

**REPORT OF THE
WORKING GROUP ON RECRUITMENT PROCESSES**

Halifax, Canada

17–20 June 1996

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1 TERMS OF REFERENCE AND PARTICIPANTS

At the 1995 ICES Statutory Meeting, resolution 2:53 was adopted as follows:

The Working Group on Recruitment Processes (Chairman: Dr. P. Pepin Canada) will meet in Halifax, Nova Scotia, Canada, from 17-20 June 1996 to:

- 1 review progress with the planning of a Workshop to further study the Relationship Between Otolith Growth and Body Growth in Fish Larvae and identify further aspects to be considered;
- 2 review progress with the Study Group on Spatial and Temporal Integration;
- 3 review progress in the application of size-based theory to recruitment problems and in particular
 - (a) develop explicit relationships between mortality and body size in early life and carry out sensitivity analyses to determine which parameters are most sensitive to changes in size-specific survival,
 - (b) examine stage-specific survival rates and their variability, and determine how variability changes with stage development,
 - (c) determine whether there are critical stages or sizes where variability in rates change significantly;
- 4 review progress in the application of otolith elemental analysis to recruitment problems;
- 5 review experimental protocols relating to experiments designed to characterise growth and condition of larval fish, and their vulnerability to predation.

The meeting was attended by the following:

S. Campana	Canada	A. Folkvord	Norway
P. Fossum	Norway	C. Fox	UK
B. Klenz	Germany	T. Lambert	Canada
T. Marshall	Norway	R. Mohn	Canada
F. Page	Canada	P. Pepin	Canada (Chairman)
H. van der Veer	Netherlands	K. Wieland	Germany

The Chairman received apologies from the following:

J. Alheit	Germany	J. Bartsch	Germany
J. Beyer	Denmark	M. Dickey-Collas	UK
J. Gagné	Canada	C. Grimes	USA
M. Heath	UK	E. Houde	USA
P. Kåras	Sweden	T. Linkowski	Poland
P. Margonski	Poland	J. Modin	Sweden
E. Moksness	Norway	P. Munk	Denmark
W. Nellen	Germany	W. Richards	USA
D. Schnack	Germany		

2 OVERVIEW

2.1 Introduction

The Working Group was greeted by Dr. M. Sinclair, Division Manager, Marine Fish Division, Bedford Institute of Oceanography. Following this, the Working Group was able to address the assigned terms of reference to varying degrees of detail. The limited attendance and high turnover in composition of the participants relative to previous meetings of the Working Group had an influence on the continuity of approach in dealing with some of the assigned terms of reference. There were four main areas of work: (1) review and evaluation of experimental protocols used in the study of growth, condition, and vulnerability to predation of ichthyoplankton; (2) progress and development of a Workshop to further study the relationship between otolith and body growth in larval fish; (3) consideration of the

influence of physical processes on populations dynamics of fish eggs and larvae; and (4) preliminary assessment of the link between the establishment of year-class strength and early life history stages.

2.2 Review and Evaluation of Experimental Protocols

The Working Group was presented with an extensive review prepared by one of the members (A. Folkvord, Norway) in collaboration with a graduate student (A. Paradis, Canada) summarising the quality and extent of information that can be used to describe laboratory procedures and the state of experimental animals in published studies dealing with growth and condition. An evaluation of the influence of experimental protocols on estimates of predation rates on fish larvae by a variety of organisms was also summarised.

Discussion centred around the frequent lack of information concerning the state and source of the study organisms and the limited knowledge of reference growth curves or criteria that could be used to assess the health of study animals. A proposal was presented outlining what critical elements are required to assess the value of experimental approaches as well as the condition of experimental animals. Physical elements essential for intercomparison among studies included those that may significantly influence the results and those which may be critical to the development and health of experimental animals. There was considerable discussion about the need to establish reference levels (e.g. size-at-age) for healthy animals, of various species, living under optimal conditions for growth and development.

2.3 Progress on Development of a Workshop Dealing with the Relationship Between Otolith and Body Growth in Larval Fish

The Working Group was presented with a summary of previous discussions outlining the need to develop a mechanistic model otolith growth by one of the members (S. Campana, Canada). The development of that model was, and is, viewed as being fundamental to improving the accuracy of growth back-calculation. However, it appears that the experiments necessary for linking otolith increment width to somatic growth, temperature, food consumption, size and protein synthesis have not yet been carried out. While these experiments are tractable, the fact that back-calculations will necessarily be based on increment width alone may mean that there are too many unknown variables for improvements to current back-calculation models. Measurements of oxygen isotopes (temperature) and protein along the otolith growth sequence may circumvent this theoretical constraint, if it indeed exists. Thus the Working Group concluded that progress in the development of the otolith growth model must await further research.

2.4 Progress in the Application of Otolith Isotopes to Recruitment Problems

The Working Group was presented with a summary of the most recent developments in the use of oxygen isotope ratios for the reconstruction of temperature histories by one of the members (S. Campana, Canada).

Reconstruction of the temperature history of individual fish would be of considerable value to those studying growth trajectories, spawning sites and migration pathways, among other things. In principle, the chemical composition of the daily growth increments formed in the otolith record the temperature history of the fish on a daily basis. However, recent applications of Sr:Ca measurements as proxies for temperature have been criticised as being heavily influenced by factors other than temperature. With recent experimental and methodological advancements, analyses of otolith oxygen isotope ratios are now being used to reconstruct temperature history without the influence of the growth effects which can confound Sr:Ca ratios. While further research is required, oxygen isotope assays appear to offer the potential for accurate temperature histories, at least in waters where oxygen isotope ratios are homogeneous.

The basis for the temperature reconstruction approach is that oxygen incorporated into carbonates (such as the otolith) at the time of formation includes both major isotopes (^{18}O and ^{16}O). Normally, one would expect them to deposit in equilibrium with the concentration in the water. However, there is a physical fractionation due to temperature at the time of deposition, such that the proportion of ^{18}O becomes increasingly depleted as temperature increases. As a result, if the $^{18}\text{O}:$ ^{16}O in the ambient water is known, and if the $^{18}\text{O}:$ ^{16}O in the otolith can be measured, temperature can be calculated. With the recent development of an otolith microsampling device, small regions of the otolith (~50 μm) can be cored and assayed, thus providing temporal resolution on the order of 1-4 weeks.

