stock discreteness.

2. Timing of spawning

- date, year-to-year variability, time of day, timing in relation to production cycle, in relation to hydrographic events, in relation to other fish species spawning in the same location.

3. Location of spawning

- geographic location, extent and variability, location in relation to hydrographic features and in relation to other species (including potential food producers), larval drift and retention.

4. Biological details

- fecundity, egg size, typical egg and larval densities, incubation rate, size of larvae at hatching, size of yolk sac in relation to total larval size, larval development rate, larval condition factors and nutritional status, egg and larval mortality rates, first feeding of larvae and food composition.

5. Recruitment

- stock to which they recruit and whether they are the only contributor (eg there are several spawning areas which contribute to the North Sea cod stock and their relative contributions may vary from year-to-year), evidence of year class variability (eg young fish survey; VPA), earliest time when year class strength can be predicted, hypotheses to account for year-to-year variability, linkages with other species (eg predation, competition, linked fluctuations in recruitment).

XI APPENDIX v. SUBTLETIES AND EPISODES IN THE EARLY LIFE OF FISHES*

Author: E D Houde

Fluctuations in the abundance of fishes may be caused by episodic mortalities or by more subtle variability in the daily growth and mortality rates of early life stages when survivorship response surfaces are used to illustrate the relative effects of episodic and subtle mortality during early life it is the subtle variability that may exert the greatest effect on recruitment. Massive advective losses of eggs or larvae, failed egg production and acute contaminant mortalities are examples of episodic events that may impact recruitment significantly by eliminating a large fraction of the population in a brief period, but such episodes need not be catastrophic. Difficult to detect, minor changes in growth or mortality rates (eg 2 to 3% per day) related to starvation, predation, chronic contaminant effects and dispersive losses easily can lead to order of magnitude variability in potential recruitment. Stabilisation of recruitments through density-dependent growth rate variability in the early life of herring, haddock, striped bass and bay anchovy was examined and shown to be potentially important. Whether this mechanism actually is important in the sea remains to be determined.

* Abstract of a paper presented at the Fish Population Biology Symposium, Aberdeen, 17-21 July 1989

XI APPENDIX VI. SIZE-SPECIFIC SURVIVORSHIP AND RECRUITMENT STABILITY[1]

Author: J.E. Beyer

Replacing chronological age by a physiological age measured as body size represents, in principle, a simple substitute form of variables in traditional age specific fish population dynamics. However, survivorship to size depends on the combined and interaction effect of growth and mortality and the outcome is usually not straightforward. Some size specific concerns are introduced in this appendix in terms of three figures relating only to the most simple treatment of a year class fish i.e. considering the year class to comprise identical fish.

Figure 1: the "physiological rate" of Mortality

Empirical evidence indicates that the rate of natural mortality decreases with body size and also is closely related to the specific rate of growth. The figure illustrates the most simple treatment of this situation using the basic elements of traditional fish population dynamics as the starting point. Thus growth takes place according to the von Bertalanffy growth equation. Using weight as the measure of size, the rate of growth attains a maximum at size 0.296 W_∞, the point of inflexion at the sigmoidal growth curve. The rate of mortality is considered inversely proportional to weight in the power of 1/3 (that is the body length). Mortality thus approaches a minimum value, denoted by M_∞ at size W_∞. The "physiological rate" of mortality is defined as the rate-ratio of mortality to growth. Note that the reciprocal value of the rate of growth at a specific size is a measure of the time spent at that size. The physiological rate of mortality attains a minimum at size 0.422 W_∞. Thus maximum survival across a small size interval occurs at this size. The cumulative mortality across a size interval is generally obtained by integrating the physiological rate of mortality that is, by the area under curve.

An example of parameter values for this size-structured extension of traditional theory is $K \cong 0.1\ yr^{-1}$, $M_\infty \cong 0.1\ yr^{-1}$ and $W_\infty \cong 3kg$ for North Sea plaice. The very high size-specific vital rates for the early life stages are included in the same picture although they are not visible in this figure. Actually, the entire first year of life with body weights from about 1/2 mg to 10 g "disappears" from the graph and is virtually represented by "the y axis" in this figure.

