Oceanography Committee

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REPORT OF THE

WORKING GROUP ON RECRUITMENT PROCESSES

Bergen, Norway
8–10 March 2000

International Council for the Exploration of the Sea

Conseil International pour l'Exploration de la Mer

Palægade 2–4 DK–1261 Copenhagen K Denmark

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1 TERMS OF REFERENCE AND PARTICIPANTS

At the 1999 ICES Annual Science Conference, resolution C.Res 1999/2C03 was adopted as follows:

The Working Group on Recruitment Processes [WGRP] (Chair: Dr P. Pepin, Canada) will meet in Bergen, Norway, from 8-10 March 2000 to:

a) Review multidisciplinary projects dealing with recruitment research, with attention to providing a synthesis of the projects and highlighting unresolved issues which deserve future consideration;
b) Synthesise on-going and past studies of the patterns of growth histories and birth date distributions of surviving individuals;
c) Synthesise knowledge concerning the influence of spawning stock characteristics on viable egg production and subsequent larval survival and recruitment with the goal of dis-aggregating the effects of spawning stock on recruitment from the effects of the environment;
d) Review knowledge of size-dependent mortality, focusing on the modelling and description of patterns of mortality as well as efforts to understanding the possible causes. Efforts should address how widely current knowledge can be applied in the estimation of Spawning Stock Abundance and in the understanding of recruitment variability;
e) Assess the possible importance of multispecies interactions (e.g., competition, predation) during the larval and juvenile stages of fish;
f) Prepare a report of "reference growth curves" for a wide range of species in the ICES area;
g) Review the development of new approaches, developments, or techniques used in the study of factors and processes that influence the development and survival of fish eggs and larvae in relation to recruitment or the formation of year-class strength;
h) Consider a synthesis of the 1999 Theme Session "Cod and Haddock Recruitment Processes: Integrating Stock and Environmental Effects" to be prepared by the Session's Conveners;
i) Review progress of SGPRISM;
j) Consider, and where feasible, develop data products and summaries that can be provided on a routine basis to the ICES community via the ICES website;
k) Examine the 1999 Oceanography Committee Working Group reports and 2000 TORs to identify where inter-group input could be provided or required with the view to formulating key questions requiring inter-disciplinary dialogue during concurrent meetings of the Committee's Working Groups in 2002.

The meeting was attended by the following:

E. Bell	England & Wales	J. Beyer	Denmark
G. Bløm	Norway	C. Clemmesen	Germany
M. Dickey-Collas	Northern Ireland	A. Folkvord	Norway
A. Gundersen	Norway	M. Heath	Scotland
K. Helle	Norway	T. Marshall	Norway
R. Nash	Isle of Man	C. Needle	Scotland
R. Sætre	Norway	P. Solemdal	Norway
P. Wright	Scotland	P. Pepin	Canada (Chair)

Apologies were received from

E. Houde (USA), W. Nellen (Germany), J. Alheit (Germany), P. Munk (Denmark), M. St.John (Denmark), F. Lagardere (France), P. Pettigas (France), Sweden, Spain, C. Grimes (USA),

2 OVERVIEW

Per Solemdal who also presented apologies on behalf of Petter Fossum greeted the Working Group (WG). The WG was able to address the Terms of Reference (ToRs) with varying degree of detail and success. Initially, it was hoped that the diversity of ToRs would attract research with a wide breadth of expertise and allow good input from a variety of perspectives. In the end, this appeared to dilute the effectiveness of the WG. As a result, the WG decided to concentrate future efforts on maintaining awareness of areas of significant progress in the study of recruitment processes and subsequently work to make this knowledge applicable to stock forecasting. As a result, the current activities of the Study Group on Incorporation of Process Information into Stock-Recruitment Models (SGPRISM) are considered to be very important for future activities of the WG.

3 REPORTS OF DISCUSSION GROUPS

3.1 The influence of spawning stock characteristics on population dynamics

ToR [c]: Synthesize knowledge concerning the influence of spawning stock characteristics on viable egg production and subsequent larval survival and recruitment with the goal of dis-aggregating the effects of spawning stock on recruitment from the effects of the environment.

Three presentations were made concerning ToR [c]. The first consisted of an extensive review and detailed synthesis by M. Heath (Scotland), T. Marshall (Norway) and P. Wright (Scotland) (see Appendix 1). The second focussed on results of a laboratory experiment aimed at the effects of exposure to alkyl phenols on some aspects of reproduction in cod conducted by A. Folkvord (Norway) (see Appendix 2). The third reported on a long term study of the changes in Spawning Stock Biomass (SSB) and April 24, 2000Annual Egg Production (AEP) of Irish Sea cod by M. Dickey-Collas (Northern Ireland) (Appendix 3).

There is no doubt that the area represents one of major concern in understanding the dynamics of marine fish populations. The key concern in all instances is the potential for changes in Egg Production that are not a reflection of the SSB measure that is currently used as a primary index of the reproductive potential of stocks under the ICES jurisdiction. Current activities associated with a number of major research projects (see Section 3.3) focuses on the implications of various aspects of stock characteristics on the dynamics of marine populations. Through discussion, the WG considered that given the progress that will be complete from research projects and the activities of the SGPRISM by the time of the next meeting, one of the key activities of the WG should be to consider how such information can be effectively used in developing projections of stock dynamics.

The STEREO project is investigating the extent to which variations in dispersal and the spatial configuration of spawning affect the proportion of the total carrying capacity that can be occupied at different levels of stock abundance, and these results will be reported at the next meeting of the RPWG. However it was also felt that the type of information considered in that project should be provided to the SGPRISM as an example case study which should be used to develop approaches for incorporation of process studies into stock-recruitment projections and advice.

Recommendations:

- M. Heath (Scotland), G. Martinsdottir (Iceland), B. MacKenzie (Denmark), T. Marshall (Norway) should present an analysis of simulations exploring the effects of stock structural factors on the parameters of stock-recruitment relationships to the next RPWG. They should also prepare a case for a Study Group (SGPRISM) on evaluating the impact of these factors on stock projections.

Justification: The current SGPRISM has been tasked with investigation how environmental effects on recruitment can be incorporated into the fisheries advice system, but one of the conclusions is that this may not necessarily reduce the uncertainty in forecasts because we are unable to forecast the environment with any precision. However, stock structural factors also affect recruitment dynamics, and these may be readily incorporated into stock projections.

3.2 Review of the synthesis of the 1999 Theme Session "Cod and haddock recruitment processes: integrating stock and environmental effects"

ToR [h]: Consider a synthesis of the 1999 Theme Session "Cod and Haddock Recruitment Processes: Integrating Stock and Environmental Effects" to be prepared by the Session's Conveners.

A synthesis of the Theme Session is included in Appendix 4. The Session attracted 32 papers, mainly from 3 projects – the STEREO project on cod and haddock recruitment (Appendix 5), the CORE/STORE projects in the Baltic (Appendix 6), and Norwegian studies on Northeast Arctic cod. The key points to emerge from the Session were:

- The distributions of phenotypic characteristics in survivors (spatial origin, temporal origin, maternal origin, RNA/DNA, growth performance) become progressively skewed relative to initial distributions due to selection.

Models are beginning to incorporate these features and generate detailed simulations of the structure of recruitment processes in realistic hydrodynamic settings. Practical methods for verifying these results in the field include birthdate distributions from otolith microstructure, and spatial origins from otolith microchemistry, but in general, the modelling capabilities are advancing ahead of our ability to resolve features in the field.

- Compensatory processes (density dependence) clearly dominate the recruitment dynamics of many stocks - but we still know very little about them - where they act, when they act, or spatial and temporal patterns. Indications from sequential surveys of abundance are that in haddock the main compensation acts at the transition from the pelagic to demersal phase. The situation is less clear for cod, but studies of diet and ingestion in the early larval phase do not any significant scope for competition for food. There is a clear need for more investigation of processes acting at settlement and the factors that determine the carrying capacity of the environment for early demersal stages.
- There is clear evidence for extensive mixing of offspring from different stocks/populations at the juvenile stage. However, we still do not know whether the extent of natal fidelity of fish migrating away from nursery areas to recruit to the adult populations. These factors affect our perception of the spatial scales appropriate for stock-recruitment relationships.
- There are STILL embarrassingly few data on mortality sources, the ontogeny of mortality rates, or spatial and temporal patterns in mortality of early life stages. This aspect is holding up the implementation of recruitment models.
- Regardless of maternal effects on egg and larval viability, spawning biomass is a very poor index of total egg production. Age, size and physiological structure of the spawning stock have a large effect on Total Egg Production (TEP).
- Egg condition varies with a range of maternal factors - impacts on early life stage survival are being modelled and studied in the laboratory. The lessons of aquaculture technology bear examination with respect to evaluating the role of these factors in the population dynamics of wild stocks.
- The use of TEP instead of Spawning Stock Biomass (SSB) as a measure of reproductive output in yield per recruit and stock-recruitment analyses could result in very different conclusions regarding the risk of collapse in some stocks. Yield per recruit decreases faster with fishing mortality when expressed in terms of TEP as opposed to SSB.

The Session generated vigorous discussion, and was a valuable opportunity to review the state-of-the-art in research on gadoid recruitment processes. Theme Sessions such as this could be a more effective means of reviewing and synthesising scientific progress than presentations during WG meetings, since they attract a wider range of active scientists and are fully documented by accompanying manuscripts.

Recommendation:

- P. Pepin (Canada) and R. Nash (Isle of Man) be charged with providing a synthesis of recruitment issues presented at the SAP (Stock Assessment and Prediction) symposium to the next WGRP meeting.
- E. Houde (USA), P. Pepin (Canada), P. Munk (Denmark) and D. Schnack (Germany) are charged with presenting a synthesis of Theme Session N ("Spatial and temporal patterns in recruitment processes") from the 2000 ASC to the next WGRP meeting.

Justification: Progress and awareness of key issues by the WG requires commitment to providing input from key areas of active research. The SAP symposium deals with integrating knowledge into stock assessment and predictions, which the WG identified as one of the key areas where it can make contributions to ICES. Similarly, Theme Session N deals with issues that are key elements previously discussed by the WGRP.

3.3 Review of Multidisciplinary Research Projects

ToR [a]: Review multidisciplinary projects dealing with recruitment research, with attention to providing a synthesis of the projects and highlighting unresolved issues which deserve future consideration.

The WG was presented with the summary of five large multidisciplinary research programs currently underway or planned within the ICES region of interest. In addition to providing a basis for information about new initiatives relating to the study of recruitment processes, these information sessions provide the WG with key areas of interest that should serve as the basis for advice to ICES. Discussion surrounding each of the summary presentations was lively and most members expressed a desire to be kept abreast of developments within each project. Furthermore, discussion surrounding the progress and activities of the STEREO project (section 3.3.2 and Appendix 5) concluded that this represents one of the key areas in the study of recruitment processes that should serve as a basis for activity at the next WG meeting.

3.3.1 Precision and Accuracy of tools in Recruitment Studies (PARS). (FAIR- CT96-1371)

A. Folkvord (Norway) provided an update on the progress in the PARS project. An outline of the project was given in connection with the report from the previous Working Group Meeting (CM 1999/C:2). The project ended January 2000, and a final report will be completed within April 2000. One of the key outcomes of this project is the production of a practical manual that includes summary of results and recommended laboratory and field procedures in connection with otolith microstructure analysis, RNA: DNA analysis, and otolith microchemistry analysis. Some of the topics that will be dealt with in the larval condition section of the manual include: sampling of fish larvae; sizing, drying and weighing; extraction of nucleic acids; laboratory protocols for fluorometric determination of nucleic acid; protocols for determination of RNA and DNA; and precision of the methods. Similar topics are being developed for the analysis otolith microstructure.

3.3.2 An operational model of the effects of stock structure and spatio-temporal factors on recruitment (STEREO) (FAIR CT98-4122)

M. Heath and P. Wright (Scotland) presented results from the STEREO project (Appendix 5). The overall objective of the project is to improve the methodology for determining limit reference points for the biomass of exploited fish stocks. This project will produce an operational scheme for refining stock-recruitment data by incorporating biological, spatial and temporal information on the stock structure, with the aim of reducing the uncertainty associated with the derived limits. The methodolgy will be developed for cod and haddock stocks around Iceland, Norway and in the North Sea as case studies

The specific objective is to build a modelling system that will predict the probability of contributions by different spatial, temporal and parental components of the spawning stock of a species to the juvenile pre-recruit population some months after spawning.

The approach will be to develop a series of interconnected models mapping the development of individual fish from the point of spawning, through the egg and larval phase, to settlement out of the pelagic phase. Variability between individuals is especially high during the early life stages and capturing this feature is the key to successful modelling.

A preliminary version of the entire model system, including spatially and temporally resolved population egg production, egg and larval dispersal, growth and survival, and settlement of juveniles to the seabed at the end of the pelagic phase, has been achieved for North Sea haddock. The inclusion of density dependent survival is a significant step forward.

For cod, a detailed model of the temporal pattern of egg production by an age structured spawning stock has been developed, utilising the available biological knowledge from the laboratory and field studies.

A new development in hydrodynamic modelling has been achieved with the design of a statistical model to summarise results from a 3-dimensional baroclinic General Circulation Model of the northeast Atlantic in terms of a matrix of atmospheric pressure gradients. Since these atmospheric data are available in near real-time, this opens up the possibility of high speed, operational use of the STEREO model, driven by realistic, time-specific hydrodynamic data.

In year 2 of the project, the component parts of the STEREO model will be assembled for Icelandic waters and the North Sea and simulations of the cod and haddock recruitment process tested against observations from the field.

It was stressed that the fish that survive are from a non-random subset of the initial population of characteristics. A brief discussion on the growth model being temperature driven took place. Wright showed evidence for differential survival throughout the season and between years for haddock larvae in the North Sea. In two years, out of three, the distribution of the hatch dates did not correspond with the distribution of egg production.

3.3.3 Environmental and fisheries influences on fish stock recruitment in the Baltic Sea (STORE) (FAIR 98-3959)

C. Clamminess (Germany) gave an overview of the progress in this EC funded project (Appendix 6). The objectives of the research project are to:

1) Determine stock-recruitment relationships for Baltic cod and sprat in relation to key environmental factors influencing the production of viable spawn and the survival of early life history stages.

2) Improve short-term predictions of stock development by integrating recruitment estimates based on the present status of the stock and its biotic and abiotic environment.

3) Develop predictive recruitment models for medium- to long-term forecasts of stock development under different environmental and fishery scenarios.

4) Estimate biological management reference points, critical stock limits and target spawning stock sizes based on stock-recruitment relationships and stock development simulation models, and considering the precautionary approach for fisheries management.

Clemmesen commented that less appeared to be known about the biology and reproductive strategies of sprat. This project uses a multispecies and trophodynamic approach to fish recruitment in the Baltic.

3.3.4 Demonstration of maternal effects of Atlantic cod: combining the use of unique mesocosm and novel molecular techniques (DNA microsatellites markers) (MACOM)

P. Solemdal (Norway) and C. Clemmesen (Germany) presented a new EU-funded project. The project will investigate the viability of offspring from first-time spawning and repeat spawning cod. The parentage of the mesocosm-reared offspring will be known through the use of DNA microsatellite markers. Twenty to thirty spawning pairs will be used and the offspring will be reared to sexual maturation (at 2 years old). They intend to analyse over 4,000 genetic samples a year. It is hoped that the investigation will improve understanding of the relative importance of individual genetic variation compared to maternal effects on the growth and survival of cod in the wild and aquaculture.

3.3.5 "Linking hydrographic frontal activity and ecosystem dynamics in the North Sea & Skagerrak: Impact on fish stock recruitment" (LIFECO)

J. Beyer (Denmark) presented a proposed EU-project (Appendix 7). The objective of the project is to investigate the scale of processes around frontal features that influence recruitment success in the North Sea. The state of funding is still unknown.

In addition to the presentation about the LIFECO project, P. Munk (Denmark) provided written summaries for two research projects underway at the Danish Institute for Fisheries Research (Appendices 7 & 8).

The group welcomed all the projects presented. Many of the proposed projects and the results of the completed projects have implications with regard to fish stock assessments and stock recruitment relationships. The group stressed that relevant work should be available in a useable format to facilitate and improve stock assessments.

3.3.6 Shelf edge advection mortality and recruitment (SEAMAR)

The WG also received an e-mail submission from the Chair of the WG on Zooplankton Ecology (L. Valdes (Spain)) concerning an EU funded project dealing with recruitment dynamics of Atlantic Mackerel.

SEAMAR is a multi-disciplinary study to develop a Bio-Physical Transport Model for the prediction of year-to-year survival during the early life-history stages of the NorthEast Atlantic mackerel (*Scomber scombrus*) and hence ultimate recruitment strength. The study will be based on an existing transport model developed as part of the SEFOS programme, which included a simulation of the physical environment but did not take account of biological interactions. Growth and mortality rates in response to environmental conditions such as food availability and temperature will be incorporated in the model as functions of the biological and physical environment. This will take predictive modelling of pre-recruit survival beyond the current state of the art and will give a fundamentally more realistic simulation of the fate of the eggs, larvae and post-larvae of mackerel in their drift from the spawning grounds to the nursery areas and an improved ability to predict recruitment. The modelled drift and survival (recruitment) of the post-larvae will be related to the observed distribution and abundance from lagrangian studies, recruit surveys and to recruitment indices from VPA stock assessment models, as validation of the model. This understanding, combined with known changes in spawning behaviour (timing, location and pattern), will allow the prediction of scenarios for successful mackerel recruitment and the establishment of operational models for stock management as proposed by IWC & ICES.

The main requirements to achieve the stated objectives of the SEAMAR programme are:

- Development of individual-based growth and mortality modules for incorporation into the transport model.

- Sampling to give the detailed geographical distribution of the planktonic stages of mackerel in relation to mesoscale hydrographic and biological features.
- Measurements of growth and mortality of the planktonic stages of mackerel as a function of the physical and biological environments.
- Incorporation of the locomotory behaviour of the larvae and post-larvae in modifying their vertical distribution and horizontal dispersion.
- Collection of recruit distribution and abundance data for model validation.