A recently completed experiment evaluated the response of stable isotopes of C and O in the otolith to 4 temperature regimes. $^{13}\text{C}:$ ^{12}C ratios were highly correlated with somatic growth rate, as would be expected on the basis of metabolic considerations. In contrast, $^{18}\text{O}:$ ^{16}O ratios were insensitive to somatic growth rate, but highly correlated with temperature. The $^{18}\text{O}:$ ^{16}O - temperature relationship was almost identical to that predicted on the basis of equilibrium deposition, and suggested that temperature differences on the order of 1-2 $^{\circ}\text{C}$ should be discernible on the basis of microsampled otolith oxygen isotope assays.

The one major constraint to the application of oxygen isotope assays is the requirement for knowledge of the $^{18}\text{O}:^{16}\text{O}$ in the water through the period of interest. Where this is known, otolith assays should provide an accurate and unambiguous temperature history of the fish. If the isotope ratio of the water is unknown, salinity can often be used as a proxy for the ratio. However, the temperature history may then become a relative one, rather than absolute. In those instances where fish migrate through various water masses characterised by large, unmeasured differences in oxygen isotope composition, reconstruction of the temperature history is likely to be flawed. Nevertheless, the microsampled isotope ratios will still record the migration through the various water masses on an age-structured basis.

Future research in this field will need to evaluate the generality of the experimental results for other species and systems. Development of a laser-based system for sampling the oxygen isotopes in an otolith is likely in the near future, and will greatly simplify the assay procedure. As with other areas pertaining to methods of studying recruitment processes, the Working Group would like to be kept abreast of any further developments in this field.

2.5 The Role of Physical Processes on the Population Dynamics of Eggs and Larvae

Motivation for this section of the meeting was based on recommendations from Study Group on Methods of Spatial and Temporal Integration (ICES CM 1995/L:7)

“To review progress in the analysis of case study data being used to develop techniques for optimising the temporal and spatial design of fish egg and larvae surveys”

and from the ICES/GLOBEC Cod and Climate “Aggregation Workshop” (ICES CM 1994/A:10)

“To identify potential data sets that could be used to assess effects of intermediate scale physical oceanographic processes on the aggregation of cod and their prey, and encourage investigators to develop models of dynamic processes that can be related to the distribution, aggregation and dispersion of eggs, larvae and pelagic juveniles”.

The Working Group was provided with several presentations from guest speakers (J. Sheng & K. Thompson, Canada; F. Page, Canada) and from members (K. Wieland, Germany; H. van der Veer, Netherlands; C. Fox, UK) detailing the application of several types of models to the study of drift and survival of ichthyoplankton. The underlying philosophy of many of the approaches dealt with establishing the relative roles of environmental versus behavioural factors in determining the distribution, and consequently transport, of fish eggs and larvae. The presentations varied in the complexity of the models used for the study of transport and illustrated the need for model validation, in terms of partitioning dynamical and statistical errors. These aspects are of particular significance not only in terms of the general characteristics and behaviour of the models but also when one attempts to estimate loss or retention of animals from regions of interest. Data assimilation methods provided estimates of drift and retention from dynamic models and indicated the potential importance of short term and small scale events on the dynamics of pelagic early life stages.

Evidence indicates that general numerical models may provide adequate representation of the processes which influence both drift and plankton production. Work along the eastern North Sea shows correspondence between wind-forced advection and supply of larvae to coastal areas with subsequent settlement in nurseries. Simulation models for the central Baltic Sea show that wind stress is a significant variable which can be used to identify years with retention or substantial larval drift towards coastal waters as well to assess the relative importance of two potential nursery areas (i.e. the Polish coastal waters south from the main spawning area or the Swedish coastal waters located north-easterly from the initial center of the egg distribution). Wind forcing may also serve as an important driving force in the Irish Sea where there was an association between estimated production and recruitment. Models used in these instances did not rely on high levels of complexity although data assimilation, as driving forces, was an essential element to understanding variability in the early life dynamics.

The underlying problem in defining the level of model complexity required to achieve a good level of predictive ability is the need to identify the key parameters which provide an adequate representation of the influence which physical processes have on early life dynamics. In cases where wind-induced residual circulation is key, then the level of model detail required may be more limited than in a case where strong baroclinic flows impose strong requirements for temperature and salinity data. Fundamental to this issue is the necessity to have an accurate understanding of the factors that govern regional circulation patterns (i.e. have validated physical models). However, there is also a need to consider the quality of information detailing the distribution of fish eggs and larvae in the regions of interest.

The Working Group concluded that there is a need to examine the robustness of plankton survey designs for the generation of distributional indices, to assess their limitations in providing information used in the evaluation of outputs from physical oceanographic models, and to assess whether existing distributional data are sufficient to detect inter and intra-annual patterns. The Working Group should invite presentations from persons with experience in the use of spatial statistics e.g. geostatistics, plant distribution analyses, etc.

2.6 Review Progress in the Application of Size-based Theory to Recruitment Problems

The Working Group was informed of developments in this field in presentations by three members (T. Marshall, Norway; K. Wieland, Germany; P. Pepin, Canada). One of the aspects addressed in all presentations dealt with the potential variability in the features of animals which may alter functional aspects of size-dependent relationships.

The significance of variations about standardised size-dependent relationships was illustrated using an analysis of the variations in egg production by spawning stocks of cod in the Barents Sea and Lofoten area. Interannual variation in the condition of spawning females, with concomitant effects on individual size-related levels of egg production, has important implications for the perceived estimates of spawning stock size. Periodic variations in availability of food for large and small cod have differential effects on their spawning potential. As a result, what may appear as relatively small fluctuations in spawning stock biomass over several years (5 fold variation) is amplified in terms of egg production (10 fold variation) due to changing physiological condition of the animals as well as variations in the size composition of the stock. When coupled with potential condition related effects on egg quality, the results suggest that the accuracy of simple metrics, such as spawning stock biomass, requires careful investigation.