Figure 2: The size specific survivorship

The weight gaining factor (p) is the most important factor in specifying the size interval. The theory of course can be applied to any selection of consecutive size intervals but two alternative definitions of p are of particular interest for early life studies. The first relates to physiological reasonably well-defined stages e.g.:

$$p_1 = \frac{\text{weight at metamorphosis}}{\text{weight at onset of feeding}} \approx 200$$

---

[1]Basic ideas presented as ELHS paper No. 86 ("The stock and recruitment problem") at Bergen, 1988 and subsequently considered in more detail by J.E. Beyer, 1989: Recruitment stability and survivorships - simple size-specific theory with examples on the early life history dynamics of marine fish (to appear in DANA, the Danish Journal of Fisheries and Marine Research). Basic equations of size structured cohort dynamics in case of continuous size at age distributions were included as an appendix to the 1986 report of the IREP Steering Group as part of a first draft on size structured prey-predation interactions.

The second relates to the size ratio between larvae and their prey:

$$p_2 = \frac{\text{weight of predator}}{\text{weight of prey}} \approx 100 \text{ (larval fish as predators)}$$

Once p is specified and the physiological rate of mortality expressed as a function of size, then the survivorship (1) may be derived. The survivorship always refers to numbers. But since we consider numbers at size, a simple p-scaling gives biomass, i.e.

$B_1 = lp\ B_0$ or

Ratio of biomass increase = Size-specific survivorship x weight gaining factor

If, for example, the survivorship is 1% and p = 100 then the biomass may change during the grow-up phase but the biomass at size W_1 is the same as the start biomass at size W_0.

To illustrate the sensitivity to changes in the vital rates, suppose the survivorship is 10%. If the growth rate is reduced by 50% then (both stage duration and) the physiological rate of mortality doubles. Hence, the survivorship is reduced to the square of its initial value or to 1% as indicated by the stipled curve. The same effect (but with unchanged stage duration) could have been obtained by a doubling of the rate of mortality. It is ONLY the ratio between the vital rates (i.e. the physiological rate) that determines survival at size.

The most simple size-specific model of the vital rates that appears to explain present knowledge on early life dynamics is the following power model:

$g(w) = Hw^{1-m}$: Rate of growth (dw/dt) at size

$\mu(w) = qw^{-m}$: Instantaneous rate of mortality at size

where H,q and m are constants. The physiological rate of mortality is thus inversely proportional to weight and q/H denotes the constant of proportionality. The survivorship becomes:

$l = p^{-q/H}$: survivorship from size w_0 to size pw_0

and is thus independent of the initial weight w_0 and the power m. Notice that the traditional model of constant mortality is obtained in the special case of m = 0, i.e. with a constant instantaneous (specific) rate of growth. A sensible value of m appears to be about 1/4. The p-specific survivorship is completely determined by the power q/H, the instantaneous rate-ratio of mortality to growth.

Figure 3: Critical Points on the Size-specific Recruitment Curve

Three domains of spawning stock densities or of initial egg or larval abundances are considered. Point C denotes the transition from density-independent to density-dependent growth. As the larval abundance increases further (caused by e.g. a reduction in adult fishing mortality), the survivorship decreases due to a progressive slower rate of growth. At point B the survivorship has reached the critical level of 1/p and the recruited biomass (of fish sized pw_0) becomes equal to the initial biomass (of fish sized w_0). Even higher larval abundances (III) reflect situations of such severe competition for food that we expect density-dependent mortality to occur caused by starvation, cannibalism etc.