Recommendations:

- The WG recommended a continued review of multidisciplinary project dealing with recruitment research, with attention to providing a synthesis of the projects and highlighting unresolved issues which deserves future consideration.

3.4 Examine 1999 Oceanography Working Group Reports

ToR [k]: Examine the 1999 Oceanography Committee Working Group reports and 2000 TORs to identify where inter-group input could be provided or required with the view to formulating key questions requiring inter-disciplinary dialogue during concurrent meetings of the Committee's Working Groups in 2002.

Two issues needed to be addressed under this ToR. First, all WGs within the Oceanography Committee were asked to consider the possibility of joint activities with other WGs. The Chair therefore provided a summary of the Terms of Reference gathered from the 1999 WG reports to highlight the possibility for joint activity. Second, the WG was asked to consider a draft letter from the Chair of the Oceanography Committee to ascertain the potential similarity in the activities of the WG with others within the Committee.

The Cod and Climate Change Working Group (WGCCC) is very focused and has a more restricted scope than the WGRP. Although there are references to recruitment and growth within the WGCCC ToRs, more effort is directed towards climate effects and forecasting of environment. Both the WGRP and the WGCCC are addressing issues of how knowledge from research projects can be incorporated into stock assessment and projections (SGPRISM for the WGRP, the workshop on cod growth in WGCCC). There is potential for interaction at a later time but it was felt that these differing initiatives should be allowed to develop before the two WGs consider a joint meeting on this subject. There was some discussion that the SGPRISM would likely be interested in the activities of the WGCCC concerning variations in growth of cod but the WG also considered that the workload and activities of SGPRISM were sufficient at this time, particularly since the next meeting of the SG is intended to be its last. Those activities should be made part of the WG ToRs in the future. This should provide an opportunity for discussion with the WGCCC concerning possible collaborations on workshops of joint meetings.

A review of the ToRs of the Working Group on Shelf Seas Oceanography (WGSSO) revealed that two were considered particularly relevant for the WGRP. The first one deals with assessing the relevance and effectiveness of monitoring programmes. Issues concerning statistical accuracy of monitoring programs have been considered critically important to the nature of recruitment research but repeated calls by the WG for Study Groups or in the development of ToRs for WG on Methods have yielded no significant progress. The discussions resulting from the WGSSO will be beneficial to discussions of the WGRP. However it was felt that at this time, this was insufficient to warrant a joint meeting since this would be greatly dependent on the progress made by the WGSSO on this topic. The second ToR of the WGSSO important to the WGRP deals with development, use and validation of numerical models. There is an increasing use of numerical circulation models in research dealing with recruitment processes and their validity and accuracy is likely to be critical in interpreting the results of any research program. Although it was acknowledge that most research projects which make use of such tools are generally multidisciplinary ones which involve physical oceanographers capable to providing a critical assessment of the validity of any model, a clear set of recommendations or guidelines could serve as a starting point for further developments as well as recognition of potential limitations and advantages of different model types. Despite the importance of the issue of numerical model accuracy, the WG considered that without a specific project requiring assessment, there was little benefit in planning joint activities at this time.

Terms of Reference from both the Working Group on Phytoplankton Ecology (WGPE) and the Working Group on Zooplankton Ecology (WGSE) are of interest to the WGRP with respect to the production of suitable prey for larval and juvenile fish. However, very few of the issues considered by either of those WGs focus on abundance or production of organisms that are of a size which makes them suitable prey for larval fish. This is probably a result of the dominant monitoring activities reviewed by the WGs, which focus primarily on phytoplankton or the abundance of adult stages of most zooplankton. Although the latter may be suitable prey for juvenile and adult fishes, their importance to larval stages is more limited. Given that the WAG has not dedicated a great deal of effort at looking into the feeding dynamics of early life stages, it was felt that at this time there was relatively little opportunity or need to pursue joint meetings with either the WIPE or the WAGS.

At this point, the WARP was joined by the Chair of the Oceanography Committee (OC) (H. Loeng, Norway) for the discussion of the overlap in activities among WGs. As our guest, he stressed the importance of the relevance of the WGs to ICES. He also indicated that the need to address the ToR was essential to improving ICES, and an integration of efforts from different WGs would be useful.

Both P. Pepin (Canada) and M. Heath (UK) raised concerns about the ICES strategy with respect to the WGs and felt that initiatives and prioritised tasks provided directly from ICES itself would promote more focussed efforts of the activities of the WGs. However, the Chair of the WGRP commented on the suggestion of merging WG groups coming from ICES and expressed some concerns about the consequences for the WGRP. It is clear from discussions within the WG that our activities represent a distinct and general set of priorities that do not appear directly under the mandate of other WGs. Although there are some similar interests to the WGCCC, members of the WG indicated that the breadth of interest of the two WGs was significantly different and that ICES would loose by merging the activities of the two groups.

The Chair of the WGRP also commented on the slow response in updating the member lists of the WG. Although there have been repeated requests by the Chair at the Annual Science Conference meetings of the OC to review membership from the various nations as well as the willingness of individuals to be working members of the WG, participation and input remains limited largely because of over-commitment on the part of individuals listed as members of the WG.

With respect to joint activities with other Groups, the Chair expressed a certain amount of concern because a number of recommendations from the WGRP to other WGs had never been acted upon. Although it is clear that joint activities would be beneficial, there are many circumstances when the members of the WGRP do not have the expertise necessary to address the questions we have asked other WGs to address through recommendations. Even when we proposed the development of a Study Group (SGPRISM), approval came so late that the SG could not achieve all its objectives within a single meeting because participation was uncertain. This not only limited the issues that could be addressed by the SG but also forced a request for a second meeting. The WGRP views this second meeting of the SGPRISM as critical for completion of the tasks were set before it.

Recommendations:

The chair of the WGRP should continue to investigate the possibility of overlapping meetings (Copenhagen 2002) with some of the other WGs in the Oceanography Committee.

3.5 Review of SGPRISM

Review progress of the Study Group on the Incorporation of Process Information into Stock-Recruitment Models (SGPRISM) (*ToR [i]*)

One of the recommendations of the 1998 WG meeting (ICES, 1999) was that a Study Group should be instigated to examine the use and incorporation of process models and environmental information in aspects of the assessment and projection process, concentrating on implications for stock-recruit relationships. The present WG meeting reviewed the SGPRISM report (ICES, 2000) and the terms of reference for the planned second SGPRISM meeting, and discussed how these might be modified or extended in light of the deliberations of the WG.

It was concluded that the SG made good progress despite late notification and restricted attendance from both stock assessment scientists and biological process modellers. The SG discussed a subset of the possible methods by which environmental information could be incorporated, specifically a) the use of environmental indices to tune sequential population analyses, and b) the incorporation of an environmental variable as a covariate in the stock-recruitment models used in medium-term projections. Analyses concentrated on the second of these. Steps were taken towards the modification and extension of the stock projection software currently used in ICES assessment working groups. There were two main aspects to this: incorporating environmental signals (represented by temperature), and making use of any time-series autocorrelation structure in the residuals to a stock-recruitment curve fitted to VPA-derived estimates of SSB and recruitment. Work has subsequently been propagated in this area by SG participants, with the intention of wide dissemination. The WG considers this to be a useful, pragmatic and indeed essential first stage in the development of methodology for using the results of more complete process models in the assessment and projection processes.

The SG also considered the *utility* of incorporation of environmental information and concluded that, for such an exercise to be worthwhile, there must be clear causal mechanistic linkages between a readily-predictable environmental signal and recruitment: without this requisite, projections may become more uncertain or even seriously misleading. On the other hand, "what-if" environmental scenario modelling may be appropriate in situations where environmental regime shifts are prevalent: the WG discussed the example of the Baltic Sea in this context, where wind-driven shifts in salinity levels are common. In these cases projections can be based on families of regime-specific stock-recruitment models. It is clear that the basing of advice on correlational studies, without an understanding of underlying mechanisms, would be extremely dangerous and is to be avoided.

Principally as a result of the interests of those attending, the SG concentrated on issues related to environmental models and data to the exclusion of more biological process considerations, such as age or spatial structure in the stock. There were clearly items and issues that the SG could not deal with because of the lateness of the approval for the meeting. The WG proposes that the next meeting of the SG should devote considerable effort to formulation of potential methodologies by which such process models could be incorporated into fishery assessments and projections, in such a way as to be appropriate for the currently institutionalised management structure. As a result, the WG determined that the SG should meet once more to consider the following tasks:

1) Investigate and evaluate medium-term projection methodology for use in fishery assessment, taking into account of characterisations (in space/time) of historical patterns in recruitment and the environment for specific case studies;
2) Incorporate realistic variability in the parameters of management simulation models and evaluate more fully the potential of environmental studies to impact management procedures;
3) To investigate the variability and predictability of environmental conditions known or supposed to affect the dynamics of fish populations.

A suitable case study for this approach would be the STEREO project, which implements age, size and spatial structure in circulation-driven simulation models of cod and haddock populations in the North Sea and the West of Scotland. In order to be successful in this, the composition of the SG should be expanded to included STEREO participants. It is further proposed that the next meeting of the WG should review and expand on the findings of this SG examination.

It is clear that the findings of the SG and the subsequent recommendations of this WG must be disseminated widely to formal ICES assessment meetings, and that current assessment practice must evolve to take account of the wealth of process information now available. What is not so clear is the changes in assessment methodology that must be implemented in order for this to be achieved. As first steps in this direction, WG members involved in assessments have undertaken to discuss these issues with assessment colleagues and investigate the possibility of running alternative assessments based of age-structure-driven measures of total viable egg production rather than SSB. The WG proposes the following as ways in which assessment recruitment models might be improved in the longer term, although it is recognised that rapid change is hardly facilitated by the large investment in infrastructure driving the current practices:

- The spatio-temporal structure of spawning needs to be considered in parallel with total egg production, in which case assessment stock units (as opposed to management units) which split biological populations (for example, West of Scotland and North Sea haddock) may have to be merged.
- Lipid energy has been proposed as an alternative to SSB for NE Arctic cod, as it integrates age and maternal condition effects on reproductive output.
- If alternate measures of reproductive potential are to be used, appropriate biological reference points will have to be developed and accepted by the management structure.
- Assessment WGs are to be encouraged to consider how structural factors distinct from environment, such as age, size, spatial and temporal population structure, might affect perceptions of stock-recruitment relationships (although it is recognised that the environment may mask the influence of structural factors). Structural considerations will be dependent on availability of biological data, and may not be cost-effective if environment is the dominant driver.

References

ICES (1999) Report of the Working Group on Recruitment Processes. *ICES CM 1999/C:2*.

ICES (2000) Report of the Study Group on Incorporation of Process Information into Stock-Recruitment Models. *ICES CM 2000/C:01*.

Recommendations

- The Study Group on Incorporation of Process Information into Stock Recruitment Models (SGPRISM) should meet for 4 days in late January of 2001, in Lowestoft, UK (Chair: C. M. O'Brien, UK) to
  1) SGPRISM should consider the research activities of the STEREO project and investigate how the resultant information on the age, size and spatial structure of the North Sea/West of Scotland cod and haddock stocks should be incorporated into the extant methodology of stock assessment and projections.
  2) Investigate and evaluate medium-term projection methodology for use in fishery assessment, taking into account of characterisations (in space/time) of historical patterns in recruitment and the environment for specific case studies;
  3) Incorporate realistic variability in the parameters of management simulation models and evaluate more fully the potential of environmental studies to impact management procedures;
  4) To investigate the variability and predictability of environmental conditions known or supposed to affect the dynamics of fish populations.

- The next meeting of the WGRP should consider the results of the SGPRISM's examination of the STEREO project, along with concurrent and subsequent investigations, in order to refine the present approach to incorporating stock structure and environmental information into assessment and projection procedures.

3.6 Review progress in the development of reference growth curves.

ToR [f]: Prepare a report of "reference growth curves" for a wide range of species in the ICES area.

The interpretation of variations in patterns of growth requires that an underlying perspective of growth potential be established. There must be development of an understanding of the fundamental processes that govern growth dynamics in larval and early juvenile fish.

A working paper was presented (Appendix 10) which updated the results presented on the last working group meeting in Texel 1998 (ICES CM 1999/C:2). The focus was on describing maximum potential growth curves for cod (Norwegian coastal cod and Northeast Arctic cod) and Norwegian spring spawning herring under optimum laboratory conditions with respect to temperature. For the specific growth rate with age, a dome-shaped relationship was observed for both stocks of cod, whereas herring revealed a linear specific growth pattern. Further studies on metabolic activities are planned to investigate why these differences occur. The temperature optimum for cod, from field observations, was defined as 7°C (Campana and Hurley, 1989) as opposed to 16°C in the presented study. The difference is probably due to the excess of food in the laboratory (present) study.

For both cod stocks there were differences in the specific growth rates of larvae and juveniles. Larval specific growth rate ranged from 5 to 25%. There was a clear temperature signal indicating higher specific growth rates at higher temperatures. Juvenile specific growth rate was always below 5%, and no significant temperature effect was observed. Such food concentrations and temperature regimes are rarely seen in the field. In recent years advances in aquaculture techniques have resulted in laboratory studies producing very high growth and survival rates.

The ensuing discussion covered many points of which the following need to be addressed, considered or will be assumed:

Should the growth curves be based on individual values or on the mean individual growth of individuals? A possible way to resolve this would be to use median growth of the fastest growing group at any given temperature, but the use of any given percentile (e.g. the 90^{th} percentile) could be used instead of the mean or median.

Should we use average values instead of interpretations of patterns related to the scatter of percentiles (e.g. non-parametric approach)? There was no resolution of this problem and it should be considered before any of the data/ideas are implemented.

The differences observed between larval herring and cod indicate that there might be different responses to temperature and food regimes. The species specific responses must be taken into account when interpreting traditional growth curves (size at age). The discussions highlight that further research is needed in this field.

Maximum potential growth curves as described in the presented papers could serve as reference points and provide yardsticks for field observations.

There are a variety of factors affecting the mean growth response in fish (temperature, food availability, light conditions, etc). Studies on maternal effects including offspring size, growth, and viability is now part of an EU-project (MACOM). Preliminary results from this project will be available as an important contribution to the next working group. This piece of research has the potential to provide the basis for meeting the objective of *understanding of the fundamental processes that govern growth dynamics in larval and early juvenile fish*.

3.7 Synthesize on-going and past studies of the patterns of growth histories

ToR [b]: Synthesize on-going and past studies of the patterns of growth histories and birth date distributions of surviving individuals.

This term of reference was addressed through presentations by M. Dickey-Collas (Northern Ireland) (Appendix 11), and P. Pepin (Canada) (Appendix 12) which covered growth rates of juvenile whiting, and measurement error in otolith increment analyses.

The otolith increment number to age relationship for Irish Sea whiting appears to be reasonable. Therefore, increment number can be used to estimate age in this species. Using data from 1997 and 1998 the summer MIK (Methot Isaacs Kidd) sampling in the western Irish Sea gave the growth rates of Irish Sea whiting larvae as 0.69-0.70 mm d^{-1}. These values are consistent with the length-based estimates from serial sampling in the area. The back-calculated birth-date data indicate a difference in distribution between the two years, which is not unexpected. However at least 50% of the otoliths were not used because the increment pattern was erratic or deemed to be suspect (when compared with other species). The major question revolved around a high variability in growth rates/birth dates in some of the older fish. Is this real or an artifact of sampling, the technique or some unknown point/factor?

The discussion focussed on a number of points and questions: It appears that whiting do have a reputation for having very difficult to read otoliths (as adults) so the 50% rejection rate is not unexpected. However, there could be problems due to juveniles being sampled both pre and post-demersal phase. This could be explained as, the survey design is sampling only at night, therefore all juveniles are sampled in the pelagic realm. The juveniles could be a mix of pre-demersal and demersal juveniles; this species has a nocturnal vertical migration. This could be a problem since each individual may experience a different thermal regime (surface versus bottom temperatures) and thus a variable temperature mediated growth rate. The variable thermal regime would, presumably, result in variation in growth rates.

A number of other points were raised, namely: DARD (Northern Ireland) scientists are still not sure of the exact origin of juvenile whiting in the Irish Sea (do some come from adjacent areas e.g. Celtic Sea, VIaN etc). If juveniles are from areas outside the Irish Sea then this could explain some of the variability seen in the growth trajectories noted in the otolith data. It should also be pointed out that this is a relatively small data set. The data set will be expanded over the years, however, in these initial stages maybe some non-parametric statistical tests should be applied to examine the scatter in the data and explore the value of this new data set.

This is a new study on an abundant species. The study so far has highlighted the problem associated with settlement/temperature/environment and growth rate. The study also raises the spectre of individuals in a population, which may have originated from another management unit. This is a major question, which must be addressed for the identification of appropriate stock population dynamics theory, stock assessment and stock management (as currently applied on an area based management strategy).

The interpretation of otolith increment width was examined in a small study using larvae of the radiated shanny (*Ulvaria subbifurcata*). The methodology consisted of repeated readings, by one reader, of number of rings and increment widths. For the purposes of presentation and analyses all data were standardised and autocorrelation functions calculated. A number of important points were highlighted in this study:

1) At young ages (small increment widths) at least 50% of the variance in increment widths can be accounted for by measurement error (reader error). Part of the problem was that the increment widths were so small that they were close to the maximum resolution of light microscopy. However, the age estimates were consistent.
2) Any environmental signal in increment widths can not be detected for approximately three to five days post-hatch.
3) Beyond age 20 days, measurement error still accounts for a significant portion of the variance in increment widths (30-35%) but there is substantial autocorrelation within individual fish, suggesting that much of the pattern in increment widths of older larvae reflects their history rather than the environment in which they are found.
4) The implications are that one can examine short-term dynamics in young larvae and this is more difficult in older larvae. However, size selective mortality can be studied in these older larvae.

The impression is that there are very few publications available on the importance of measurement error on the interpretation of growth patterns in otolith increment widths. This will probably be addressed in the final report of the PARS project. The potential importance o measurement error on the interpretation of otolith increment patterns should be re-examined once the report from PARS becomes available to the broader scientific community.

3.8 Multispecies interactions during the larval and juvenile stages of fish

ToR [e]: Assess the possible importance of multispecies interactions (e.g., competition, predation) during the larval and juvenile stages of fish.