Variation in vulnerability to predation also highlighted possible changes in size-dependent relationships. Summary information from a collation of laboratory studies showed that maximum vulnerability appears to occur when fish eggs and larvae are approximately 10% of the length of a given predator, whether it be a crustacean, gelatinous or vertebrate predator. Below that level, vulnerability appears to increase whereas the opposite holds above that value. However, detailed analysis of laboratory and field information reveals that vulnerability of Baltic cod eggs to predation by herring appears to increase with decreasing size. This pattern is due to the changing egg size, which decreases during development, and the increasing visibility of the later stages of development, due to increasing size of the embryo as well as pigmentation. Whether this is reflected in stage-dependent mortality remains to be determined.

The findings from these studies emphasise the value of size-dependent models in the investigation of recruitment processes. At the same time, there is a need to consider that the use of simple relationships, as the basis for population studies, requires careful assessment of the factors that influence them.

2.7 Linking Recruitment Variability and the Establishment of Year-Class Strength with Events in the Life History of Marine Fish

The Working Group conducted a round table discussion concerning areas of interest to of importance to the Group's future activities. There was general agreement that tasks previously undertaken by the Working Group (e.g. cod checklist, analysis of fish larvae otolith data) had been useful in achieving a better understanding of recruitment processes as well as stimulating the development of new concepts and ideas among the members. There was also agreement that future activities of the Working Group should provide a mixture of discussion topics as well as task-oriented activities.

There was considerable discussion about linking events during the egg, larval and juvenile stages of the life history with the formation of year class strength and subsequent recruitment. Because of the difficulty in studying individual stocks for a protracted number of years, if not decades, the Working Group discussed the advantages of studying the generality of patterns among several species and stocks. The topic was referred to one of the discussion groups which concluded that the Working Group should initiate the collation and analysis of available data on the abundances of various early life history stages from a variety of stocks with a view to determining patterns in the stages at which relative year class strength is established.

2.8 Other Business

The Working Group was provided with a summary presentation concerning the Large Scale Facility Activity for Pelagic Marine Food Chain Research (Bergen, Norway) by one of the members (A. Folkvord, Norway). The facility provides a venue for EU scientist to concentrate efforts at sites well suited for research on pelagic marine food chains under the auspices of the Human Mobility and Training Program. The facility includes: controlled laboratory (temperature, salinity, light) facilities at the High Technology Center at the University of Bergen; similar facilities at the

Austevoll Aquaculture Research Station as well as a land based and floating mesocosms; the Marine Biology Field Station with floating mesocosms and a macrocosm used for juvenile fish production; and one research vessel suited for coastal navigation in model environments. Only research teams conducting their research in the Member States of the Union and Associated States are eligible for funding under the present project. Other researchers, national and international, are able to engage in joint projects with local scientists provided they have separate funding.

P. Fossum (Norway) presented an announcement concerning the 2nd International Symposium on Fish Otolith Research and Application which is to be held in Bergen, Norway, 20–25 June 1998. The objectives are to bring together scientists to exchange knowledge on fish otolith research and to provide a forum where group discussion will result in clarification of issues and the development of new directions in this rapidly evolving field. Themes for the meeting include areas of Otolith Growth and Morphology, Estimation of Fish Growth, the Use of Otoliths in Studies of Populations, and Studies of Otolith Composition.

The limited number of participants at the meeting of the Working Group raised serious concerns and may be indicative of a watershed point for the group. Continued progress may be limited if participation follows current trend (18 people in 1992; 15 in 1994; 12 in 1996). As a result, the Chairman agreed to conduct a survey Working Group members to determine if timing, cost, location, excessive workloads or the contents and agenda of the Working Group have influenced participation. In addition, the survey will gauge the interest of Working Group members in participating in future meetings.

3 REPORTS OF DISCUSSION GROUPS

During the afternoon of the third day, two discussion groups were formed to review the presentations from the previous two days, determine the issues of specific concern to the Working Group, and develop recommendations for future work and consideration. One group was asked to focus on general issues pertinent to the study of early life dynamics and the link with formation of year class strength whereas the second group focused on the methodological aspects of experimental protocols.

3.1 Recruitment Variability and Events in the Early Life History

The term biological recruitment means the process whereby juvenile fish attain sexual maturity and join the reproductive population. This definition then includes the factors affecting the fish between the post-juvenile stage and maturity. In unexploited stocks density dependent processes may occur at these stages. Most 'recruitment' studies actually deal with the determination of year-class strength of the fish entering the fishery at a certain year e.g. year 1. As concern rises about the sustainability of stocks, interest in biological recruitment is likely to increase. We currently have relatively little data to address biological recruitment and most of our studies will be concerned with the establishment of year-class strength. It has been frequently stated that year-class strength is determined at some point during the egg and larval stages for marine fish. Recently this view has been challenged with the assertion that processes occurring during the late larval and early juvenile stages may also be significant. However, it is not entirely clear if these later stage processes merely damp the variance in year-class strength without altering the pattern or can alter the pattern in year-class strength. By comparing estimates of abundance at different stages with resulting year-class strength one can come to some conclusions about the stages in the life history which are important in fixing year-class strength. Several studies (e.g. the FOCI study of walleye pollock) have carried out this type of analysis for a single stock. A number of studies in the literature have carried out this type of analysis for a limited number of stocks. We suggest that an analysis across a wider range of stocks would be potentially useful and therefore recommend that the Working Group initiate the collation and analysis of available data on the abundances of various early life history stages from a variety of stocks with a view to determining patterns in the stages at which year-class strength is fixed.

Ideally, the range of information collected for each stock would include estimates of egg abundance over the whole spawning time and range, estimates of early larval abundance, estimates of late larval/pelagic juvenile abundance, estimates of late juvenile/settled juvenile abundance and an estimate of abundance at year 1 for a number of years. Only a few stocks will be able to provide this level of detail but we suggest that stocks which cannot supply this idealised data set will still be useful. Table VII.1 details a range of stocks with an estimate of the level of data available within each study. The table is by no means exhaustive and other potentially interesting stocks may include Peruvian anchovy, South African sardine, Japanese stocks, and southern hemisphere stocks.

A number of analytical methods are suggested as means of exploring the data.