Using the simple power model, recruitment in the intermediate domain (II) is described by:

$$N_1 = p^{-q/H} N_0 \qquad : \text{H density-dependent}$$

To the first approximation we consider the size-specific rate of mortality density-independent (i.e. q is constant). The maximum size-specific rate of growth occurs at the critical point C and is described by $H = H_{max}$. Minimum size-specific rate of growth is described by $H = H_{min}$ and occurs at the critical point B of no biomass increase. That is:

$$q = H_{min} \underset{\longleftarrow}{\leq H \leq} H_{max} \quad \text{as} \quad E \underset{\longrightarrow}{\leq N_0 \leq} E_b$$

The question is here how we determine the value of H, the coefficient of the size-specific rate of growth for a certain start-density N_0, the initial number of larvae in domain II. It is tempting simply to let H decrease in inverse proportion to a linear function of N_0 in which case recruitment in domain II becomes part of a Ricker curve. However, this recruitment curve is very sensitive to changes in mortality (i.e. q) because the rate of growth is unaffected by a change in mortality since growth only depends on size and the start density in such a simplistic description of density-dependent growth. A rational approach, consists of deriving the H value from a requirement to say, the total amount of food consumed by the year class during the time required for the individual fish to gain the factor of p in weight. Considering this amount of food as being constant from one year to next, one can show that domain II represents a large intermediate range of stock-sizes ($E_b/E_c \approx 10$) while the extreme range of variation in growth rate is relatively small (representing a ca. 50% reduction from point C to point B.) Recruitment will decrease (from point C to point B) in domain II and in this sense C represents a (catastrophic) maximum point of recruitment. In this model the rate of growth depends on the amount of food available and the rate of mortality as well as size and start-density. As a consequence recruitment is stabilised against variations in the vital rates and the dominant factor in determining the level of recruitment is the amount of food available.

The basic point in these considerations is that the degree of long term stability in recruitment that many stocks appear to show can be explained alone by the first couple of months during which the larvae gain a factor of 100 in weight (while depending entirely on the production of copepod nauplii as food). Recruitment is further more unaffected by even considerable year-to-year fluctuations in the rate of mortality (say ± 50%). Deviations from stable conditions due to year-to-year variations in the copepod nauplii production <u>available</u> as larval food (causes here presumable also include variations in hydrographic conditions such as stability of fronts and microturbulence-dependent contact rates) and other causes that temporarily will change or cause a breakdown of "the overall degree of competition among young fish and invertebrates for pelagic food" can easily explain the magnitude of "observed" variability in recruitment for most stocks.

Figure 1

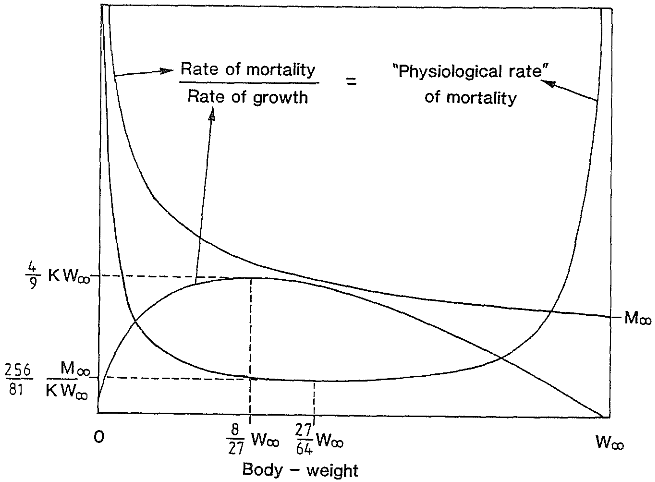

Figure 2

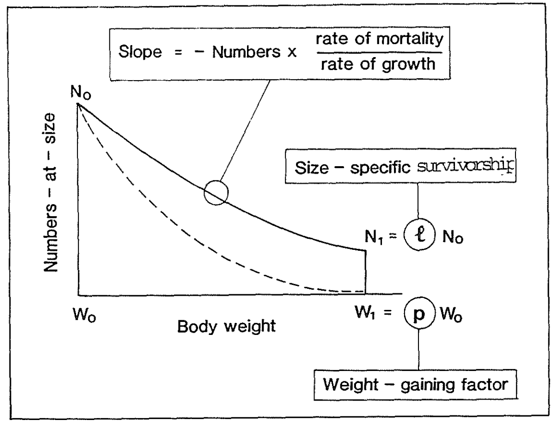

Figure 3