The topic was addressed through a presentation on ‘feeding by a larval fish community – Impact on zooplankton’ by P. Pepin (Canada) (Appendix 13). The presentation covered a study in Conception Bay, Canada using Bongo net samples over diel periods. A total of 11 fish species were studied and gut fullness indices (GFI) calculated for each species. The objective was to examine consumption rates over diel periods with the intention of examining whether fish larvae can have an impact on the abundance of their zooplankton prey and whether there is scope for intra- and/or interspecific competition for resource.

The study showed that there was diel periodicity in the ingestion rate with less food in larval fish guts during day than night and elevated ingestion rates at dusk. The highest consumption rates occurred in winter flounder, however, this may be due to measurement error. The lowest consumption rates occurred in the two species with straight guts (herring and capelin), possibly due to egestion at capture. There was very little seasonality in the densities of zooplankton available for the larvae, generally at approximately 10,000 individuals m^{-3}. The principal prey was copepod nauplii. The consumption was less than 1% of the standing stock leading to the general conclusion that multi-species larval feeding, in this area, had little impact on the density of zooplankton. In this case there is no evidence that there is density dependence operating at this stage.

In discussion the question of prey quality was raised. In this study, prey quality was not considered. However, the WG felt that, for example, essential fatty acids should be considered in larval fish predator/prey studies. The WG also considered whether standing stocks or production should be used in these studies. There was no firm conclusion on this matter. Large-scale variability in prey densities and naupliar production was noted in the bay, however, this could not be taken in to account in this study.

The WG was supposed to examine the potential for competitive or predator-prey interactions among larval and juvenile stages of marine fish in a diversity of environments. However, only one environment was available at this meeting. An examination of diverse environments needs to be conducted at some later date. Further studies are needed to confirm the conclusion that density-dependent effects in larvae, in relation to feeding, are insignificant and generally do not need to be included in simulation modelling.

3.9 Review of development of new approaches

ToR [g] Review the development of new approaches, developments, or techniques used in the study of factors and processes that influence the development and survival of fish eggs and larvae in relation to recruitment or the formation of year-class strength.

There was a presentation by K. Helle on an evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua*) using regression techniques. Abundance indices were analysed to determine which index provided the earliest reliable prediction of year class strength. The analyses imply that there is considerable inter-annual variation in mortality prior to the early juvenile stage. Based on the analyses a cohorts’ relative abundance as early juveniles is the best early indication of its abundance as to 2- and 3- year-olds. A full description of the methods and analyses are given in Helle *et al.* (2000).

This presentation generated a wide range of discussions what factors determine year class strength and when it is laid down. The data clearly showed that in some years abundance changed very rapidly between years suggesting variable mortality rates within a cohort. There was speculative discussion to the causes of year classes dominating or disappearing to intra and interspecific interactions. This was visualised by the relationship between changes in abundance over time ((stage specific), density dependence and the carrying capacity. Between year variations can be partially explained by variations in abundance of younger age stages, variation in density dependent processes and the carrying capacity.

There is a potential problem with indices based on pelagic juveniles where the surveys are close to settlement period. In these surveys variations in index may be caused by variation in year class strength or the timing of the survey relative to the ontogeny of the juveniles.

3.10 Dependent processes

ToR [d]: Review knowledge of size-dependent mortality, focusing on the modelling and description of patterns of mortality as well as efforts to understanding the possible causes. Efforts should address how widely current knowledge can be applied in the estimation of Spawning Stock Abundance and in the understanding of recruitment variability.

There were no submissions specifically concerned with size-dependent processes during the course of the WG meeting. However, the WG considered that the subject was of sufficient importance that the major points from Houde's (1997) analysis should be re-emphasised to the general ICES community. The following summarises the conclusions put forth in that study.

In a comparison of five species, Houde (1997) identified major patterns and trends in both mortality (*M*) and growth (*G*). The instantaneous morality rate in marine fishes declines rather predictably with increases in size and age of fish during early life, nit the rates are highly variable between species, cohorts, and year classes. Levels of *M*, rates of decline in it, and its overall variability are higher and more variable than weight-specific growth rates (*G*). It is probable that *M* is a more important cause of variability in recruitments than is *G*, because it is more variable and because of its initial, relatively high level, compared to *G*. The consequence of high *M/G* for cohorts of marine fish during the larval stage is an initial, and sometimes dramatic, loss of biomass. The trend is usually reversed later in the larval stage, but only after most of the cohort's original biomass has been lost.

Houde (1997) found that while the pattern in *M* was predictable, that of *G* was not. Declines in *M* were faster than predicted by simple size-spectrum theory (-0.32 to -0.62 (Houde 1997) vs -0.25 predicted by Peterson and Wroblewski (1984)). While most taxa experience a decline in *G* throughout the larval stage, there were many exceptions. Variability in stage-specific mortality derives from changes in either *M* or *G*, or in both. Unless both *M* and *G* are estimated, little can be learned about the patterns or causes in stage specific mortality.

At the outset of his study, Houde (1997) hypothesised that the body size at which the ratio of weight specific mortality-to-growth rates (*M/G*) shifts from > 1 to < 1 was a transition size and might be a predictor of cohort (i.e. year class) success. Results of the analyses have lent support to this idea in the cases of American shad, walleye pollock and striped bass, where recruitment indices are related to trends in growth, stage specific mortality, and biomass proliferation. However, there are contradictions and inconsistencies in each of the cases indicating, not surprisingly, that larval stage dynamics do not account folly for year-class success or failure. Houde (1997) concludes that the wide variation in stage specific mortality among species and years suggests that individual life histories and adaptive strategies are important in determining the influence of environmental variability on early life dynamics.

The work of Houde and a number of other researchers have shown the potential significance and usefulness of size-based theory and observations in the study of population dynamics. A number of issues remain to be studied in greater detail. The comparative approach (among species or year classes) has proven successful in making progress in this area of marine science. However, greater benefit to understanding changes in population dynamics may be gained by extending the size-dependent observations and theory to stages beyond the early life history as well as by obtaining data from a greater number of species.

References

Houde, E. D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. J. Fish Biol. 51 (Suppl. A) 52-83.

Peterson, I., and Wroblewski, J. S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries Aquatic Science, 41: 1117-1120.

Recommendations:

The WG proposes to organise a Theme Session for the ASC in 2002 focussed on “Size-dependency in population processes of marine and freshwater organisms” to be co-convened by E. Houde (USA) and P. Pepin (Canada).

Justification: Research has shown the potential significance and usefulness of size-based theory and observations in the study of population dynamics. The objective of the Theme Session is to provide a basis for extending the observations and theory beyond the early life stages of fish by including presentations that deal with organisms from the entire food web.

4 RECOMMENDATIONS

A synthesis of the 2000 Theme Session “Spatial and temporal patterns in recruitment processes” should be prepared by E. Houde (USA), P. Pepin (Canada), P. Munk (Denmark) and D. Schnack (Germany) for presentation at the next meeting of the WG.

During 2001 the chair of the WGRP should investigate the possibility of overlapping meetings (Copenhagen 2002) with some of the other WGs in the Oceanography Committee.

The Study Group on Incorporation of Process Information into Stock Recruitment Models (SGPRISM) should meet for 4 days in late January of 2001, in Lowestoft, UK (Chair: C. M. O’Brien, UK) to:

1) SGPRISM should consider the research activities of the STEREO project and investigate how the resultant information on the age, size and spatial structure of the North Sea/West of Scotland cod and haddock stocks should be incorporated into the extant methodology of stock assessment and projections (based on a presentation by M. Heath (Scotland), G. Martinsdottir (Iceland), B. MacKenzie (Denmark), T. Marshall (Norway)).
2) Investigate and evaluate medium-term projection methodology for use in fishery assessment, taking into account of characterisations (in space/time) of historical patterns in recruitment and the environment for specific case studies;
3) Incorporate realistic variability in the parameters of management simulation models and evaluate more fully the potential of environmental studies to impact management procedures;
4) To investigate the variability and predictability of environmental conditions known or supposed to affect the dynamics of fish populations.

The next meeting of the Working Group on Recruitment Processes (Co-chairs: P. Pepin (Canada) and R. Nash (Isle of Man)) will work by correspondence in 2001 to prepare for a meeting in 2002

1) Review multidisciplinary projects dealing with recruitment research, with attention to providing a synthesis of the projects and highlight unresolved issues which deserve further consideration;

   Justification: There currently exists a large number of on-going and planned multidisciplinary and multinational studies which are investigating some of the fundamental processes which influence recruitment patterns and stock dynamics. Since many are not supported through ICES, it is essential that the WG keep abreast of developments, results and conclusions of such projects in order to inform ICES of the applicability and utility of these findings and identify potential avenues of research which should be pursued.)
2) WGRP should consider the results of the SGPRISM's examination of the STEREO project, along with concurrent and subsequent investigations, in order to refine the present approach to incorporating stock structure and environmental information into assessment and projection procedures.
3) Review the development of new approaches or techniques used in the study of factors and processes that influence the development and survival of fish eggs and larvae in relation to recruitment or the formation of year-class strength;

   Justification: The dynamic nature of research on recruitment processes requires that ICES be kept informed of new developments in approaches used in to study of various elements affecting recruitment processes.)
4) P. Pepin (Canada) and R. Nash (Isle of Man) are charged with providing a synthesis of recruitment issues presented at the SAP symposium to the next WGRP meeting.
5) M. Heath (Scotland), G. Martinsdottir (Iceland), B. MacKenzie (Denmark), T. Marshall (Norway) should present an analysis of simulations exploring the effects of stock structural factors on the parameters of stock-recruitment relationships to the next RPWG.

Justification: The current SGPRISM has been tasked with investigation how environmental effects on recruitment can be incorporated into the fisheries advice system, but one of the conclusions is that this may not necessarily reduce the uncertainty in forecasts because we are unable to forecast the environment with any precision. However, stock structural factors also affect recruitment dynamics.

6) Consider a synthesis of the Theme Session "Spatial and temporal patterns in recruitment processes" from the 2000 ASC to be prepared by E. Houde (USA), P. Pepin (Canada), P. Munk (Denmark) and D. Schnack (Germany).

The WGRP will report to the Oceanography and Living Resources Committees at the 90th Statutory meeting.

5 TIMETABLE OF WORKING GROUP ON RECRUITMENT PROCESSES

Wednesday 8 March, 2000

9:15-10:40 General Introduction and Outline of Objectives (Pepin)

ToR [c] – "The influence of spawning stock characteristics on population dynamics"

"Results from a generation experiment in cod (effects of pollutants to parent fish on the survival and viability of offspring)" (Folkvord)
"Transport from the North Sea of larvae and juvenile fish into coastal and northern Norwegian waters" (Sætre)

10:40-11:00 Break

11:00-11:30 ToR [c] – Continued

"Retention areas and their importance for spawning and recruitment of the Norwegian spring spawning herring" (Sætre)
"Relationship between spawning stock biomass and reproductive potential in Irish Sea cod" (Dickey-Collas)

11:30-12:30 Lunch

12:30-14:30 ToR [h] – Review a synthesis of 1999 Theme Session "Cod and Haddock Recruitment Processes: Integrating Stock and Environmental Effects" (Heath)

General discussion
Issues to be addressed:
Are there general conclusions to draw or is it too early?
How should the findings from such studies affect activities of ICES Assessment WGs?
Are there issues that can be pursued as part of activities of WGRP (workshop, recommendation to SGPRISM) in reference to ToR [c]?

14:30-15:00 Break

15:00-17:00 ToR [a] – Review multidisciplinary projects

Summary of PARS project report (Folkvord)
Summary of STEREO project activities (Heath)
Summary of STORE project activities (Clemmesen)
Summary of MACOM project objectives (Solemdal, Clemmesen)

ToR [k] – "Examine the 1999 Oceanography Committee Working Group reports and 2000 TORs to identify where inter-group input could be provided or required with the view to formulating key questions requiring inter-disciplinary dialogue during concurrent meetings of the Committee's Working Groups in 2002." (Pepin)

General Discussion ToR [a] and [k] concerning the use of input from multidisciplinary projects and WG activities/requirements: How should WG provide input to ICES for use of findings from such projects? Can we identify major gaps that can be addressed by this or other WGs?

Thursday 9 March, 2000

09:00-10:40 ToR [i] – "Review progress of SGPRISM"

Summary of SG activities and recommendations (Pepin)

ToR [j] – Consider, and where feasible, develop data products and summaries that can be provided on a routine basis to the ICES community via the ICES website.

General Discussion:
Issues: Scope of work to be done to meet SG recommendations.
Participation by WG members in SGPRISM.
Commitment to reporting on either of three ToRs for next SG meeting.
Importance of SG work to assessment WGs.
Linking process studies with incorporation into stock assessment/projection, are there aspects that were missed by the SG?
Where should the WGRP direct its efforts as a result of progress from SGPRISM?

10:40-11:00 Break

11:00-11:30 General Discussion Continued-

11:30-12:30 ToR [f] – "Review the progress in the development of reference growth curves"

"Summary of work/progress to date (cod and herring)" (Folkvord)
ToR [b] – Synthesize on-going and past studies of the patterns of growth histories:
"Preliminary investigations into the growth rates of 3 month old whiting in the Irish Sea in 1997 and 1998" (Dickey-Collas)

12:30-13:30 Lunch

13:30-15:00 "Analysis of the effect of measurement error of otolith increment width in the study of growth" (Pepin)

ToR [e] – "Assess the possible importance of multispecies interactions"
"Feeding by a larval fish community – Impact on zooplankton" (Pepin)
General Discussion of ToR [f], [b] and [e]

15:00-15:20 Break

15:20-17:00 Break off into small groups to summarise discussion, draft report.
Outline recommendations.

17:00-17:30 Business Session: Election of new Chair

Friday 10 March, 2000

09:00-12:00 Presentation and discussion of draft report.

APPENDIX 1 TERM OF REFERENCE C

***Term of reference c*:** Synthesise knowledge concerning the influence of spawning stock characteristics on viable egg production and subsequent larval survival and recruitment with the goal of dis-aggregating the effects of spawning stock on recruitment from the effects of environment.

M Heath[1], T Marshall[2] and P Wright[1]

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For any given level of spawning biomass of a fish stock there has usually been a wide variation in historical rates of recruitment. Often, this variation is attributed to the effects of environment on survival, but there is increasing evidence that the age, size and spatial structure of the adult spawning stock, and the physiological condition of spawners, can also influence the number of surviving recruits independent of environmental variations. Such 'structural' effects on recruitment have high potential for incorporation into medium term forecast analyses since they reflect aspects of the internal dynamics of stock-recruitment and as such are not dependent upon external predictors of the environment.

The task of dis-aggregating the effects of environment and stock structure on recruitment may be more complicated that has been recognised in most analyses to date. A clear consequence of the role of compensatory processes in stock-recruitment dynamics, must be that (i) different aspects of stock structure will be important over different intervals of spawning stock size, and (ii) environmental factors should not necessarily be expected to act continuously over the range of stock sizes. In other words, quite different aspects of the environment and stock structural factors are probably affecting the maximum reproductive rate (slope at the origin of the stock-recruitment relationship), and the carrying capacity of the ecosystem (saturated level of recruitment). The consequence of this is that attempts at identifying continuous correlative relationships between environmental variables or stock structure indices, and residuals from stock-recruitment relationships fitted to historical data may be, at best, misleading, and at worst, flawed.

There are some possible solutions to the above problem. With respect to statistical analysis of historical stock and recruitment data, the possibility of incorporating discontinuities into statistical relationships between residuals and environmental or structural indices could be considered. Another possibility may be to use process based modelling approaches such as STEREO to simulate the dependence of maximum reproductive rate and carrying capacity on stock structural aspects under defined climatic scenarios. In what follows, we consider the aspects of population biology which need to be taken into account in a simulation based approach to determining the role of stock structure on recruitment. The discussion is divided into three parts: a) maternal effects on population egg production and viability of eggs and larvae, b) effects of demographic structure on the timing of spawning, and c) variability in the spatial structure of spawning and possible effects on recruitment.

a) Maternal effects on population egg production and viability of eggs and larvae

Several correlative studies have suggested that structural characteristics of the stock (e.g., age diversity, condition, spawning experience) can affect recruitment. For example, there is a higher probability of above average recruitment when age diversity is high for Norwegian spring-spawning herring (Lambert, 1987; 1990) and Icelandic cod (Marteinsdottir and Thorarinssin, 1998). Recruitment in Scotian Shelf haddock was positively correlated with mean size and condition of spawners (Marshall and Frank 1999a). For Georges Bank haddock the fit of the stock/recruit relationship was improved if estimates of spawning stock biomass excluded the first-time spawners (Wigley 1999). These findings have stimulated interest in re-evaluating the stock/recruit relationship using more precise estimates of reproductive potential (Solemdal 1997; Murawski *et al.* 1999).

Total egg production by a stock can vary due to changes in reproductive parameters such as age or size at maturity (Stearns and Crandall, 1984; Jørgensen, 1990) and age- or size-specific fecundity (Hodder, 1965; Hislop, 1988; Kjesbu, *et al.*, 1991). Such changes may be density-mediated (Ware 1980; Marshall and Frank 1999b) or related to density-independent factors affecting growth. Interannual variation in condition of spawners affects age or size-specific fecundity for many fish species (Hislop *et al.* 1978; DeMartini 1991; Koslow *et al.* 1995; Ma *et al.* 1998; Kjesbu *et al.* 1998). Poor condition can also result in delayed maturation (Lehmann *et al.* 1991) and in skipped spawning seasons (Burton *et al.* 1997).

In addition to their effects on maturation and fecundity, there is growing evidence that maternal size and condition influences offspring viability (Chambers 1997; Trippel *et al.* 1997; Trippel 1998; Marteinsdottir and Steinarsson, 1998). In Atlantic cod the size, age and condition of females affects the size of eggs and larvae (Kjesbu, 1989; Chambers and Waiwood 1996; Marteinsdottir and Steinarsson, 1998). Larvae from large eggs have been shown to start feeding earlier, exhibit greater feeding success, have a greater likelihood to develop functional swimbladders and exhibit higher rates of swimming activity and growth (Knutsen and Tilseth, 1985; Solemdal *et al.* 1992; Marteinsdottir and Steinarsson, 1998). Positive correlations have also been detected between female condition and larval feeding success and larval specific growth rates (Marteinsdottir and Steinarsson, 1998). Furthermore, eggs from first-time spawners have a lower hatching success compared to second or third time spawners (Solemdal, *et al.*, 1995).