- I. Correlation plots -- These explore the strength of association between the life history stage and the resulting year-class strength. The strength of association can be tested statistically at a selected probability. This analysis requires a

large number of years of data to be available for each stock considered. Since there will usually not be more than 10 years available the issue of statistical power should be considered. There will likely be a high probability of generating Type II errors and thus failing to identify the earliest life history stage at which year-class strength is fixed.

II. Plots of coefficient of variance against life history stage -- These try to indicate at which stage the CV peaks. Mechanisms operating upon subsequent life history stages damp the variance but do not alter the pattern of year-class strength. This method also requires a large number of years of data.

III. Paulik diagrams -- Plot sets of graphs of adjacent life history stages with a view to identifying underlying functional forms.

IV. Many of the identified data sets consist of relatively short time series. We will need to develop methods for examining these data sets. At the individual study level trajectory analysis may be a useful tool. Meta-analysis may be useful in detecting general patterns across stocks.

Action: The table of available information needs to be completed with details of the type and level of data available for the stocks. The required format for the data needs to be agreed and the data sets compiled for analysis. A coordinator for this will need to be appointed.

Output: A paper detailing the results of the study will be produced. The results will be useful in targeting future research at those life history stages at which year-class strength is determined. Our ability to examine the links between year-class strength and biological recruitment should also be considered. This will also affect the directions of future research as stock sustainability becomes an ever more urgent concern.

3.2 Distributional Studies

Several studies are now attempting to link physical hydrographic models and distributions of ichthyoplankton to examine transport processes for fish eggs and larvae. In other studies comparisons of ichthyoplankton distribution data are made between surveys and years with the aim of examining broad geographical patterns. While hydrographic models now typically resolve on grid scales of between 0.5 to 10 km in the horizontal and 2 – 50 m in the vertical, ichthyoplankton surveys are typically conducted on much coarser grids (5 to 20 km in the horizontal and often no vertical resolution except at limited sites). The question arises as to whether the ichthyoplankton surveys can capture sufficient spatial information to allow us to detect distributional changes between surveys. The traditional approach to this type of study is to produce distributional maps of survey data and to compare them qualitatively. It is suggested that there may exist a number of spatial statistical methods which might provide more sensitive analytical tools but which are not widely used. One group of analytical tools are termed geostatistics. This class attempts to make use of autocorrelation information which exists in spatial data to improve the derived estimates. A second class of tools attempt to derive univariate indices which capture some aspects of the spatial distribution of one or multiple species (e.g. Lloyd's index of patchiness). These methods have been mainly developed in the field of plant community ecology but their suitability for use in plankton studies is currently unclear. The group concluded that there is a need to examine the robustness of plankton survey designs for the generation of distributional indices and to assess whether existing distributional data are sufficient to detect inter and intra-annual patterns.

The Working Group should invite presentations from persons with experience in the use of spatial statistics e.g. geostatistics, plant distribution analyses, etc. Actual data required would include distributional data from a series of ichthyoplankton surveys. Suitable candidate data sets might include US GLOBEC George's Bank, Southwest Nova Scotia Fisheries Ecology Program, Shelikof Strait FOCI, Norwegian spring-spawned herring and Irish Sea 1982 and 1995 ichthyoplankton surveys. In addition a simple sampling model which can generate simulated data sets from an underlying known distribution should be developed.

Two complementary approaches are suggested. First, the sampling model will be run with different levels of underlying spatial aggregation and pattern with different survey patterns commonly used e.g. regular grids of varying spacing, stratified sampling schemes etc. Spatial statistics will then be computed from the artificially generated data sets and the degrees to which they could capture aspects of the known distributions examined. This would provide an exploratory tool to allow the workshop to become familiar with the possible statistical methods and to gain some insight into their characteristics. Secondly, the real data sets could have typical sampling variability added to them, spatial statistics computed and the distribution of the statistics compared. This would essentially be a bootstrapping process.

Action: Invitation of individuals to provide presentations on spatial statistics. Compilation of suitable data sets. Production of the sampling model.

Output: A paper describing the range of spatial statistical tools available and their utility in the analysis of ichthyoplankton data. The paper should clearly describe how to apply the methods to plankton data, the characteristics of each method, its advantages and disadvantages and its application to real data sets. This might be similar to the ICES paper describing the use of geostatistics for the analysis of acoustical data.

3.3 Experimental Protocols

This section of the working group dealt specifically with aspects of experimental protocols in growth, condition, and predation studies. An extensive review of the effect various explanatory variables have on predation rates on early life stages of fish had been carried out using published results (Paradis, *et al.*, 1996). In addition a review of the level and quality of information in larval growth and condition studies from three international journals was presented. This review was restricted to laboratory and mesocosm experiments extending beyond the yolk-sac stage (excluding strictly developmental papers). Both reviews were restricted to papers published in the period 1976-1995. We distinguish between the extent of information given in a paper and the quality of underlying data presented. Both aspects have implications on the applicability of the information presented. There are different recommendations regarding possible improvements on data presentation and data quality.

Keeping in mind that the amount of available information on the early life stages varies considerably between species, the sequence of tasks (and experiments) needed to be undertaken for any given species will depend on how much information is already available. Basic tolerance experiments will have to be carried out in less studied species, whereas upper and lower lethal limits are available for a number of factors in well studied species. These studies will serve as necessary starting points for further studies.

Predation studies: Container size, duration of experiment and several other experimental protocol variables were shown to be significantly correlated with predation rates. Given the large potential impact on predation rates by these variables it is important that information regarding these variables are reported in the papers dealing with predation rates. Information of specific interest in predation studies include container volume, experimental temperature, criteria to determine the state of experimental animals, duration of experiments and criteria to determine appropriate end points. The quality (or suitability) of the prey and predators was not assessed in this review, but it is likely that some of the variability in observed predation rates are due to the condition (or state) of either predator and/or prey. In only one of the studies included in the review did the authors actually comment on the possibility of the prey being in less than optimal condition. The prey growth rate up to the point of experimentation was reported in less than 7% of the predation trials, and the age of the prey was given for less than 50% of the trials. The possibility therefore exists that a substantial proportion of the prey used in these predation trials were growing at lower rate than expected based on rearing temperature and food density. The consequences of varying prey condition in laboratory experiments is not entirely clear, but it is conceivable that it may influence the assessment of predation rates in the field when using laboratory derived relations.

Larval growth and condition studies: A lack of basic information was also apparent in larval growth and condition studies (Table VII.2). More seriously, in a large proportion of the papers the missing information was considered essential. Overall survival during the experiment and size variation information was missing in about half of the papers which makes it difficult to assess the quality of the larval groups used in these studies. Further, the presented growth relations are subject to potential bias due to possible size-selective mortality, and the calculation of approximate individual growth rates in the absence of survival data is highly uncertain. Regardless of the underlying quality of the larval material used in the study, the lack of essential information presented poses two major problems. Firstly it reduces the confidence other researchers will have in the paper and secondly it unavoidably limits the possibility of comparison with results from other papers and experiments. A preliminary list of information that should be included in different types of studies is given in Table VII.3.

Recent advances in rearing technology of marine fish larvae and growth data from various mesocosms suggest that many of the previous laboratory larval growth studies are characterised by relatively low growth rates in spite of feed being offered in excess. The quality of some of these growth studies is therefore suspect. A subjective evaluation of the quality of some of the aspects of larval data from growth and condition studies is given in Table VII.4. Measures of growth rates and condition using inappropriate rearing protocols may seriously bias the results obtained and conclusions inferred (Folkvord and Moksness, 1995). We encourage the establishment of reference maximum growth curves for species investigated, such that size-at-age and growth of larval groups fed in excess (fed controls) can be compared to expected values. An analogy to these yardstick measures is currently used to monitor human length,

weight, and condition development during first years of life (e.g. Knudtson *et al.*, 1988; Waaler 1983). The development of such relations in humans is of course much easier due to extensive empirical databases available from public health records, and due to human homeothermy. In the case of poikilothermal animals as fishes, such relations will be temperature dependent, and therefore require temperature correction. In addition, within species differences may exist between groups from different stocks or stock units.

Near maximal size-at-age and growth of fish is in this context used as a health or quality proxy of individuals used in experiments. We are well aware of possible limitations of such a measure in terms of abnormal development, malnutrition and malfunction. The observed growth rates should preferentially also be accompanied by high survival figures indicative of a healthy group. High survival rates during an experiment also has the immediate advantage that the need of documentation to infer suitable rearing conditions is necessarily reduced. Once the opposite is the case, there should be sufficient extra information on physical and environmental conditions to rule out any side effects of these conditions on survival.

Suggestions for future tasks

- compile a list of measures to be recorded/reported in experimental studies
- establish reference growth curves (yardsticks) for early life stages of important species
- write up recommended protocols for future experimental growth, condition and predation studies (e.g. What is a good growth experiment?)
- compare a 1996 "yardstick" with available literature growth data

References

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4 RECOMMENDATIONS

- 1 Recommend that work underway to establish standard operating protocols for future experimental studies of larval growth, condition and predation be completed and that the results be published for broad dissemination to the scientific community.
- 2 The next meeting of the ICES Working Group on Recruitment Processes should be held in October of 1998 in Texel, Netherlands, to include the following draft terms of reference which may be revised in 1997:
 - (a) To collate and analyse available data on the abundances of various life history stages from a variety of stocks with a view to determining patterns in the stages at which year-class strength is fixed.
 - (b) To examine the robustness of plankton survey design for the generation of distributional indices and to assess whether existing distributional data are sufficient to detect inter and intra-annual patterns.
 - (c) To review the development of reference growth curves for early life stages of important species and contrast those with existing data on the development from both wild and laboratory studies from various species (e.g. cod, herring, sole, plaice).
 - (d) To review the development of new approaches, developments, or techniques used in the study of factors and processes which influence the development and survival of fish eggs and larvae in relation to recruitment or the formation of year-class strength.

5 TIMETABLE OF THE WORKING GROUP ON RECRUITMENT PROCESSES

Monday 17-June-1996

- am Opening remarks, outline of terms of reference, group activities, acceptance of agenda, round table discussion.
- pm Presentation by Arild Folkvord (Norway) detailing his review of experimental protocols used in the study of fish eggs and larvae.

Tuesday 18-June-1996

- am Review progress in the application of size based theory to recruitment problems and in particular
- pm Presentations dealing with the role of physical processes in population dynamics.

Wednesday 19-June-1996

- am Presentation by S. Campana (Canada) detailing progress with the planning of a Workshop to further study the Relationship Between Otolith Growth and Body Growth in Fish Larvae and identify further aspects to be considered as well as review progress in the application of otolith elemental analysis to recruitment problems.
- pm Break off into small groups to summarise the discussion from each session, outline recommendations and actions required.

Thursday 20-June-1996

- am Presentation and discussion of draft report.
- pm Completion of draft report and presentations of ongoing work.

6 APPENDIX [SUMMARIES/ABSTRACTS OF PRESENTATIONS]

Irish Sea production

C.J. Fox (Ministry of Agriculture, Food, and Fisheries, Lowestoft, UK)

Distributional data for fish eggs, larvae and gadoid juveniles were presented to show that in the western Irish Sea the main gadoid spawning areas are in the shallow coastal waters. There follows a gradual move offshore with the concentration of pelagic juveniles in June/July being associated with an area of stratified water. A simple model has been constructed which simulates copepod egg production for *Acartia* and *Calanus*. Copepod egg production is driven in the model by phytoplankton availability and temperature. Phytoplankton production in turn is controlled by the availability of nitrate and light. The underlying physical model simulates patterns in stratification as three-layers on a 5 km grid. The model has been run in hindcast for 26 years using meteorological data from Dublin airport. Patterns in simulated copepod egg production suggest that the ichthyoplankton distributions observed maybe linked to changes in secondary production. There was a significant correlation between year-class strength of Irish Sea cod and simulated copepod production in the stratified region. This tentatively suggests that year-class strength for Irish Sea cod might be linked to the timing of secondary production on a local geographical scale.

Modelling the cod larvae drift in the Bornholm Basin in summer 1994.