These results have important implications for quantifying reproductive potential of a stock. High fishing mortality reduces the number of old/large spawners (Trippel *et al.* 1997 and references therein). These age/size classes may contribute disproportionately to the number of successful recruits (Scott *et al.* 1999) such that the reproductive potential of heavily exploited stocks may have undergone decreases that are disproportionately large relative to the decrease in spawner biomass. Many stocks exhibit a larger degree of interannual variation in condition. Positive associations between condition and recruitment for stocks which show no relationship between spawner biomass and recruitment (Marshall and Frank 1999a; Marshall *et al.* 1999) suggest that spawner biomass does not accurately represent the effect variation in condition has on reproductive and recruitment potential. Interactions between different aspects of stock structure (e.g., size and condition) affect the magnitude of variation in reproductive potential of the stock. For example, the effect of condition on the reproductive potential of the stock is greater when stocks are dominated by smaller spawners (Kvalsund and Marshall, in prep.). Consequently, high age diversity may buffer the effects of variation in food resources and condition on stock reproductive potential.

Quantifying total viable egg production requires comprehensive databases describing stock composition (age or size, sex, maturity, spawning experience), fecundity, atresia, maturation, offspring viabilities, and/or possibly environmental factors. Replacing the spawner biomass term with estimates of total viable egg production can lead to an improved stock/recruit relationship (Jarre-Teichmann in press) which may permit the development of biological reference points that are more effective in conserving the reproductive potential of stocks. For many stocks the databases required to estimate total viable egg production are unavailable. In some cases, it may be possible to develop proxies for total viable egg production using existing databases (Boyd *et al.* 1998; Marshall *et al.* 1999). It may also be possible to design biological reference points based on these proxy variables (Painting *et al.* 1998).

Methods for quantifying the reproductive potential of individuals and stocks are currently being reviewed and summarized by the NAFO Working Group on Reproductive Potential (Chair: E.A. Trippel). The terms of reference for this group are to: (1) explore and review availability of information and existing data on reproductive potential by area and species; (2) explore possibilities to develop standard internationally co-ordinated research protocols to estimate egg and larval production; (3) explore and evaluate alternative methods to estimate reproductive potential as part of routine in monitoring and sampling schemes; and (4) review possibilities to develop methods and applications to estimate stock reproductive potential for assessment and management. The final report of the working group will benefit researchers seeking to re-evaluating the stock/recruit relationship by incorporating information on stock structure.

b) Effects of demographic structure on the timing of spawning

Variation in the timing of spawning is potentially an important source of variability in recruitment since it affects the initial synchrony between offspring production and favourable environmental conditions. For example, there are a variety of hypotheses on recruitment processes in fish in which the underlying mechanism relates spawning times to plankton production cycles (e.g. critical period; Hjort, 1914; match-mismatch; Cushing, 1975;1990) or optimal windows of environmental conditions (Sinclair and Tremblay, 1984; Cury & Roy, 1989). Spawning times together with maternal influences on larval size and growth are also relevant to the bigger-is-better hypothesis and the size-spectra hypothesis (Leggett and DeBlois, 1994; Pope *et al.*, 1994). Whilst many of these hypotheses consider spawning as a relatively discrete event the spawning season of many temperate fish species extends over several weeks to months and can show considerable inter-annual variation. Evidence from otolith birthdate analysis indicates that cohorts spawned very closely together can experience widely differing mortalities. Consequently, there can be considerable selective advantages to spreading reproduction over time to ensure that not all offspring experience sub-optimal conditions for growth and survival (Gillespie 1977; Mertz and Myers, 1994).

Protracted spawning within a fish stock may be achieved by individuals spawning repeatedly. In addition to this trait individuals may begin spawning at different times of year and spawn for longer, as they get older and/or larger (DeMartini and Fountain 1981; Parrish *et al.*, 1986; Hutchings and Myers, 1993; **see also report on theme session Y ASC Apppendix 4** An example of this age related spawning trait in North Sea haddock is given in Figure 1.1. Single spawning species may also extend their spawning period through age related differences in the timing of spawning (Lambert, 1990). In most of the species studied it is the older and larger females that begin spawning earlier in the season and continue for longer than younger and smaller females. For all species that exhibit an age or size related spawning trait the removal of older members of a stock will shorten the population spawning season and change the peak time of egg production.

Changes in the timing and duration of spawning induced by a truncation of age and size composition of spawning fish could have consequences for the match of larvae with conditions for survival. Further, a reduction in the population spawning period has implications to the effect of short-term mortality episodes on year class strength (Mertz and Myers, 1994) and the growing season available to larvae. Whilst it is difficult to directly quantify this attribute in the estimation of a stock's reproductive potential, the STEREO project is using simulation modelling to assess the relative contribution of variability in spawning times to year class variability (**Annex X**). Empirical studies using birthdate analysis of survivors may also give some indication of the relative contribution of the early spawning older females to a year class **(see report on theme session Y ASC; Appendix 4**). Further, the use of hatch check diameter as an indicator of egg size together with information on birthdate may provide a tool for investigating parental size and age contribution to survivors (e.g. Meekan and Fortier, 1996).

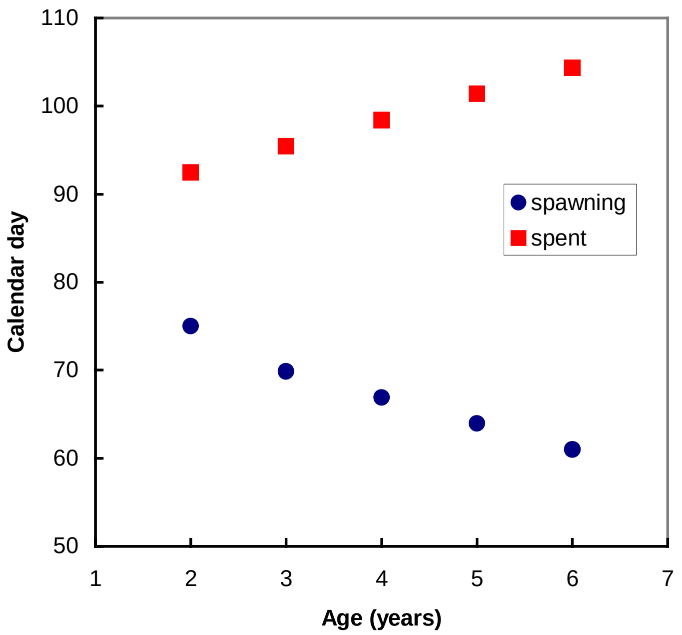

Figure 1.1 Age comparison of the calendar date at which 50% of female haddock were either spawning or spent during the 1996 spawning season based on probit regression. P. Wright unpublished data

c) Variability in the spatial structure of spawning and possible effects on recruitment

Variability in the geographic extent and location of spawning has been observed in many fish stocks, including those of cod (MacCall, 1990; Hutchings, 1996). Changes in spawning location may have a profound effect on the early survivorship of progeny due to its effect on the conditions which larvae experience at hatching (Sinclair, 1988; deYoung and Rose, 1993; Watanabe *et al.*, 1996). Egg surveys conducted by Saville (1959) and Heath *et al.* (1994) provide indirect evidence for changes in the extent of spawning in cod and in the location of spawning haddock in the North Sea. Heath *et al.* (1994) found that most haddock eggs were concentrated in relatively warm Atlantic water along the continental shelf, which may have reflected a preference for specific environmental conditions or regional variability in egg production at the time of the egg survey. In Iceland, the spatial dynamics of spawning areas appear complicated by the unequal distribution of age and size classes on the main spawning grounds. Investigations since 1994 have indicated that larger and older cod tend to spawn close to the coast releasing eggs into the westward flowing coastal current, formed by the discharge of large rivers on the South coast (Marteinsdottir and Petursdottir, 1985). Smaller and younger cod spawn in deeper water out on the Bank and the youngest individuals are found along the continental edge. Additional spawning does also occur at numerous other locations along the West, North and East coast. However, the sizes of these spawning units are only a fraction compared to the size of the main spawning aggregation off the Southwest coast. Changes in spatial distribution and abundance of spawning cod are therefore expected to be influenced both not only by the population size but also by the size/age composition of the spawning stock at each time.

Changes in fish distribution have been explained in terms of a reduction in 'population richness' (Sinclair, 1988), density-dependent habitat selection theory (MacCall, 1990; Swain & Wade, 1992), responses to physical changes, or some combination of these factors. In populations comprising several co-existing sub-populations or races (e.g. Northern anchovy, *Engraulis mordax* Vrooman *et al.*, 1981; Atlantic herring, *Clupea harengus*, Sinclair, 1988) stock contractions have often been associated with an unequal reduction in the size of sub-stocks (MacCall, 1990). In cases where density has been implicated in altering the extent of a population's distribution, expansions and contractions in range have tended to occur around an area or areas of high 'suitability' (MacCall, 1990). Habitat suitability may be related to factors influencing fitness, such as preferred physical characteristics. As such, large-scale changes in sea circulation may affect the location of spawning through changes in actual 'suitability' of reproductive habitat (Bakun, 1993). Failure to recognise the importance of density related changes in distribution has been implicated in several stock collapses where fishery yields were believed to be sustainable (Murphy, 1977; MacCall, 1990).

Optimum patterns of stock and recruitment for a particular stock must be an evolutionary adaptation to growth and mortality conditions in a given ecosystem. It is clear that this evolutionarily adapted state has been significantly altered in some stocks by the intensive exploitation of the late 20th century, such that the current spatial configuration of reproduction may be far from optimal. The genetic basis for sub-regional spatial structuring of fish stocks is not well understood, and we currently have no estimates of whether stock collapses through over-exploitation have resulted in gene flow events equivalent to those which must have occurred through natural events in the geological past. However, understanding of such processes is an important component of any assessment of the likely time scales for restoration of over-exploited stocks.

The key questions regarding relationships between stock-recruitment dynamics and the spatial structure of spawning are:

- ***What effect have observed variations in the spatial configuration of spawning had on maximum rates of recruitment?***
- ***What factors affect the recruit carrying capacity of the ecosystem – and what effects do the different spatial configurations of spawning have on the fraction of the total carrying capacity that can be occupied?***
- ***Is there a systematic relationship between age and spatial distribution of spawners, and/or between stock abundance and the spatial distribution of age classes?***

If maximum recruitment rates (the slope at the origin of the stock-recruitment curve), carrying capacity, or the ability to occupy the carrying capacity are altered by the changing spatial structure of the stock, then stock-recruitment relationships cannot be regarded as stationary, even under constant environmental conditions.

One of the objectives of the STEREO project is to simulate exactly these relationships. Initial results for haddock in the North Sea and west of Scotland indicate clear spatial and temporal structuring of survival rates from spawning to. For example, in a simulation based on climatological hydrodynamic and temperature conditions, spawning stock age and spatial configuration based on the late 1980's, and not including any maternal effects on egg and larval mortality rates (Heath and Gallego, 1998), the west of Scotland sub-region produced 14% of the annual egg whilst 24% of the survivors to the end of the pelagic phase originated from this area (Figure 1.2). The haddock spawning stock to the west of Scotland is dominated by 3 year and older repeat spawners. 2-year old recruit spawners are mainly found in the North Sea (Figure 1.3). Hence, a conclusion of these results would be that progressive loss of older age classes from the population should reduce the maximum recruitment rate purely due to spatial factors, and in addition to any maternal effects of recruit spawners on egg and larval survival rates. The STEREO model also includes an explicit representation of density dependent processes acting at the transition from the pelagic to demersal phase in haddock, and of the spatial structure of the carrying capacity of the ecosystem. The project is investigating the extent to which variations in dispersal and the spatial configuration of spawning affect the proportion of the total carrying capacity that can be occupied at different levels of stock abundance, and these results will be reported at the next meeting of the RPWG.

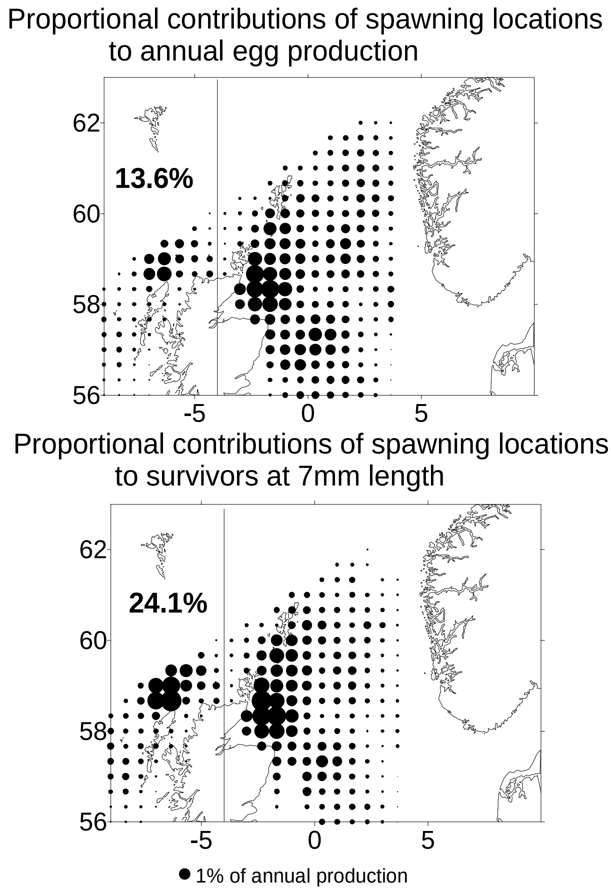

Figure 1.2. Results from a simulation of the spatial structure of pelagic phase survival of North Sea haddock eggs and larvae using the STEREO bio-physical model.

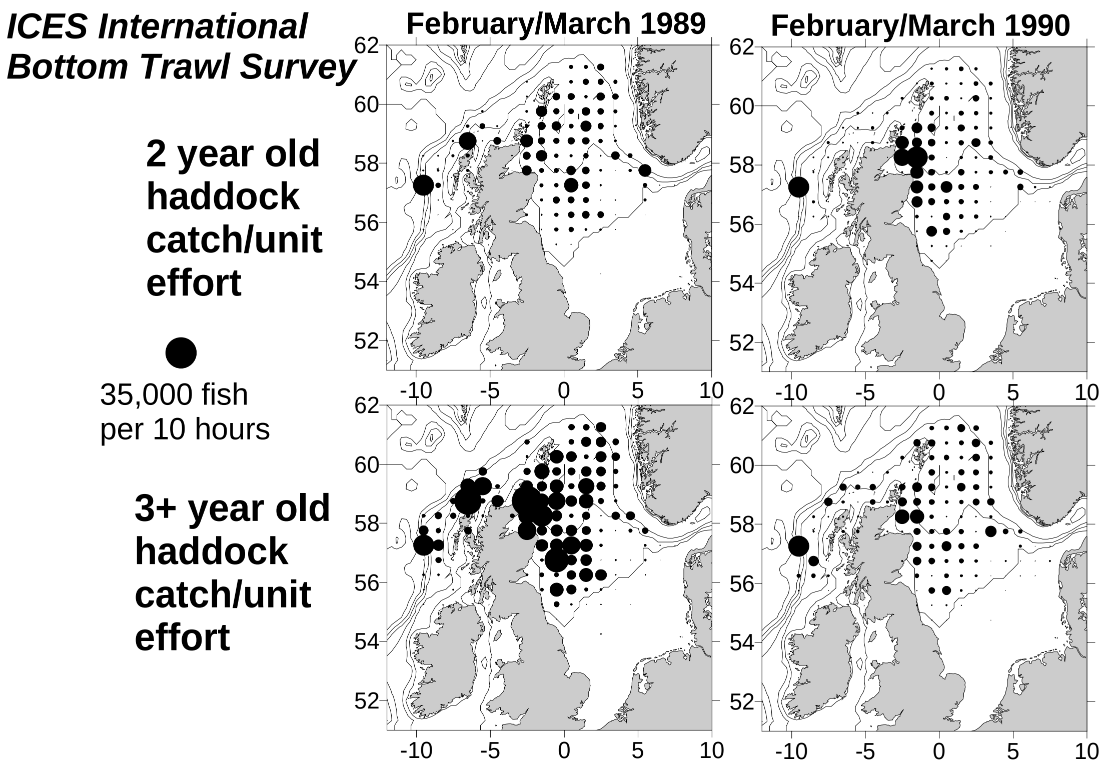

Figure 1.3. Spatial distribution of recruit-spawner (age 2) (upper panels), and repeat-spawner (age 3+) (lower panels) haddock in two years of bottom trawl surveys in the North Sea and west of Scotland region.

References

Bakun, A 1993. The California Current, Buenguela Current, and Southwestern Atlantic Shelf Ecosystems: A Comparative Approach to Identifying Factors Regulating Biomass Yields. In: Large Marine Ecosystems, Stress, Mitigation and Sustainability. 1st ed. (Eds: Sherman, K; Alexander, L M., Gold, B. D.) AAAS Press, Washington DC, 199–224.

Boyd, A. J., Shannon, L. J., Schülein, F. H., and Taunton-Clark, J. 1998. Food, transport and anchovy recruitment in the southern Benguela upwelling system of South Africa. In Global versus local changes in upwelling systems. Editted by M.-H. Durand, P. Cury, R. Mendelssohn, C. Roy, A. Bakun, and D. Pauly. Pp.195–209. Éditions de l'Orstom, Paris.

Burton, M. P. M., Penney, R. M., and Biddiscombe, S. 1997. Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 122–131

Chambers, R. C. 1997. Environmental influences on egg and propagule sizes in marine fishes. In Early Life History and Recruitment in Fish Populations (Edited by R. C. Chambers & Trippel, E. A.), pp. 63–102. Chapman & Hall, Fish and Fisheries Series 21. London, UK.

Chambers, R. C. and Waiwood, K. G. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Si. 53, 1986–2003.

Cury P. and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Science 46: 670–680.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge and New York.

Cushing, D. H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26: 249–293.

DeMartini, E. E. and R. K. Fountain. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

DeMartini, E. E. 1991Annual variations in fecundity, egg size, and the gonadal and somatic conditions of Queenfish *Seriphus politus* (Sciaenidae). Fish. Bull. 89: 9–18.

deYoung, B. and Rose, G. A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Canadian Journal of Fisheries and Aquatic Science 50, 2729–2741.

Gillespie, J. H. 1977 Natural selection for variances in offspring numbers: a new evolutionary principle. American Naturalist 111: 1010–1014.

Heath, M. R., Rankine, P. and Cargill, L. (1994). Distribution of cod and haddock eggs in the North Sea in 1992 in relation to oceanographic features and compared to distributions in 1952–1957. ICES mar.Sci.Symp. 198, 438–439.

Heath, M. R. and Gallego, A. (1998). Biophysical modelling of the early life stages of haddock in the North Sea. Fish.Oceanogr. 7, 110–125.

Hislop, J. R. G. (1988). The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of haddock, *Melanogrammus aeglefinus,* in British waters. Journal of Fish Biology 32, 923–930.

Hislop, J. R. G., Robb, A. P., and Gauld, J. A. 1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish. Biol.13: 85–98.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapp. P. -v. Reun. Cons. int. Explor. Mer 20:1–228.

Hodder, V. M. 1965: The possible effects of temperature on the fecundity of Grand Bank haddock. International Commisssion on Northwest Atlantic Fisheries, Special Publication 6, 515–522.

Hunter, J. R., N. C. H. Loand R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. In. R. Lasker (ed), An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*. NOAA Technical Report NMFS 36. U.S. Dept. Commerce

Hunter, J. R and Macewicz, B. J. 1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fisheries Bulletin, US 21, 139–149.

Hutchings, J. A. (1996). Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. 53, 943–962.

Hutchings, J. A. and R. A. Myers. 1993. Effect of age on the seasonality of maturation and spawning of

Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 50:2468–2474.

Jarre-Teichmann, A. in press. Stock-recruitment relationships for cod (*Gadus morhua calleria*s L.) in the central Baltic Sea incorporating environmental variability. ICES J. Mar. Sci.

Jonsson, E. 1982. A survey of spawning and reproduction of the Icelandic cod. Rit Fiskideildar VI (2): 1–45.9

Jorgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). J. Cons. int. Explor. Mer. 46:235–248.

Kjesbu, O. S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biology 34, 195–206.

Kjesbu, O. S., J. Klungsyr, H. Kryvi, P. R. Witthames and M. Greer Walker. 1991. Fecundity, atresia, and egg size of captive Atlanttic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48, 2333–2343.

Kjesbu, O. S., P. R. Witthames, P. Solemdal and M. Greer Walker. 1990. Ovulatory rhythm and a methoid to determine the stage of spawning in Atlantic cod (*Gadus morhua* L.), Can. J. Fish. Aquat. Sci. 47, 1185–1193.

Kjesbu, O. S., J. Klungsyr, H. Kryvi, P. R. Witthames and M. Greer Walker. 1991. Fecundity, atresia, and egg size of captive Atlanttic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48, 2333–2343.

Kjesbu, O. S., Witthames, P. R., Solemdal, P., and Greer Walker, M. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. J. Sea Research 40: 303–321.

Knutsen, G. M. And Tilseth, S. (1985). Growth, development, and feeding success of Atlantic cod larvae *Gadus morhua* related to egg size. Transactions of the American Fisheries Society 114, 507–511.

Koslow, J. A., Bell, J., Virtue, P., and Smith, D. C. 1995. Fecundity and its variability in orange roughy: effects of population density, condition, egg size, and senescence. J. Fish Biol. 47: 1063–1080.

Lambert, T. C. 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. Mar. Ecol. Prog. Ser. 39: 209-220.

Lambert, T. C. 1990. The effect of population structure on recruitment in herring. J. Cons. int. Explor. Mer 47: 249–255.

Leggett, W. C. and Deblois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32 (2): 119–134.

Lehmann, G. B., Karlsen, Ø., and Holm, J.C. 1991. The impact of feeding on growth and sexual maturation in cod. Final project report to BP Nutrition ARC.

Ma, Y., Kjesbu, O. S., and Jørgensen, T. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). Can. F. Fish. Aquat. Sci.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program, Seattle.

Mackenzie, B., J. Tomkiewicz and F. Köster and A. Nissling. 1998. Quantifying and Disaggregation the Spawner Effect: Incorporating Stock Structure, Spatial Distribution and Female Influences into Estimates of Annual Population Egg Production. ICES. CM 1998/BB:11.

Marshall, C. T., O. S. Kjesbu, N. A. Yaragina, P. Solemdal and Ø. Ultang. 1998. Is spawner biomass a sensitive measure of the reproduction and recruitment potential of North-east Arctic cod? Can. J. Fish. Aquat. Sci. 55: 1766–1783.

Marshall, C. T., and Frank, K. T. 1999a. The effect of interannual variation in growth and condition on haddock recruitment. Can. J. Fish. Aquat. Sci. 56: 347–355.

Marshall, C. T., and Frank, K. T. 1999b. Implications of density-dependent juvenile growth for compensatory recruitment regulation. Can. J. Fish. Aquat. Sci. 56: 356–363.

Marshall, C. T., Yaragina, N. A., Lambert, Y. and Kjesbu, O. S. 1999. Total lipid energy as a proxy for total egg production by fish stocks. Nature 402: 288–290.

Marteinsdottir, G. and K. Thorarinsson. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. Can. J. Fish. Aquat. Sci. (In press)

Marteinsdottir, G. and A. Steinarsson. 1998. Maternal influence on the size and viability of Iceland cod (*Gadus morhua* L.) eggs and larvae. J. Fish. Biol. 52 (6) : 1241–1258.

Marteinsdottir, G. and G. Petursdottir. 1995. Spatial and temporal variation in reproduction of Icelandic cod at Selvogsbanki and nearby coastal areas. ICES CM 1995./G:15.

Meekan, M. G. and Fortier, L. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Mar. Ecol. Prog. Ser. 137, 25–37.

Mertz, G. and R. A. Myers. 1994. Match/mismatch predictions of spawning duration versus recruitment variability. Fisheries Oceanography 3:4, 236–245.

Murawski, S. A., Rago, P. J., and Trippel, E. A. 1999. Impacts of demographic variation in spawning success on reference points for fisheries management. NOAA Tech. Memo NMFS-F/SPO-40: 77–85.

Murphy, G. 1977. Clupeoids. In: Fish Population Dynamics. 1st ed. (Ed: Gulland, J.) John Wiley, New York.

Myers, R. A. And G. Mertz. 1998. The limits of exploitation: A precautionary approach. Ecological Applications, 8(1) Supplement, pp S2165–S169

Painting, S. *et al.* 1998. Environmental and biological monitoring for forecasting anchovy recruitment in the southern Benguela upwelling region. Fish. Oceanogr. 7: 364–374.

Parrish, R. H., Mallicoate, D. L. and R. A. Klingbeil 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in Northern Anchovy, *Engraulis mordax*. US Fishery Bulletin 84: 503–517.

Pope, J. G., Shepherd, J. G., and Webb, J. 1994. Successful surf-riding on size spectra: the secret to survival in the sea. Phil. Trans. Royal Soc. Lon 343B. 41–49.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11.559–623.

Saville, A. 1959. The planktonic stages of the haddock in Scottish waters. Marine Research : Scottish Home Department 3, 23.

Scott, B., Marteinsdottir, G., and Wright, P. 1999. The potential effects of maternal factors on spawning stock-recruitment relationships under varying fisheries pressure. Can. J. Fish. Aquat. Sci. 56: 1882–1980

Sinclair, M. 1988. Marine Population Regulation and Speciation. Seattle, University Washington Press, 252pp.

Sinclair, M. and M. J. Tremblay 1984. Timing of spawning of Atlantic herring (*Clupea harengus harengus*) Populations and the Match-Mismatch theory. Canadian Journal of Fisheries and Aquatic Science 41: 1055–1065.

Solemdal, P. 1997. Maternal effects - a link between the past and the future. J. Sea Res. 37: 213–227.

Solemdal, P., Bergh, O., R. Finn, N, Fyhn, H. J., Grahl-Nielsen, O., Homme, O., Kjesbu, O. S., Kjorsvik, E., Opstad, I., and Skiftesvik, A. B. 1992. The effects of maternal status of Arcto-Norwegian cod on egg quality and vitality of early larvae. II. Preliminary results of the experiment in 1992. International Council for the Exploration of the Sea Committee Meeting 1992/G**,** 79.

Solemdal, P., Kjesbu, O. S. and Fonn, M. 1995. Egg mortality in recruit- and repeat-spawning cod - an experimental study. International Council for the Exploration of the Sea Committee Meeting 1995/G,35

Stearns, S. C. and Crandall, R. E. 1984. Plasticity for age and size at sexual maturity: a life history response to unavoidable stress. In Fish reproduction: strategies and tactics, pp. 13–33. Edited. by G. W. Potts and R. J. Wootton. Academic Press. London.

Swain, D. P. and Wade, E. J. 1992. Density-dependent geographic distribution of Atlantic Cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. Can.J.Fish.Aqua.Sci. 50, 725–733.

Trippel, E. A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Transactions of the American Fisheries Society 127:339–359.

Trippel, E. A., Kjesbu, O. S., and Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In Early Life History and Recruitment in Fish Populations (Edited by R. C. Chambers & Tripple, E. A.), pp. 63–102. Chapman & Hall, Fish and Fisheries Series 21. London, UK.

Vrooman, A. M., Paloma, P. A., and Zweifel, J. R. 1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*. Cal. Fish Game 67, 39–51.

Ware, D. M. 1980 Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012–1024.

Watanabe, Y. Zenitani, H. and R. Kimura, 1996. Offshore expansion of spawning of the Japanese sardine, *Sardinops melanosticus*, and its implication for egg and larval survival. Can. J. Fish. Aquat. Sci. 53, 55–61.

Wigley, S. E. 1999. Effects of first time spawners on stock-recruitment relationships for two groundfish species. J. Northw. Atl. Fish. Sci. 25, 215–218.

Wooton, R J. 1984. Strategies and Tactics. In: Fish reproduction strategies and tactics. 1st ed. (Eds: Potts, G. W.; Wotton, R J) Academic Press, London, 2–34.

APPENDIX 2 PROJECT SUMMARY – ARILD FOLKVORD

Summary of project "The hormonal effects of alkyl phenols in cod – generation effects. Start feeding, juvenile production and differences in sexual determination"

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Adult cod were fed diets containing different levels of alkyl phenols to determine effects on growth, survival and sex determination of the offspring (0 ppb, 5 ppb and 500 ppb per fish per day). The results indicated that exposure of parental cod to alkyl phenols did not influence growth and survival of the offspring, either in the larval stage or as early juveniles. The survival in all groups was high, from 51–62% from hatching to day 56 post hatching (approx. 20 mm length). Furthermore, the data on sex determination of the offspring from the different treatments did not indicate hormonal influences and generation effects on sex differentiation in cod, and the observed sex ratio was close to 1:1 in all groups. However, it cannot be ruled out that the choice of exposure (oral versus immersion), the dosage, and the timing relative to the developmental state of the parental fish can influence the results. The parental fish used in this study were 700–900 g first time spawners, and it was concluded that offspring of first time spawners may have a high growth and survival potential when provided with suitable feeding conditions.

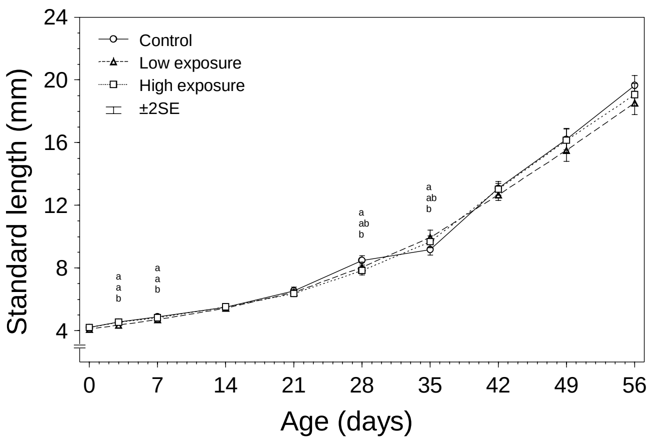

Figure 2.1. Mean standard length at age of larvae and juvenile cod, offspring of females exposed to low- and high concentration of alkyl phenols, together with a control group.

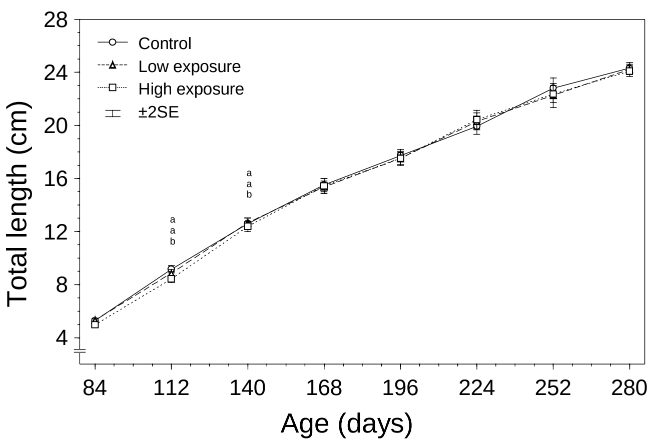

Figure 2.2. Average growth in total length at age of juvenile cod, offspring of females exposed to low- and high concentration of alkyl phenols, plus a control group.

APPENDIX 3 RELATIONSHIP BETWEEN SPAWNING STOCK BIOMASS AND REPRODUCTIVE POTENTIAL IN IRISH SEA COD

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Relationship between spawning stock biomass and reproductive potential in Irish Sea cod

In 2000, the European Commission closed for 10 weeks the fishery that targets Irish Sea cod. This was based on the advice of ICES that the fishing mortality experienced the fish stock was too high (F averaged 1.0 in the 1990s) and the biomass in recent years was well below the precaution reference point of B_{pa}. The state of the stock was further worsened by a series of recruitment failures. Hence it is important that the stock/recruit relationship of Irish Sea cod is considered in greater detail. For this reason and with the findings of recent research on the fecundity of Irish Sea cod, an initial investigation of the reproductive potential of the stock was carried out and compared to the time series of SSB.

The current ACFM stock summaries date back to 1968 and these were used to obtain mean size at age and numbers at age for Irish Sea cod. The maturity ogives and sex ratio of cod in the Irish Sea appear not to have changed since the early 1970s (Brander, 1975; Armstrong *et al*., *in press*). There were no estimates of size dependent fecundity from the beginning of the series, however recent research has determined estimates of potential fecundity (Armstrong, *et al*., *in press*). These estimates were used throughout the series to determine the potential egg production of the stock. Unfortunately there are no data on egg viability from cod in the Irish Sea and time series on the condition of adult cod are very short.

The trends in the reproductive potential of the stock were very similar to the trends in the SSB since 1968 (Figure 3.1). Changes in the estimates of reproductive potential are highly influenced by changes in the age structure of the population but also by the relative condition of the fish (Marshall, *et al*, 1998; 1999; Scott *et al*., 1998), which was not assessed in this study. It is apparent that the Irish Sea cod stock has been heavily exploited throughout the last three decades and hence the overall age structure of the population has remained fairly stable (Figure 3.2). Hence, the trends in the SSB are similar to the trends in the reproductive potential. The reproductive potential of the stock is only likely to vary if interannual differences in the size dependent fecundity are great or if the eggs are less viable in some years. So the resulting reproduction/recruit relationship is almost identical to that shown by the recruitment numbers and SSB (Figure 3.3).

References

Amstrong, M.J., Connolly, P. Nash, R.D.M., Pawson, M., Alesworth, E., Coulahan, P.J., Dickey-Collas, M., Milligan, S.P., O'Neill, M., Witthames, P.R. and Woolner, L. (in press). An application of the annual egg production method to estimate the spawning biomass of cod (*Gadus morhua* L.), plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) in the Irish Sea. ICES J Marine Sci.

Brander, K. (1975). The population dynamics and biology of cod in the Irish Sea. PhD thesis, University of East Anglia.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P. and Ulltang, Ø (1998). Is spawner biomass a sensitive measure of the reproduction and recruitment potential of Northeast Arctic cod? Can. J. Fish. Aquat. Sci. 55: 1766–1783.

Marshall, T.M., Yaragina, N.A., Lambert, Y., Kjesbu, O.S. (1999). Total lipid energy as a proxy for total egg production by fish stocks. Nature, 402: 288–290.

Scott, B.S., Marteinsdottir, G. and Wright, P. (1998). Potential effects of maternal fators on spawning stock-recruitment relationships under varying fishing pressure. Can. J. Fish. Aquat. Sci. 56: 1882–1890.

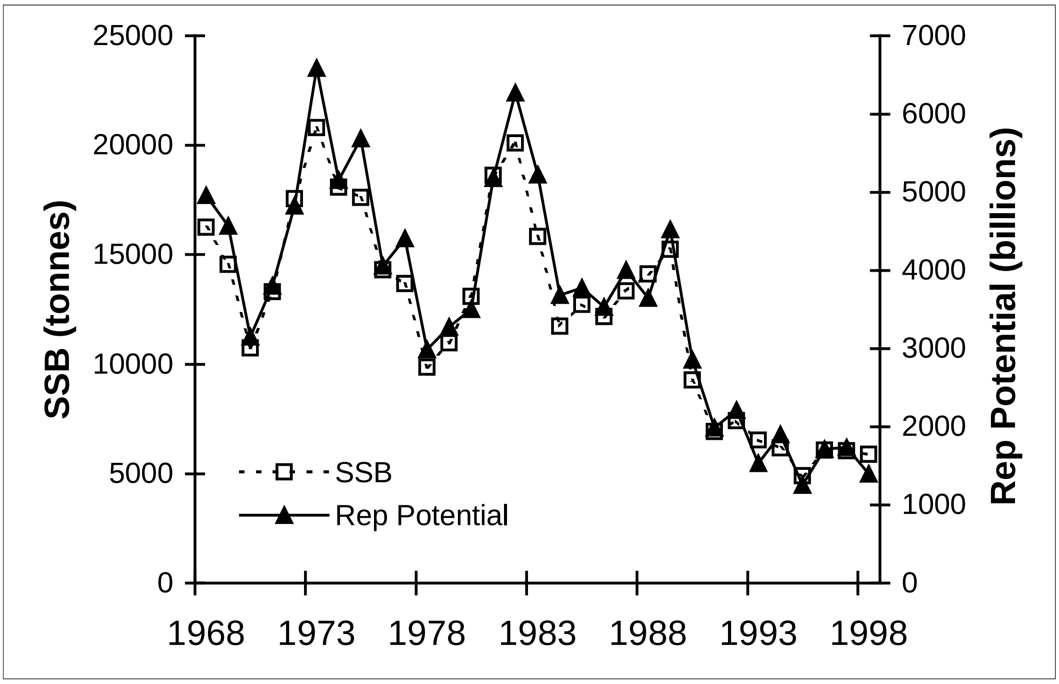

Figure 3.1. The reproductive potential (billions of eggs) and SSB of Irish Sea cod from 1968 to 1999.