H.-H. Hinrichsen, A. Lehmann (Institut für Meereskunde, Kiel, Germany), M. St. John (Danish Institut for Fisheries and marine Research, Charlottenlund, Denmark), and B. Brügge (Institut für Meereskunde, Kiel, Germany)

Research on the early life history stages of Baltic cod has primarily focused on the survival and distribution of the egg and larval stages. Very little knowledge exists on the ecology and distribution of larvae and juveniles > 1cm. As observed in other systems, variations in larval drift may influence transport to or retention in nursery areas potentially resulting in variations in recruitment success.

In order to investigate the drift of Baltic cod from the centre of the spawning effort in the Bornholm Basin, Baltic Sea, a three-dimensional eddy-resolving baroclinic model of the Baltic Sea coupled with hydrographic and ichthyoplankton measurements has been used to examine changes in larval distribution. Larval drift is simulated by incorporation of a passive tracer into the model representing individual cod larvae. Additionally, simulated Lagrangian drift trajectories are presented. For model purposes initial fields of temperature and salinity for the Bornholm Basin are constructed by objective analysis using hydrographic observations taken during a research cruise survey in early July 1994. Outside the Bornholm Basin horizontally uniform distributions of temperature and salinity are assumed. The baroclinic model was forced by realistic wind data taken from meteorological observations. Verification of simulations was performed by comparison with ADCP-measurements and hydrographic observations taken during a survey at the beginning of August, 1994. Most of the hydrographic features observed during the research cruise are correctly simulated, with variations attributed to the prescribed initial conditions outside the Bornholm Basin.

The goal of this modelling exercise was to predict the drift trajectories of cod larvae in the Bornholm Basin thereby aiding in the development of a sampling program for a second survey based on the predicted distribution of the larvae. The modelled results based on the coherence of the flow fields and hydrographic properties with observed features indicate that predictions of larva distributions can be made with a high degree of confidence. However, results from larval sampling during the second cruise could not entirely confirm the modelled results due to low numbers of larvae captured.

Using individual-based measures of reproductive potential to estimate the realised egg production of Northeast Arctic cod

C.T. Marshall, O.S Kjesbu, P. Solemdal, O. Ulltang (Institute of Marine Research, Bergen, Norway) & N.A. Yaragina (Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, Russia)

Interannual variation in realised egg production by Northeast Arctic cod was quantified using individual-based measures of fecundity and condition in combination with the length, maturity and sex composition of the stock obtained from annual research surveys of the Barents Sea and the spawning area off of Lofoten. Condition indices (liver condition index and length-specific weight) indicated that mature female cod were in poor condition in the late 80's and that condition subsequently improved after 1990. These temporal trends were similar to the trends observed in capelin biomass. Fecundity of pre-spawning females was measured for five years (1986-91, excluding 1990). Analysis of covariance indicated that there were significant differences among years in both the slope and intercept of the log length-log fecundity relationship and that these differences were related to interannual variation in condition. For example, the fecundity of a 50 cm cod in poor condition was less than half of the fecundity of a 50 cm cod in good condition. Fecundity differences between cod in poor and good condition decreased with increasing length. This result suggests that the reproductive potential of stocks comprised of small cod is more sensitive to interannual variation in

condition relative to stocks comprised of large cod. Data from research surveys indicated that in the years when cod were in poor condition the proportion of females was well below 50% for cod in intermediate length classes. Maturity ogives for the poor condition years were also anomalous relative to good condition years: a higher than expected proportion of female cod in intermediate length classes were classified as immature. The two results suggest that mature females in intermediate length classes may experience higher spawning mortality and/or skip spawning seasons when conditions for growth are poor. Both of these responses will affect total egg production by the stock. For the short time period available for this analysis (1988-95), estimates of total egg production by the stock were positively correlated with recruitment to age 1. These results suggest that interannual variation in reproductive potential influences the recruitment dynamics of Northeast Arctic cod. Furthermore, the lack of a relationship between spawning stock biomass and recruitment for the same time period suggests that spawning stock biomass is an insensitive measure of the reproductive potential, and hence recruitment potential, of the stock. Future work is planned which will incorporate interannual variation in egg quality to give improved estimates of the realised egg production.

Modelling of Early Life History Distributions Within the US GLOBEC Georges Bank Study

F.H. Page (St. Andrews Biological Station, New Brunswick, Canada)

The primary objective of the US GLOBEC program is to develop a spatial and temporal understanding of the underlying physical and biological processes that control the population dynamics of populations of cod, haddock, *Calanus* sp. and *Pseudocalanus* sp. on Georges Bank. The working concept with respect to the physical transport of cod and haddock early life stages is that spawning occurs over the northeast peak of Georges Bank and that the eggs and larvae are displaced toward the southeast so that by the time the pelagic juveniles are descending toward the bottom they are distributed along the southern flank of the bank and near the Great South Channel. The demersal juveniles then become distributed over the shallow, central regions of the bank. This sequential change in the distribution pattern of the pelagic stages is consistent with the rate and direction of the residual circulation. One of the challenges is to determine the relative contributions of water circulation, early life stage behaviour and mortality to the observed distributions. The Lynch et al. project¹ has been approaching this issue from the modelling point of view. It has focused on developing realistic diagnostic and prognostic circulation models, bio-physical transport and trophodynamics models and descriptions of observed distributions and behaviours of the early life stages of the cod and haddock. The team has succeeded in producing a 3-D finite element circulation model of the mean seasonal circulation that agrees well with observations. In the context of egg and larval transport the model has been used to estimate the spatial and temporal patterns in residence times of particles on Georges Bank and the displacement patterns of cod and haddock early life stages. The results indicate that eggs are released in areas having residence times of 35-40 days or greater, the observed and modelled egg and larval distributions are in qualitative agreement for the first 60-90 days and the early life stage distributions are sensitive to interannual variation in the circulation, particularly the wind driven component. The team hopes to further these efforts by improving the circulation model so events can be simulated, improving the early life stage transport and trophodynamics models so they are more realistic and use these models to help improve understanding of the processes controlling the distribution and abundance of the cod and haddock populations on Georges Bank and use this understanding to help assess the impact of physical climate change on these fish populations.