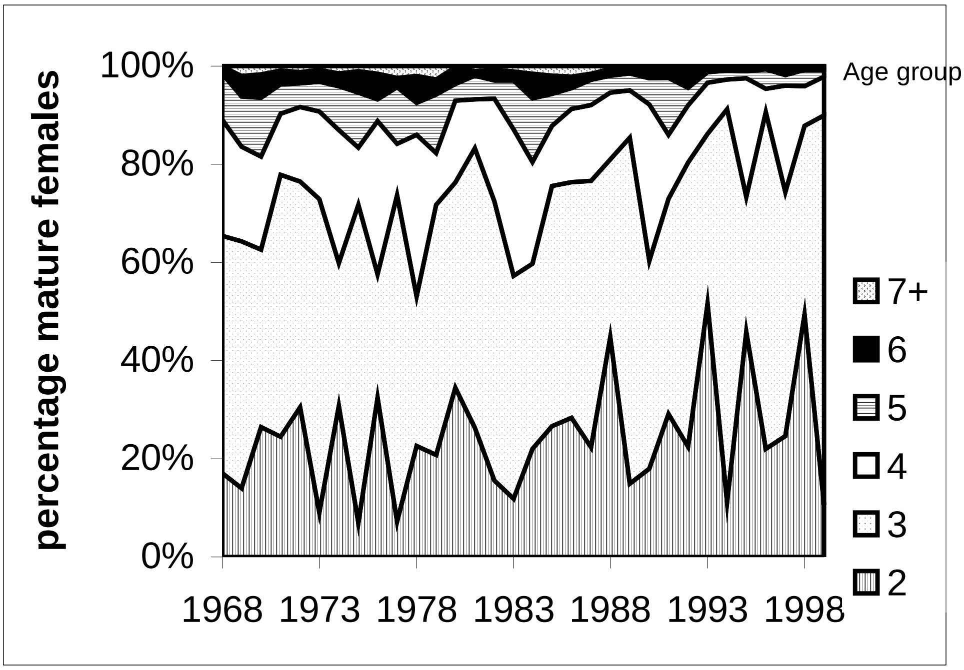

Figure 3.2. Proportion of mature females at age in Irish Sea cod since 1968.

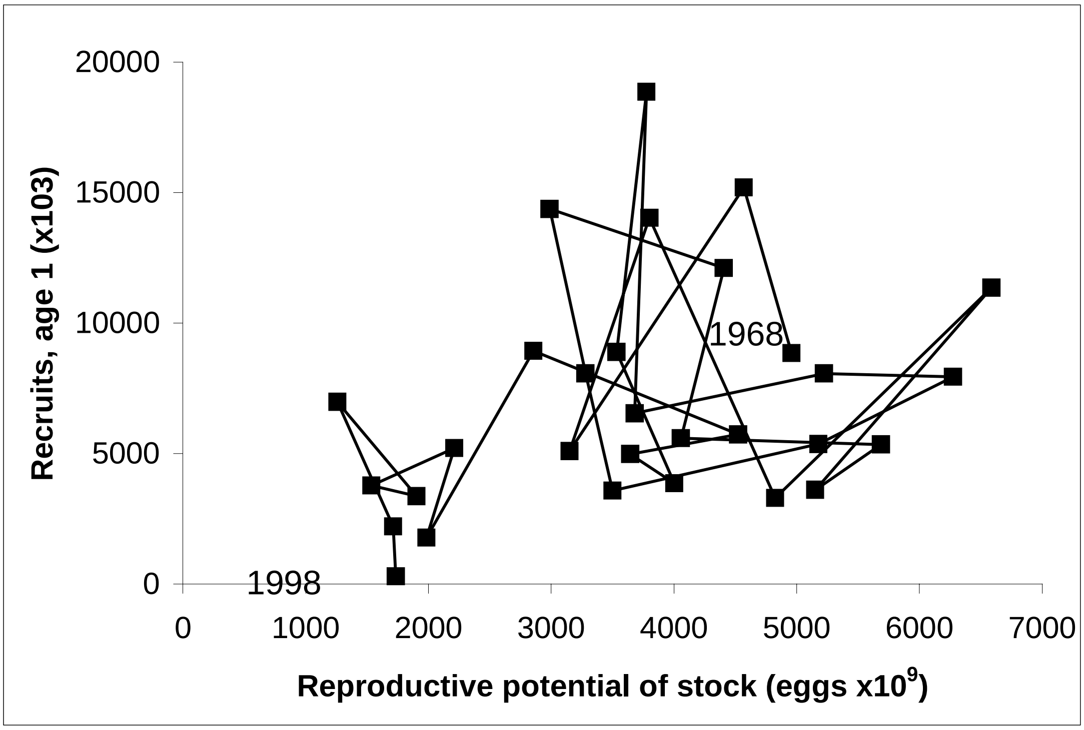

Figure 3.3. Recruits (aged 1) over reproductive potential of Irish Sea cod from 1968 to 1998, recruit values taken from XSA analysis.

APPENDIX 4 THEME SESSION Y REPORT

Report on Theme Session Y "Cod and Haddock Recruitment Processes – Integrating Stock and Environmental Effects"

Co–convenors: Mike Heath, UK; Brian MacKenzie, Denmark; Gudrun Marteinsdottir, Iceland

The session included 32 programmed presentations and one poster (Table 1). The authors of two papers were not present to present their manuscripts (Y:12 and Y:33). Manuscripts were not available for 2 presentations although they were logged as having been received in Copenhagen, and were dispatched to Stockholm within the specified time.

Overall, the Session stimulated considerable interest among the Symposium participants and vigorous question and discussion sessions.

The Session was born out of two papers presented at the 1998 ASC which described results from field programmes directed at haddock early life stages in the North Sea and cod reproductive parameters at Iceland, conducted as part of an EU funded project entitled "Recruitment processes in cod and Haddock: Developing new approaches" (1996–1998) (FAIR-CT95–0084). The participants in this project subsequently obtained further EU funding ("Stock Effects on Recruitment Relationships (STEREO)" (1998–2001) (FAIR-CT98–4122)), and 12 of the papers presented in the Session were attributable to the members of these two projects. A further 12 papers were derived from the Baltic CORE and STORE projects, also funded by the EU FAIR programme. There is clear overlap of approach between the STEREO and Baltic research groups, and the Session was a valuable opportunity for interaction between the investigators.

The first paper in the Session (Y:10) described the underpinning philosophy of STEREO, which is that the survivors of the recruitment processes are a select subset of the initial egg production by virtue of their parental, spatial and temporal properties. Various evidence indicates that the feeding conditions and age composition of the adult stock, have a profound effect on the timing, intensity and duration of spawning, and on egg size. In general, large eggs produce fitter larvae, and slow growing larvae suffer lower survival to the size of recruitment than fast growing individuals. The hypothesis underlying the projects is that a high proportion of the survivors to recruitment can be traced back to fractions o f the spawning stock producing high quality eggs at times and locations which confer high growth potential on larvae. These concepts are being assembled into coupled biological-physical models of cod and haddock stocks in the North Sea and Icelandic shelf waters. Ultimately, these rather complex models will be used to inform the production of new types of stock-recruitment relationships which take account of spatial and temporal features in a simpler way, and which may be of value in fisheries management procedures.

Four papers on the first day focussed on studies of larval haddock growth and survival in the North Sea. Y:01 showed that the survivors are indeed drawn from rather discrete parts of the temporal distribution of spawning, but that there is considerable year-to-year variation in the particular part of the spawning season which contributes most recruits. Y:13 and Y:14 focussed on studies of larval growth rates as estimated from otolith microstructure analysis and on environmental factors affecting vertical distribution. Y:11 discussed the processes that might be acting to control survival at around the time when juveniles switch a pelagic life-history to demersal. For North Sea haddock there are indications that the 1–2 months around settlement is extremely influential in setting the level of recruitment.

Patch studies are being used in the North Sea (Y:14; haddock) and off western Iceland (Y:30; cod) to investigate the ontogeny of various processes. There are parallels between some aspects of these studies and those carried out in the NW Atlantic during the Canadian OPEN programme and US-GLOBEC.

Very similar approaches to analysis of historical data from stage-abundance surveys to were presented by Y:11 (North Sea haddock), Y:15 and Y:20 (North-east Arctic cod). Correlations between sequential measures of stage abundance over several years were used to infer when the influential processes in recruitment were occurring. On face value there appears to be a difference between cod and haddock in that pelagic juvenile stages of cod correlate with abundance at age 1 and 2, whilst the equivalent correlation in haddock is not established until after settlement.

Hydrodynamic and particle tracking models are being used in both STEREO (Y:10) and STORE (Y:04) to investigate the dispersal of eggs and larvae in the North Sea, Baltic and will ultimately at Iceland during STEREO. At Iceland, an impressive analysis of historical data from surveys of pelagic juvenile abundance (Y:28) exposed previously unsuspected mixing of offspring from spawning grounds distributed widely around the coast of Iceland. The main spawning grounds are in the SW area, and it is suggested that the various dispersed spawning sites may provide a buffer against survival or egg production failure at the main site. These data will provide a strong foundation for investigation with particle tracking. In the Baltic, particle tracking was in use to try to resolve questions about the mixed spawning origins of juveniles found along the Polish coast. Westerly winds were found to promote dispersal of cod eggs and larvae from the western stock into the Arkona Basin and Polish coast. It appears that ultimately the survivors of this dispersal may return to the west, but there is some debate as to whether they contribute to spawning in the eastern region before returning to the west. Length distributions of juveniles sampled by trawl surveys in the eastern Baltic were used to 'verify' the conclusions of the particle tracking models (Y:08). Almost exactly analogous approaches are being used to tackle similar problems involving haddock spawning on Browns Bank, NW Atlantic (Theme Session K, K:05 and K:10) There is a clear requirement to develop molecular, chemical, meristic or other probes of the spawning origins of juveniles to diagnose the mixing of progeny in field samples of juveniles.

A number of papers (Y:02, Y:06, Y:07, Y:25, Y:27, Y:19, Y:29, Y:31, Y:34) focussed on field studies, experimental investigations and modelling of the reproductive biology of cod. It is clear that not only does the annual fecundity per unit body mass of fish vary with age and size, but also the timing and duration of spawning, and the size and quality of the eggs. Taken together this means that Spawning Stock Biomass is an extremely poor measure of potential population egg production. Elimination of old fish from the stock by exploitation severely depletes the egg production per unit biomass and potentially shifts the timing and duration of the spawning season (Y:25, Y:34), which may have consequences for the match-mismatch of larvae with conditions for survival. Y:06 and Y:07 demonstrated that recruitment also responds to the condition of the spawning stock. In North-east Arctic cod stock, variation in the liver condition index introduced more variation into total egg production than did the age or size composition. The liver index was related to the abundance of capelin which are the major food of Arctic cod. These papers showed that cod stocks dominated by recruit spawners are especially vulnerable to failure of egg production due to ecosystem effects leading to feeding conditions. Paper Y:19 showed that that maturation rates, as indicated by the age and size at maturity of North-east Arctic cod, are also related to feeding condition. In poor condition the year classes mature at age 5, whilst in good condition they may mature at least 1 year earlier. There was some discussion of the potential and benefits of introducing better indices of total egg production than spawning biomass into fisheries management procedures. Routine monitoring of spawning stock condition may be demanding due to seasonal variation in the various available indices. Age structure information are clearly readily available for many stocks, but the necessary information on age-specific reproductive traits for relatively few. Y:23 provided some information on the development of histological indices of maturation state for Baltic cod that will be necessary for 'operational' collection of reproductive data. Y:05 presented analysis of Baltic cod otolith annual increments which may provide a methodology for estimating interannual variations in spawning time within age classes.

In discussion, it was suggested that there may be a interaction between spawning stock abundance and age structure, and the spatial and temporal structure of larval survival as indicated by the field and modelling studies. In some cases, different age classes have different spatial distributions of spawning, whilst there is evidence from some stocks and species that as abundance is reduced so the stock retreats into core areas of the spawning range. The latter process may represent an important compensatory process which acts to

Y:03, Y:16, Y:29 and Y:32 described the unique impact of mesoscale oceanographic processes on the reproduction of Baltic cod. The deep layers of the basins of the western Baltic have a propensity to stagnate, resulting in oxygen depletion beneath the halocline. The spawning volume of cod is defined by the envelope of oxygen concentration and water density, which influences the neutral buoyancy depth of eggs. During prolonged stagnation this volume is diminished, and is not renewed until deep inflow events involving saline oxygenated water from the Kattegat and Belt Seas. Y:32 showed that interannual variations in the proportion of the adult stock participating in the spawning in March is very influential on recruitment to the western stock, and appears to be related to the incidence of inflow events during the previous winter. The situation in the 1990's, when most of the process orientated studies of recruitment have been carried out has been very different from conditions prior to 1970. The carrying capacity of the system appears to have declined since the 1950's, and seems to be related to inflow events and the spawning volume. Y:16 elaborated on this hypothesis and identified a mismatch during the 1980's between the spatial distribution of spawning and the distribution of spawning volume between the various basins, as being the likely cause of the decline in carrying capacity. Positive spawning volume is seen to be a necessary, but not sufficient condition for good recruitment.

Y:21 began to explore the consequences of variations in egg quality, as indicated by the amount of yolk, for the development and early survival of larvae. An elegant combination of rearing experiments and strategic modelling was being applied to investigate the problem.

There was a vigorous discussion following the presentations on the first day, and much interest in the notions that survivors are a select subset of the initial egg production, and that spawning biomass is a poor index of total egg production. It was questioned whether incorporating age structure and condition into stock-recruitment models would provide a significant benefit in terms of better resolving the underlying relationship. Data presented during the session clearly showed that at least for Arctic cod there is considerable benefit, and that the use of spawning biomass in management procedures risks overestimating recruitment potential in years when the stock is dominated by small fish and conditions are poor.

Historical data were central to Y:17, Y:18 and Y:26, which focussed on methods for improving the traditional stock recruitment relationship models for cod stocks. Throughout the Baltic, there has been a marked decline in the recruitment per unit spawning stock between the mid-1970's and mid-1990's (Y:26). This is related to the spawning volume (Y:03 and Y:16), and also to predation on cod eggs and larvae by planktivorous fish (herring and sprat). Spawning volume explains only apart of the variability in the survival from late egg stage to larvae. A statistical model of recruitment was developed which incorporated the potential egg production (from stock age abundance and maturity ogives), predation on eggs (from MSVAP data), effects of spawning volume, and a transport index, and Y:26 presented an in depth analysis of its performance in relation to observations. Similar compilation of stock and environmental factors into a multivariate model of recruitment processes was presented for Bay of Biscay anchovy (Y:22).

Y:17 and Y:18 presented results from a meta-analysis of stock and recruitment data across the range of cod stocks in the North Atlantic. The carrying capacity (recruit per spawner) differs widely between stocks, but there was a remarkable coherence of mean stock biomass and mean recruitment across the geographical range. By sharing data between stocks and accounting for the differences in carrying capacity, it may be possible to considerably refine the parameterisation of traditional stock-recruitment models.

Session Y, Summing up points

- The distribution of properties such as growth rate and size in individuals surviving to various stages in the recruitment process becomes progressively skewed relative to that of the initial population. The implication is that there is selective pressure for larger, faster growing individuals. The incorporation of this feature into bio-physical models of the early life history indicates that we can expect rich patterns of spatial, temporal and maternal structure to the origins of the survivors of the recruitment process.
- Model predictions of temporal pattern to the spawning origin of survivors is borne out by field observations. We do not yet have the methodology to verify predictions regarding spatial or maternal origins.
- The locus of density dependent survival steps in the early life history of most fish stocks is still not known, despite the fact that such processes are clearly dominant in setting the functional form of the stock-recruitment relationship. More research effort needs to be directed towards this topic.
- In many cases, populations of demersal juveniles are thought to be composed of surviving offspring from several disparate spawning locations. Identification of the spawning origins of juveniles sampled in the field remains a significant problem. Particle tracking models have been used in many studies to investigate such issues.
- There is still no significant information on the predation mortality of eggs, larvae or juveniles.
- Regarding maternal effects, investigations show that spawning stock biomass is a poor index of total egg production. Age and size structure, and in particular physiological condition of the adult stock have strong influences on total egg production. Stocks dominated by recruit spawners are more vulnerable to egg production failure due to poor feeding conditions than those with a more complete age structure.
- The timing and duration of spawning is strongly related to the age and size composition of the spawning stock. Temperature and feeding conditions of the adult stock may also influence spawning times.
- Egg condition varies with female age, size and condition, and has implications for the development and survival of early larvae.
- Fisheries management models traditionally employ spawning stock biomass as an index of total egg production in yield and recruitment simulations. There is evidence that these models would benefit from incorporating the newly emerging evidence on effects of spawning stock condition and age structure on egg production, where the relevant biological information is available. This is an immediate, practical way in which the outputs of recruitment process research can by utilised by management activities.
- Stock condition and age structure effects also have implications for the functional form of stock-recruitment models, and may explain some of the autocorrelation in recruitment time series. Combining these effects with simple representations of the spatial and temporal structures in survival exposed by computationally intensive bio-physical models should be a focus for studies in the coming years.
- Meta-analyses of stock and recruitment data across the range of cod stocks in the North Atlantic was presented as an alternative way of improving stock-recruitment relationships. The carrying capacity (recruit per spawner) differs widely between stocks. By sharing data between stocks and accounting for the differences in carrying capacity, it may be possible to considerably refine the parameterisation of traditional stock-recruitment models.
- The activities of the forthcoming Study Group on Incorporation of Process Information into Stock-Recruitment Models (first meeting, Lowestoft, UK, 23–26 November 1999) , and the Recruitment Processes Working Group (Bergen, 7–9 March 2000), are highly relevant to the activities of the participants in this Theme Session.

Table 1: Contributions to Theme Session Y, ICES Annual Science Conference, Stockholm 1999

Code	Paper or Poster	Authors	Institution	Country	Title
Y:01	Paper	P.J. Wright, F.M. Kennedy, I.M. Gibb, J.R.G. Hislop and W.S. MacDonald	FRS Marine Laboratory		Age related differences in spawning time and its significance to reproductive success in North Sea haddock
Y:02	Paper	Beth Scott, Gudrun Marteinsdottir, Peter Wright and Olave Kjesbu	Department of Zoology	UK	Sensitivity of potential recruitment to stock structure in the presence of temporally varying survival
Y:03	Paper	Fritz Thurow,		Germany	On the biomass of cod in the Baltic Sea during the 20th century
Y:04	Paper	H.-H. Hinrichsen, U. Böttcher, R. Oeberst, R. Voss and A. Lehmann	Institute für Meereskunde an der Universität	Germany	Drift patterns of cod early life stages in the Baltic: exchange between the western and eastern stock, a physical modelling approach
Y:05	Paper	T. Baranova, I. Shics	Latvian Fisheries Research Institute	Latvia	Reproduction of Eastern Baltic cod (*Gadus morhua* c*allarias* L.) and formation of annual growth zones on the otoliths in 90-s
Y:06	Paper	Merete Kvalsund, C. Tara Marshall	Institute of Marine Research	Norway	Food and fishery effects on the spawner-recruit relationship for North-east Arctic cod (*Gadus morhua* L.)
Y:07	Paper	C. Tara Marshall, O.S. Kjesbu, A. Thorsen	Institute of Marine Research	Norway	Spawner quality effects on two indices of reproductive potential: have we been counting our eggs before they've hatched?
Y:08	Paper	R. Oeberst,	Bundesforschungsanstalt für Fischerei Hamburg	Germany	Exchanges between the western and eastern Baltic cod stocks using the length distributions of trawl surveys
Y:09	Paper	M. Heath, A. Gallego	Marine Laboratory Aberdeen	UK	Process based simulation of the stock recruitment relationship in North Sea haddock
Y:10	Paper	M. Heath, J. Backhaus, A. Gallego, O. Kjesbu, B. MacKenzie, G. Marteinsdóttir, E. McKenzie	Marine Laboratory Aberdeen	UK	Overview of the EU FAIR Project 'Stereo' (Stock Effects on Recruitment Relationships
Y:11	Paper	M. Heath, A. Gallego, J. Hislop, C. Needle, B. Scott, P. Wright	Marine Laboratory Aberdeen	UK	The importance of the late pelagic and demersal settlement phases for recruitment dynamics in North Sea haddock
Y:12	Paper	V.L. Tretyak,	Polar Research Institute of Marine Fisheries and Oceanography (PINRO)	Russia	On possibility of applying the "stock-recruitment" Ricker's model to assess the recruitment of the north-east Arctic cod population
Y:13	Paper	A. Gallego, M.R. Heath, P. Wright, G. Marteinsdóttir	Zoology Department	UK	An empirical model of growth in the pelagic early life history stages of cod and haddock
Y:14	Paper	A. Gallego, M.R. Heath	Zoology Department	UK	Short-term changes in the vertical distribution of haddock larvae as a function of environmental factors

Code	Paper or Poster	Authors	Institution	Country	Title
Y:15	Paper	N.V. Mukhina,	Polar Research Institute of Marine Fisheries and Oceanography (PINRO)	Russia	The use of Russian ichthyoplankton survey data in forecasting of recruitment to Arcto-Norwegian cod stock
Y:16	Paper	Brian MacKenzie, M. Plikshs, F. Köster, H.-H. Hinrichsen	Danish Institute for Fisheries Research	Denmark	Does spatial match-mismatch of spawning and environmental conditions affect recruitment in Baltic cod?
Y:17	Paper	Brian MacKenzie, Ransom A. Myers and Keith Bowen	Danish Institute for Fisheries Research	Denmark	Stock-recruitment meta-analyses reveal differences in fish stock productivity between marine ecosystems
Y:18	Paper	Ransom A. Myers, Brian R. MacKenzie	Danish Institute for Fisheries Research	Denmark	Empirical models of carrying capacity, maximum reproductive rate, and species interactions using a meta-analytic approach
Y:19	Paper	H.-H. Eikeseth, Odd Nakken	Institute of Marine Research	Norway	Maturation in North-East Arctic Haddock
Y:20	Paper	Kristin Helle, Bjarte Bogstad, C. Tara Marshall, Kathrine Michalsen, Geir Ottosen, Michael Pennington	Institute of Marine Research	Norway	An evaluation of recruitment indices for North-east arctic cod (*Gadus morhua* L)
Y:21	Paper	Oyvind Fiksen, Arild Folkvord	Dept of Fisheries and Marine Biology	Norway	Maternal effects and the benefit of yolk supply in cod larvae in different environments - a simulation model
Y:22	Paper	G. Allain, P. Petitgas, P. Lazure	IFREMER	France	Environmental and stock effects on the recruitment of anchovy in the Bay of Biscay: a multivariate analysis
Y:23	Paper	L. Tybjerg, J. Tomkiewicz	University of Copenhagen	Denmark	Histological evaluation of gonadal and sexual maturity in Baltic cod (*Gadus morhua*)
Y:24	Paper	J. Tomkiewicz, M. Hansson, T. Baranova, V. Feldman, H. Müller, K. Ratke	Danish Institute for Fisheries Research	Denmark	Sex specific maturity ogives and sex ratios of Baltic cod: Implications for stock assessment
Y:25	Paper	J. Tomkiewicz, F.W. Köster	Danish Institute for Fisheries Research	Denmark	Maturation processes and spawning time of central Baltic cod
Y:26	Paper	F.W. Köster, H.-H. Hinrichsen, D. Schnack, M.A. St. John, B. MacKenzie, J. Tomkiewicz, M. Plikshs	Institute of Marine Research	Germany	Stock-recruitment relationships of Baltic cod incorporating environmental variability and spatial heterogeneity
Y:27	Paper	Gerd Kraus, A. Müller, K. Trella, F.W. Köster	Institute of Marine Research	Germany	Variability in fecundity of Baltic cod
Y:28	Paper	Gudrun Marteinsdottir, Björn Gunnarsson, Iain M. Suthers, Gavin Begg	Marine Research Institute	Iceland	Origin of juvenile cod in Icelandic waters based on statistical modelling of historical data on spatial distribution, abundance and demographic characteristics

Code	Paper or Poster	Authors	Institution	Country	Title
Y:29	Paper	E.I. Karasiova,	Atlantic Scientific Research Institute of Marine Fisheries of Oceanography (AtlantNIRO)	Russia	On the possible relation of the cod peak spawning time with the environmental conditions in the Gdansk Deep of the Baltic Sea
Y:30	Paper	Konrad Thorisson, Thor H. Asgeirsson	Marine Research Institute	Russia	Short term changes in a cod larvae patch West of Iceland 1997
Y:31	Paper	M. Plikshs, H.-H. Hinrichsen, F. Köster, J. Tomkiewicz, V. Berzins	Institute of Marine Sciences	Germany	Baltic cod reproduction in the Gotland Basin: annual variability and possible causes
Y:32	Paper	R. Oeberst, M. Bleil	Bundesforschungsanstalt für Fischerei Hamburg	Germany	Relations between the year class strength of the western Baltic cod and inflow events in the autumn
Y:33	Paper	Eric Grist,	Center for Marine Science and Technology	USA	Cod and haddock spatio-temporal dynamics within the multi-species fishery
Y:34	Paper	Gudrun Marteinsdottir,	Marine Research Institute	Iceland	Variable time duration and amplitude of egg production by cod in Icelandic waters (*Gadus morhua*): Influenced by stock or environmental effects?
Y:35	Poster	Ramiro P. Sánchez, John L. Butler	Instituto Nacional de Investigación y Desarrollo Pesquiro (INIDEP)	Argentina	The effect of vital rates on population growth. The application of a stage-specific matrix model to the SW Atlantic anchovy

APPENDIX 5 STEREO

An operational model of the effects of stock structure and spatio-temporal factors on recruitment (STEREO) (FAIR CT98–4122)

Commencement date: 1 December 1998 Duration: 36 months
Completion date: 30 November 2001
EC contact: DGXIV

Coordinator: Dr S. Mellergaard, Danish Institute for Fisheries Research, KavalergDrden 6, Charlottenlond, Denmark, tel: +45 3396 3403, Fax: +45 3396 3434, E-mail: brm@dfu.min.dk

Partners:		
	Danish Institute for Fisheries Research, DK.	Coordinator
	University of Aberdeen, UK	Contractor
	Institute of Marine Research, NO	Contractor
	Marine Research Institute, IS	Contractor
	University of Strathclyde, UK	Contractor
	University of Hamburg, DE	Contractor
	Marine Laboratory Aberdeen, UK	Contractor (Science coordinator)

SCIENTIFIC SYNTHESIS

Introduction

The overall objective of the project is produce an operational scheme for refining fisheries stock-recruitment relationships. This will be achieved by incorporating biological, spatial and temporal information on the stock structure. The aim is to provide the information necessary for improving the scientific basis of limit reference points in fisheries management. These are the biological criteria against which the state of the stocks are judged and form the basis for management. The methodology will be developed for cod and haddock stocks around Iceland, Norway and in the North Sea as case studies

The specific objective is to build a modelling system that will predict the probability of contributions by different spatial, temporal and parental components of the spawning stock of a species to the juvenile pre-recruit population some months after spawning. The system must be formulated in such a way as to address the following strategic questions for a given stock:

1. *What are the relative contributions of different age and size components of the spawning stock to the surviving juvenile population of a year class?*
2. *What are the relative contributions of different spatial and temporal components of the annual egg production to the surviving juvenile population of a year class?*
3. *What is the sensitivity of 1) and 2) to exploitation strategies?*
4. *What is the sensitivity of 1) and 2) to spawning stock size?*
5. *What is the sensitivity of 1) and 2) to climatic scenario?*

The approach will be to develop a series of interconnected models mapping the development of individual fish from the point of spawning, through the egg and larval phase, to settlement out of the pelagic phase. The individual based nature of the models is the key element that will confer the ability to achieve the desired aims. In essence, it is recognised that each individual in the population has a unique parental origin and experience of the environment which confers a particular survival probability. Variability between individuals is especially high during the early life stages and capturing this feature is the key to successful modelling.

The project is divided into 6 tasks (Table 1) which fall under four categories of activity:

- model development
- supporting initiatives to improve the representation of processes in the models
- data assimilation
- regional implementation

Model development will involve the coding and testing of four modules, followed by their coupling together to form an integrated system. The modules will be:

- A conventional Virtual Population Analysis (VPA) based model to predict the whole-stock age composition and abundance of fish under different exploitation strategies, linked to routines for estimating the spatial probability distribution of fish based on statistical analyses of historical data and allowing for different scenarios of spatial distribution in fishing mortality. The module will draw heavily on the catch statistics assembled by annual ICES Assessment working Groups and the outputs will be spatially resolved data on the abundance of fish age classes.

- An egg production module. This will predict the spatial and temporal distribution of eggs by the spawning stock, and the distribution of egg quality. The basis of the module will be that fish of different size, age and spawning experience have different reproductive outputs.

- An egg and larval dispersal, growth and survival module. This will simulate the dispersal through space and time of a population of individuals, starting life as eggs and developing into larvae and pelagic juveniles. The growth and development of each individual in the model will be simulated from the estimated exposure to key environmental conditions along the dispersal trajectory, and survival probability will be coupled to individual growth rates and at appropriate stages, to the concentration of individuals to mimic density dependence. The output of the module will be the spatial and temporal distribution of individuals by age, size, and cumulative survival probability.

- A pelagic juvenile settlement module. This will determine which of the individual larvae surviving to a particular size and/or age may join the demersal juvenile population. Settlement success will be on the basis of spatial criteria parameterised from observational data, and temporal criteria based on the cumulative number of individuals already settled in a particular area. The total number of successfully settled individuals, and their distribution, will be the final output from the system as a whole.

Supporting initiatives will be essential to the optimum formulation and parameterisation of the modules. These must include investigations of:

- The relationships between fish age, size and condition, and the timing, duration, quantity and quality of reproductive output.

- Characterisation of the vertical distributions of eggs and larvae and functional relationships describing spatial and temporal variability in growth and survival.

Where necessary, the supporting initiatives will depend on the collection and analysis of new field observations and experimentation, but maximum usage will be made of existing data and resources.

Data assimilation will be a significant task in the project. Oceanographic and hydrodynamic data will be required to configure the modules to particular regions, especially the egg and larval module. Historical trawl survey data will be required to configure the settlement success module. Analysis of historical survey data will be necessary to provide the parameters for simulating adult stock distributions, and to provide testing data against which some of the results can be evaluated.

Regional implementations will be the vehicle for demonstrating and testing the operational system. The aim will be to hindcast the histories of effective reproductive output for cod and/or haddock stocks in the northern North Sea and at Iceland, as substitutes for the spawning biomass term in stock-recruitment relationships. Fitted relationships between observed recruitment and effective reproductive output will be compared with the conventional spawning biomass-recruitment models to assess the improvement in resolution achieved.

Table 1

MODEL DEVELOPMENT

TASK 1 Model assembly, testing and sensitivity analysis
1.1 Exploitation strategies and corresponding stock structures.
1.2 Development and testing of an egg production model.
1.3 Development and testing of an egg and larval dispersal and survival model.
1.4 Coupling of the egg production model to VPA model output.
1.5 Coupling of the stock model to the egg and larval survival model.
1.6 Identification of settlement criteria and sensitivity analysis of the model.

SUPPORTING INITIATIVES

TASK 2 Spatial and temporal structure in stock composition and egg production.
2.1 Relationship between spawning age class distribution, stock abundance and environmental conditions.
2.2 Relationship between egg viability, batch frequency and size, and female age, size and condition.
2.3 Relationship between spawning time and duration and female age, size and condition.

TASK 3 Spatial and temporal structure in egg and larval survival.
3.1 Age and spatial variability in the vertical distribution of eggs and larvae.
3.2 Spatial and temporal variability in larval growth and survival rates and the relationship with environmental conditions.
3.3 Spatial structure in the spawning time origin of surviving juveniles.

DATA ASSIMILATION

TASK 4 Historical data analysis
4.1 Statistical modelling of historical data on large-scale distributions of mature fish.
4.2 Statistical modelling of historical data on large-scale distributions of pelagic O-group fish
4.3 Statistical modelling of historical data on large-scale distributions of demersal juvenile fish

TASK 5 Assembly of forcing data
5.1 Assembly of historical meteorological and hydrographic data.
5.3 Hydrodynamic and turbulence closure modelling.

REGIONAL IMPLEMENTATIONS

TASK 6 Stock hindcasts
6.1 Model hindcasts of North Sea cod and haddock stock histories.
6.2 Model hindcasts of Icelandic cod stock history.

Results from year 1 of the project

Model development

The STEREO model development has proceeded along three tracks in the first year of the project – modelling of egg production, modelling of pelagic phase dispersal, growth and survival, and analysis of stock assessment model and catch data to determine stock age structures at spawning dates.

The egg production modelling started out by developing a representation of annual reproductive output at the whole stock level. This model was used to examine the potential significance of age and size-specific differences in fecundity and as well as the effect of maternal size on offspring viability (Scott *et al*., 1999). The model indicated that, at constant biomass, changes in the age composition of the spawning stock significantly affected the potential reproductive output because of age related differences in specific fecundity. The conclusion was that spawning biomass is a poor index of the state of a fish stock, and that management advice should take account of the age structure as well. Exploitation of stock to the point that recruit spawners make up the bulk of the population, is clearly a high risk strategy for management.

The reproductive modelling then focused on simulating the temporal patterns of egg production from mean individuals of given age and size. This work is the essential pre-requisite to implementing a population egg production model. The spatial dimension to such a model will be provided by coupling to a statistical analysis of the spatial distribution of age and size classes in the population. A preliminary test of the methodology was carried out to assess the reliability of the methods, using VPA values and a simplified egg production model production based on field sampling of maturity compositions during a survey carried out during the peak spawning period in 1992. An additional motivation for this implementation was development of the particle tracking scheme for simulating egg and larval dispersal and survival (subtask 1.3). The particle tracking scheme was successfully coupled to the egg production model of the North Sea haddock stock and demonstration results produced.

The particle tracking model can be conceptually divided into 2 parts; a model of the dispersal of eggs and larvae (physical processes) and a model of growth and survival (biological processes). A preliminary model of egg and larval dispersal and survival is operational, in advance of the 18 months deadline, developed from the scheme described by Heath and Gallego (1998), although several aspects of the physical and biological modelling will be further developed and improved throughout the life span of the project. As described above, the model is currently implemented for North Sea haddock (including the west of Scotland), and is coupled to a preliminary population egg production model. The results indicate significant spatial variability in the survival of eggs and larvae from different parts of the spawning distribution.

At present, the physical aspects of the dispersal model are based on simulated flowfields inherited from previous EU-funded projects, and a data-driven representation of the time-evolving temperature field. Work is currently in progress to substitute the hydrodynamics scheme developed in this project into the particle tracking system.