¹ Lynch, D.R., F.E. Werner, J.W. Loder, M.M. Sinclair, R.G. Lough, R.I. Perry, F.H. Page, D.A. Greenberg, P.C. Smith and W.C. Smith. US GLOBEC: Importance of Physical and Biological Processes to Population Regulation of Cod and Haddock in Georges Bank; A Model-Based Study. Proposal funded by US GLOBEC for the period July 1993- June 1996.

Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator.

A.R. Paradis (Ocean Sciences Center, Memorial University, St. John's, Newfoundland, Canada), P. Pepin (Fisheries & Oceans, St. John's, Newfoundland, Canada), & J.A. Brown (Ocean Sciences Center, Memorial University, St. John's, Newfoundland, Canada)

We investigated the potential influence of relative body size of early life stages of fishes on their vulnerability to predation by crustaceans, ctenophores, medusae and fishes, and contrasted the patterns with predictions based on different conceptual models. We found that vulnerability of ichthyoplankton to predation by ctenophores and by predatory fishes was dome-shaped. Laboratory estimates of predation rates of these two predator types were negatively influenced by volume of the container in which the experiments were conducted and by duration of that experiment. Medusae and crustaceans showed decreasing predation rates with increasing relative size of fish larvae. Laboratory estimates of predation rates of medusae were influenced by container volume, temperature and duration of the experiment while predation rates of crustaceans were influenced by container volume alone. Independent of predator type, the maximum vulnerability to predation of ichthyoplankton occurred when fish larvae are 10% the length of the predator.

Modelling Circulation on the Scotian Shelf: Assessing Predictive Skill and Hindcasting Retention Indices, 1956-1993
Keith Thompson and Jinyu Sheng (Dalhousie University, Halifax, Canada)

The first part of the presentation focused on ways of assessing the performance of shelf circulation models. We showed that statistical models can provide a useful upper bound on the performance of circulation models. The statistic we have found most useful is the variance of the model errors divided by the variance of the observations. Applying this statistic to a three-dimensional barotropic model of the Scotian Shelf we showed that the skill of the model is reasonable, particularly within about 100km of the coast and over offshore banks. We then showed how the model skill could be improved by assimilating coastal sea-levels and moored current meter data. An assimilative version of this model has recently been coupled with the Atmospheric Environment Service wind forecast model to provide 48-hour forecasts of surface circulation on the Scotian Shelf on a daily basis.

In collaboration with Dr Ken Frank of the Bedford Institute of Oceanography, we have used the numerical model to calculate retention indices for banks on the Scotian Shelf for each March-April, 1956 to 1993. The model was driven by observed wind at Sable Island and coastal sea level at Halifax. A statistical approach was used to infer flows through model open boundaries from observed coastal sea level. A diagnosed density-driven current pattern was used as the model background flow. From the predicted currents we could then calculate trajectories of near-surface particles. We found that most of the particles seeded on the Scotian Shelf are carried to the southwest by the Scotian Current. However some particles are retained over several offshore areas including the Gulley, Western Bank and Emerald Bank. We then compared year to year changes in retention with the year-class success of Scotian cod spawned in Spring on Western Bank. We found statistically significant positive correlations between our spring retention index and the catch rate of cod of length 18-23 cm collected during the regular July research vessel surveys. This supports the hypothesis that successful year-classes may be associated with reduced dispersion of larvae from their nursery on Western Bank.

Level and variability of recruitment in plaice *Pleuronectes platessa* L. in relation to latitude
Henk W van der Veer (Netherlands Institute for Sea Research, Texel, The Netherlands)

The mean recruitment level in North Atlantic flatfish species appears to be related to the size of the nursery area for the 0-group. These relationships have been found both within and between species. This finding has resulted in a 'nursery size' hypothesis. As extensive research in the nursery areas never suggested the presence of density-dependent growth or mortality processes, the key factor underlying the above relationship between level of recruitment and nursery size is thought to be the larval supply. Water exchange and hence larval supply will be directly related to the size of a nursery area. However, it is expected that this relationship varies with latitude. Since temperatures increase with decreasing latitude, the metabolic costs will increase and the scope for reproduction decrease. Thus, two relationships are expected to determine the ultimate level of recruitment. Since there is every indication that year-class strength is generated in the larval stage, larval transport is also thought to be a key factor in determining the ultimate level of between-year variability in recruitment. Beverton's 'concentration' hypothesis states that the level of variability in recruitment appears to be inversely related to the degree of concentration of juveniles in nursery areas. So far no clear mechanism has been suggested which might explain such a relationship. Based on the assumption that especially the larval phase is the critical period in the early life history of flatfish, an inverse relationship is expected between duration of the larval stage and ultimate variability in recruitment. A long larval stage might result in a greater dispersion of pelagic larvae than in the case of a shorter larval period. If true, it means that over the range of distribution of a species, the variability in recruitment will increase with increasing latitude. Water temperature decreases with increasing latitude and hence larval development will be longer and potential dispersion greater.

Size and visibility of Baltic cod eggs with reference to size-selective and stage-dependent predation mortality.
K. Wieland & F.W. Köster (Institut für Meereskunde, Kiel, Germany)

Size of Baltic cod eggs from incubation experiments and from field samples was determined by microscopic analysis. Results from plankton samples were compared with corresponding size distributions of cod eggs found in herring stomachs. The influence of fixation on size of different developmental stages was studied. Live eggs from incubation experiments were also sized separately throughout the developmental period with an optical plankton counter (OPC) based on light attenuation measurements because this was assumed to be more closely related to the visibility of the eggs for potential predations than egg diameter as obtained by microscopic analysis.

Preservation in formaldehyde solution caused a small reduction in egg diameter (2.2%) whereby no differences between the developmental stages were detected. Egg size decreased slightly during incubation (6.9%) while the OPC measurements revealed a substantial increase in light attenuation during egg development (42.2%). In the field, a

general decrease in egg size with increasing depth was observed while no change between the developmental stages was detectable. The mean size of eggs ingested by herring was slightly lower than in the water column which was most pronounced for the late stages containing a well developed embryo. The frequency of eggs in an advanced stage of development was considerably higher in the stomachs than in corresponding plankton samples. Therefore, it is suggested that the selection of further developed egg stages by predatory fish in the central Baltic Sea, i.e. herring and sprat, is due to an increase of visibility during egg development in relation to growth and pigmentation of the embryo. Thus it is likely that egg mortality due to predation is stage-dependent rather than strictly size-dependent.

Table VII.1 Summary of stocks for which stage specific information on interannual variations in cohort abundance are believed to be available. Values indicate the number of years for which it is believe data may be available. Contact names indicate the individuals which Working Group members suggested should be able to assist in guiding compilation of the information.

Stock	Eggs	Early larvae	Late larvae	Juveniles	Age 1	Biological Recruitment
Arcto Norwegian cod	3	10	15	30	Acoustic	
North Sea herring						
North Sea plaice	15	10	10	10	VPA/RV	10
North Sea sole						?
North Sea saithe						
North Sea haddock						
Celtic Sea mackerel	7					
Irish Sea cod/sole/whiting	2	2	1	1	VPA/RV	2
Blackwater estuary herring		3		8	VPA/RV	
Baltic spring herring		19		7	Acoustic 7 VPA 19	
Norwegian spring herring	25	38	15	30	Acoustic	
Baltic cod	10	10			15	
Barents Sea capelin		15		30	15	
4X cod/haddock	3	3	3	25	VPA/RV	
4 VW cod/haddock	3	3			VPA/RV	
Georges Bank cod/haddock	8	8		5	VPA/RV	
4X herring		20		20	VPA	
Gulf Maine herring						
Chesapeake anchovy	2	2	2	2	?	
mid Atlantic Bluefish		3		3		
Chesapeake striped bass						
CALCOFI	20	20	20	20	VPA	
English sole	3	3	3	3	3	
Alaskan pollock	10	10	10	10	10	?
Pacific Hake						

Table VII.2 Summary of information given in experimental larval growth and condition studies in three selected journals. The results were categorized into studies that contained information (yes) and those that did not (no). In some studies the information was partly available (part).

Journal	ICES J mar Sci			ICES mar Sci Symp			J Exp Mar Biol Ecol			Total		
	yes	part	no	yes	part	no	yes	part	no	yes	part	no
Larval background												
Species	6			20			14			40	0	0
Stock	4	1	1	10		10	1		13	15	1	24
Wild/cultivated	5		1	6	7	7	5	4	5	16	11	13
Parental size, age			6	1		19			14	1	0	39
Larval numbers												
Initial number	4		2	16		4	6	1	7	26	1	13
Mortality count			6	4		16	3	1	10	7	1	32
Final survival	3	1	2	14		6	3		11	20	1	19
Larval size measures												
SL	5		1	18		2	11		3	34	0	6
DW	3		3	11		9	6		8	20	0	20
Otolith	2		4	2		18	3		11	7	0	33
Other	2		4	5		15	4		10	11	0	29
Size variation	2	1	3	10		10	11		3	23	1	16
Setting												
Duration	6			20			14			40	0	0
Container volume	5		1	19	1		9		5	33	1	6
Container shape	4		2	12		8	3		11	19	0	21
Replicates ^a		1	5	8	2	10	3	1	10	11	4	25
Environment												
Temperature (mean)	1	4	1	10	1	9	12		2	23	5	12
Temp. variability	5		1	11		9	10		4	26	0	14
Oxygen	4		2	6		14			14	10	0	30
Salinity	3	1	2	9		11	6		8	18	1	21
Light regime	4		2	14		6	11		3	29	0	11
Algae included ^a	4		2	11		9	2		12	17	0	23
Zooplankton/food												
Density in tank	4		2	12		8	9	3	2	25	3	12
Food restriction ^a	2		4	5		15	2		12	9	0	31

^a studies where these methodologies are applied and described

Table VII.3 Suggestions for minimum information required from different types of larval experiments.

	Predation studies	Growth studies	Condition studies/ Otolith validation studies	Developmental studies	Response studies	
Larval background						
Species	X	X	X	X	X	X
Stock		X	X		X	
Wild/cultivated	X	X	X	X	X	X
Parental size, age		X	X			
Larval numbers						
Initial number	X	X	X	X	X	X
Mortality count	X	X	X	X	X	X
Final survival	X	X	X	X	X	X
Larval size measures						
SL	X	X	X	X	X	X
DW		X	X	X		
Otolith				X		
Other			X		X	
Size variation	X	X	X	X	X	X
Setting						
Duration	X	X	X	X	X	X
Container volume	X	X	X	X	X	X
Container shape	X					
Replicates	X	X	X			X
Environment						
Temperature (mean)	X	X	X	X	X	X
Temp. variability	X	X	X	X	X	X
Oxygen ^a						
Salinity ^a						
Light regime	X	X	X	X		X
Algae included ^b		X	X			
Zooplankton/food						
Density in tank ^c	X	X	X	X	X	X
Food restriction	X	X	X			

^a as long as values are within common range.

^b most studies would benefit from the use of added algae, but the marked studies should also give taxonomic information on algae used.

^c taxonomic information should also be included.

Table VII.4 Questions regarding quality of larval data used in experimental growth and condition studies, and the number of papers that had included the relevant information. Number of papers reviewed is 40 (including 12 on condition).

	Yes	Part	No
Viability			
Q1: Was viability (starvation) control included?	11	2	27
Mortality and survival			
Q2: Was mortality (survival) accounted for?	19	1	20
Q3: Was cause of mortality given?	0	7	33
Q4: Was size information on dead available (SL, DW, OTO)?	0	0	40
Growth			
Q5: Was individual growth distinguished from population growth?	1	1	38
Q6: Was growth corrected for possible size-selective mortality?	1		39
Q7: Was observed growth rate reasonable compared to maximum growth rate at respective temperature?	12	1	27
Condition (12 studies)			
Q8: Was growth performance of starved/restricted fish contrasted with fed fish?	8		4
Q9: Was survival performance of starved/restricted fish contrasted with fed fish?	5		7
Q10: Was condition (quality) of fed groups assessed by independent methods?	5		7
Q11: Was condition of fed groups compared to other groups (studies) with high survival and growth rate?	0		12
Other			
Q12: Was it likely that sampling of larvae was random and representative?	10	2	28 ^a
Q13: Were adequate samples taken to discover individual extremes (n > 30 per sampling)?	4	2	34

^a Most of the studies gave insufficient information suggesting that the sampling was random