Density dependence is one of the most important biological processes that must be represented in the STEREO model system. Without explicit inclusion of the key density dependent steps in the recruitment process, it will not be possible to simulate the stock-recruitment relationship. Density dependence reduces the variability in numbers between cohorts within a year class, and causes the characteristic flattening or doming of stock-recruitment relationships. The biology of reproduction and early life histories of cod and haddock were reviewed by the partners at the first project meeting. A variety of processes may lead to density dependence, including competition for food or space, and cannibalism. There is no evidence to support the existence of competition for food during the larval phase. However, competition for food in the adult stock may lead to reduced body condition and reproductive output. Most importantly though, the pelagic juvenile settlement phase was identified as being the likely focus for density dependent processes, involving competitive exclusion, impacts on growth, and predation mortality (including cannibalism in cod). A representation of competitive exclusion at the end of the pelagic phase has been implemented in the particle tracking model, and the methodology for implementing alternative processes has been developed. To our knowledge, this is the first example of density dependent survival processes having been implemented in a particle tracking model, and the initial results indicate that the system has high potential to reflect the underlying form of stock-recruitment relationships.

Underpinning both the egg production and pelagic phase components of the model system will be a good analysis of the state of the stocks in any particular year to be simulated. The task of compiling and analysing VPA model output and catch data for haddock and cod in the North Sea and west of Scotland, and cod in Iceland is also under-way. However, it is too soon to report results from this undertaking.

Supporting Initiatives

The supporting initiatives in the project cover a wide range of field and data studies of the biological properties and responses of spawning adult fish, eggs, larvae and juveniles. Ultimately, the studies are designed to feed knowledge and parameters into the modelling effort, but they also represent strong, free standing scientific contributions in their own **right.**

Studies of spawning stock distribution and biology

The factors affecting the distribution of spawning haddock in the North Sea and west of Scotland, and cod at Iceland and Lofoten, have been extensively studied in 1999 during the annual trawl surveys for stock assessment, and by a programme of tagging with data storage tags (DST's). Application of Generalised Additive Models (GAM) to analysis of the haddock data from the North Sea indicates that depth was the most important explanatory variable for both mature and spawning fish. Smoothed partial fits for depth were obtained in both North Sea and west of Scotland surveys indicated that the highest catch rates of mature and spawning fish occurred in depths of 60 –100 m. Temperature also appeared to have a significant influence on the distribution of spawning haddock but not mature haddock. Spawning fish CPUE increased to the highest temperature recorded in the North Sea survey and around the mid-temperature range in area west of Scotland surveys. For both areas this temperature range was around 8°C. This possible temperature preference will be further investigated for different length-classes of spawning fish. Future work will also explore the size-stratified data with reference to information available and collected on sediment and topography.

Cod occurred down to 355 m depth in the North Sea and west of Scotland, although the highest densities of cod were found in depths <60m in the North Sea and around 250 m along the shelf edge to the west. In the North Sea the highest concentration of cod occurred in the temperature range of 7–8 °C. However, this factor was not retained as a significant explanatory variable in the preliminary GAM analysis. At Iceland, three adjacent cod spawning areas were shown to differ with respect to age and size distributions. Larger (mean weight = 10.7 kg) and faster growing cod were shown to spawn closer to the coast. Medium sized (mean weight = 7.7 kg) cod spawned in deeper waters out on the bank (Selvogsbanki), and the smallest cod (mean weight = 5.6 kg) tended to spawn along the continental edge.

The data recovered from data storage tags (DST's) attached to cod captured on the Icelandic spawning grounds indicated that temperature and depth profiles could be used to identify periods spent by spawners on the spawning grounds. Arrival and departure, on and from, the spawning grounds were indicated by abrupt changes in depth reflective of the depth range of the spawning grounds. Furthermore, the duration of stay on the spawning grounds was characterized by reduced vertical migrations. In addition, individual cod appear to reselect similar depth ranges as those experienced a year earlier. Unfortunately, nearly all of the recovered DST's were obtained from males. Only one female with a DST was recaptured during this period. The results obtained for the males indicated that larger males arrived and left the spawning grounds earlier than smaller males. Generally, males stayed for 2–4 weeks on the spawning grounds. Therefore, at least with regard to the males, the duration of the spawning period appeared to be achieved by protracted spawning of individuals as well as asynchronisity of spawning represented by variable time of arrival and departures of individual males.

The timing and duration and output of spawning in relation to the age and size of fish was investigated by time series sampling of haddock in the North Sea, and cod at Iceland and Lofoten. Data on haddock collected in 1999 were compared with those from similar collections in 1994–96 to consider inter-annual variability in the onset and duration of spawning. In all years there was a tendency for large and old fish to spawn earlier than small and young fish and the duration of spawning was positively related to size and age. However, there were marked inter-annual differences in the timing and duration of fish spawning at a given length and age-class. Investigations into the effect of size, age and condition on egg production in 1999 are ongoing. To date, potential fecundity at length based on 59 fish was within 1996 range although smaller fish had relatively higher fecundity. As in previous years, residual variation in the potential fecundity - length relationships could be partly be explained by the hepatosomatic index (see FAIR CT - CT95–0084). Information gained from field programmes in 1994–96 have been used to provide preliminary input into the egg production model

The time and duration of cod spawning at Iceland was shown to vary from one year to the next, as well as within spawning season between different size/age groups of spawning female cod (Marteinsdottir and Björnsson, 1999). Onset of spawning was in all cases related to the size of females, with larger females initiating spawning earlier than the smaller ones. Duration of spawning was also related to body size, where larger females spawned over a longer period. Furthermore, over a six year period (1994–1999), the duration of spawning among large females was significantly related to the proportion of cod greater than 105 cm in the population sampled, while the duration of spawning among small females was significantly related to the proportion of cod below 6 years of age.

Data on fecundity of cod in Icelandic waters have been collected and analysed for the years 1995–1999. These data are presently being assimilated for a manuscript that will be submitted for publication next year. Data to predict the start of spawning have been collected and analysed for the years 1997–1999. Additional data on egg size and batch fecundity are presently being analysed.

For Arcto-Norwegian cod at Lofoten, a multiple regression model has been established in which fecundity is the dependent variable and fish length, liver index and condition factor are the independent variables (Marshall *et al*., 1999). For the 1999 material, the model explains 81 % of the observed variation in fecundity

Studies of egg and larval dispersal and survival

Vertical distribution patterns of eggs and larvae can have an impact on their horizontal dispersal in situations where there is strong vertical shear in the water column. This feature is incorporated in the STEREO particle tracking model, but the vertical distributions of larvae require parameterisation from field observations. Field sampling of the abundance of eggs and larvae of cod and haddock was carried out during 1999 in Icelandic waters. Similar surveys have previously been carried out in the North Sea and west of Scotland in 1992, 1995 and 1996. The data from both regions are being analysed to determine the ontogenetic changes in vertical distributions of the two species in both regions, and for validation of the horizontal dispersal patterns simulated by the drift models. Results from the North Sea show that haddock larvae, particularly those belonging to the larger length classes, are highly reactive to environmental conditions cues and modified their vertical distribution, especially in response to wind induced turbulence. At Iceland, cod eggs were distributed mainly in the upper 10m, and the larvae became gradually deeper with increasing size. Horizontal distributions of cod eggs and larvae at Iceland were shown to follow the drift route from the spawning areas in the south onto the nursery areas off the north coast. Satellite tracked drifters indicated that the transport off the spawning banks in 1999 was particularly rapid.

A key component of the pelagic phase of the STEREO model is the link between growth rate of larvae and environmental conditions along the drift trajectory of each particle. Field studies have been able to resolve the effects of temperature on spatial variability in growth rates of larvae, but rarely the effects of food abundance. There may be several reasons for the lack of an obvious effect of food. First, it is very difficult to quantify the abundance of the relevant prey items in the field, and bulk zooplankton abundance is certainly not an appropriate measure. In addition, if food abundance is saturating for growth then spatial variability will not have any effect on growth rates. Finally, temperature and food abundance almost certainly do not vary independently in the field, either spatially or temporally, so that the field relationship between growth and temperature may in fact include an element of the effects due to food abundance.

The approach taken in the STEREO modelling is to use temperature as a proxy variable for the assemblage of environmental factors affecting growth, including food and temperature. The likely covariance between all these factors and temperature implies that the field relationship between growth and temperature will not be the same as might be measured in a controlled experiment in the laboratory, but some other ecosystem-specific function. Following from Heath and Gallego (1998), the STEREO model has initially adopted the precedent of Campana and Hurley (1989), and applied a parabolic form to the relationship between growth and temperature. Campana and Hurley (1989) derived parameters for the temperature-growth relationship for cod and haddock on Browns Bank (NW Atlantic). An important task in the first year of STEREO has been to parameterise the parabolic relationship to represent haddock in the North Sea and cod at Iceland. A new parameter set has been derived for haddock, based on a large collection of otolith microstructure data, and work is underway to estimate the parameters for Icelandic cod. At the same time, fisheries oceanography literature has been reviewed in order to evaluate field evidence for the influence of turbulence on larvae fish ecology, with a view to incorporating such connections into the STEREO model.

Ultimately, the STERO model will simulate the spatial and temporal connection between surviving populations of demersal juvenile fish, and the initial distributions of spawning adults. It will be important to be able to evaluate these results at the macro-scale by, if possible, verifying these connections. To this end, data on age and size of North Sea haddock and Icelandic cod juveniles have been collected. Analysis of the samples has started. First results on juvenile cod, indicate that reconstructed hatch date and spawning periods of surviving 0-group captured along the north and the east coast of Iceland, and the recorded hatch and spawning time for cod on the main spawning grounds in the south were not congruent. The data strongly indicate that some of the surviving 0-group cod may have originated from spawning that occurred in spring and early summer, in the colder water temperatures prevailing in the Western, Northern and Eastern fjords.

Data assimilation

The operational STEREO model will require substantial inputs of data to set the initial conditions and drive the dynamics of a given year class of recruiting fish. The initial conditions that need to be specified are the age composition and distribution of the adult spawning stock. Initially, these will be derived directly from survey data, and stock assessment VPA outputs as described in the description of modelling results above. By the end of the project however, it is hoped to be able to produce a statistical model of the spatial distributions of haddock age classes in the North Sea and west of Scotland region, and cod at Iceland, in terms of geographic, topographic and environmental variables. Preliminary analyses of the Icelandic surveys, although incomplete, indicates high variability in both abundance and length and age distributions between spawning grounds and between years within spawning grounds. Changes in size distributions appear to follow changes in the population structure. Environmental factors such as temperature are being estimated for incorporation in explanatory models. As regards the North Sea, the datasets are currently being explored to extract the relevant data, and work on spatial and temporal distributions will begin shortly.

The main driving data for the model runs will be hydrodynamic. These will dictate the current fields that disperse eggs and larvae, and the temperature records along each drift track. These data cannot be observed in the field with sufficient spatial or temporal resolution, and must be themselves simulated by a separate model system. Hydrodynamic modelling is costly exercise in terms of computing time and assembly of meteorological forcing data. Therefore, in STEREO, we sought alternative means of generating hydrodynamic data on an operational basis without having to implement a full hydrodynamic model to generate each new dataset. The original idea was to use a so called ‘drawer model’, in which stationary flow fields are simulated for a range of constant climatic scenarios, and stored for re-use. The flow regime for a particular year is then assembled by selecting stored flow patterns in sequence, according to the sequence of meteorological conditions experienced in that year. This approach has the advantage of being low cost, and rapid to implement in the particle tracking model. However, it has a number of disadvantages, most particularly that it is very difficult to classify the observed patterns of weather in the north-east Atlantic into a manageable suite of standard types. Here, we describe a completely different, and much superior approach which has been developed in the first year of the STEREO project, and which will be adopted instead of the drawer model approach.

A 3-D hydrodynamic model (Harms *et al*., 1999a,b), was adapted for the STEREO area. Initial data and forcing data was collected from institutional records and other sources, including:

- topographic data for the region of interest,
- meteorological data (various data bases),
- climatological temperature and salinity data,
- climatological sea surface elevations for open boundaries,
- tidal elevation data for open boundaries and
- air pressure data from selected points in the STEREO matrix.

The first three data sets were gridded and interpolated on the 3-d model matrix. All other data were collected and converted into the required format.

The 3-d model was run with a repeating annual cycle of climatological forcing for 11 years by which time it reached a stationary state. Time dependant flow fields were deduced and analysed. It was found that the simulated 3-D flow fields were highly correlated with surface air pressure data from eight meteorological stations within the STEREO model matrix. This offers the possibility to determine time dependent 3-D flow fields simply from air pressure data using a 'statistical model' instead of the drawer model. At the meeting of STEREO partners in Stockholm (3. Oct. 1999) results from this statistical model were presented. During the meeting it was decided to use this statistical model approach instead of the 'drawer model' specified in the technical annex. Validation of hydrodynamic and statistical model results is in progress, based on further runs of the hydrodynamic model with realistic meteorological forcing for the period 1979 – 1981.

To generate temperature fields for driving growth and survival in the particle tracking model, a mixed-layer model was set up for three different regions of interest: a) Scottish waters, b) North-Icelandic and c) South-Icelandic waters. The model was converted into a user-friendly version. Initial and forcing data were collected which encompass meteorological data and initial temperature and salinity data. The model coding, initial data and forcing data were transferred to the partners responsible for implementing the particle tracking.

Discussion/Conclusions

All of the components necessary to implement the STEREO stock-recruitment model for cod at Iceland and haddock in the North Sea, are now in place. A preliminary implementation for North Sea haddock has been successfully accomplished. The incorporation of density dependence into the model has been a particularly significant development.

The new statistical model of hydrodynamic model results is an exciting development, which opens up new prospects for high speed, near real time simulation of water circulation patterns, and true operational use of the STEREO model, perhaps even at sea during survey operations.

Outstanding new collections of data on the distribution and reproductive biology of cod and haddock have been accomplished in 1999. The spatial and temporal coverage, and coordination of sampling methods and strategies makes these data of unique value.

References

Campana, S.E. and Hurley, P.C.F. (1989). An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the gulf of Maine. *Can. J. Fish. Aquat. Sci*. **4**6, 603–613.

Harms, I.H., Backhaus, J.O. & Hainbucher, D. (1999a): Seasonal variability in the Iceland-Faroe-Shetland overflow area – Implications for the migration of *Calanus finmarchicus.* ICES Symposium 'Population Dynamics of Calanus in the North Atlantic: Results from TASC', 24–27 August 1999, Tromsø, Norway. Manuscript submitted to ICES-Journal of Marine Science

Harms I.H., J.O. Backhaus & D. Hainbucher (1999b): Modelling the seasonal variability of circulation and hydrography in the Iceland-Faeroe-Shetland overflow area. *ICES CM 1999/L:10*, Annual Science Conference, 29 September to 2 October 1999, Stockholm, Sweden.

Heath, M.R. and Gallego, A. (1998). Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. *Fish. Oceanogr*. **7**, 110–125.

Marshall, C.T., Yaragina, N.A., Lambert, Y. & Kjesbu, O.S. 1999. Total liver energy as a proxy for total egg production by fish stocks. *Nature* 402: 288–290.

Marteinsdottir, G. and H. Björnsson. 1999. Time and duration of spawning of cod in Icelandic waters. ICES C.M. 1999/Y:34 Annual Science Conference, 29 September to 2 October 1999, Stockholm, Sweden.

Scott, B., Marteinsdottir, G. and Wright, P. (1999). Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. *Can. J. Fish. Aquat. Sci*. **56**, 1882–1890

Future Actions

In the second year of the project, the constituent parts of the STEREO model system will be assembled and implemented for Icelandic cod and North Sea haddock. There will be strong emphasis on the production of manuscripts for publication, based on the basic science carried out in the supporting initiatives during year 1, and the emerging model developments.

APPENDIX 6 STORE

Environmental and fisheries influence on fish stock recruitment in the Baltic Sea (STORE, FAIR 98 3959)

Project period: 01.01.1999 – 31.12.2001

Partners:

- Institute of Marine Sciences, Kiel, Germany, Coordinator
- Danish Institute for Fisheries Research, Charlottenlund, Denmark
- Finnish Game and Fisheries Research Institute, Helsinki, Finland
- Gotland University College, Ar Research Station, Gotland, Sweden
- Baltic Sea Research Institute Warnemünde, Germany
- Federal Research Centre for Fisheries, Institute for Baltic Sea Fishery, Rostock, Germany
- Sea Fisheries Institute, Gdynia , Poland
- Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, Kaliningrad, Russia
- Institute for Hydrobiology and Fisheries Research, Hamburg, Germany
- Water Quality Institute, Hørsholm, Denmark
- Finnish Institute for Marine Research, Helsinki, Finland,
- Estonian Marine Institute, Tallinn, Estonia,
- Latvian Fisheries Research Institute, Riga, Latvia,

Background:

An integral part of applying the precautionary approach in fisheries management is the determination of key stock reference points, with a priority set for limit biological reference points that result in medium- and long-term sustainability of the stock. A crucial factor in determining the biological reference points is the quantification of processes causing recruitment variability and uncertainties in stock and recruitment parameters. Presently, ICES Assessment Working Groups develop reference points based mainly on single species considerations, thus being susceptible to failure due to multispecies interactions (e.g. predator/prey) or fluctuating environmental conditions (e.g. deep water oxygen conditions in the Baltic).

A first prerequisite of accepted management strategies is that there is a quantifiable relationship between spawning stock (or some more precise measure of viable egg production) and recruitment. Such a relationship is in general very difficult to derive from given time series of stock and recruitment observations due to the large environmentally-induced variation in recruitment success. In practice, target values identifying recruitment-limiting stock sizes are generally poorly defined and are often taken simply as the lowest value of spawning stock size recorded for a specific stock. Depending on the available time series and observed range of variation in stock size, the perceived limit value can be very different, giving different implications for the long-term exploitation levels and sustainable yield. It is clear that the potential for reducing a fish stock to a range of recruitment-limiting stock sizes, or to commercial extinction, appears to be high if the stock is at a low level and environmental conditions are prohibitive for recruitment success.

In the case of cod in the Baltic, there is some evidence of a relationship between spawning stock biomass and recruitment. However, this relationship is sensitive to environmental conditions and trophic interactions. For example, low oxygen concentrations at cod spawning sites and clupeid predation on cod eggs have both been shown to be important determinants of recruitment. The close coupling between cod and sprat, where sprat, the principal prey of adult cod influence the predators reproductive success via consumption of cod eggs at high sprat stock levels and possibly via reduced viable egg production at low sprat availability, necessitates the inclusion of this species in management initiatives on cod. Sprat and cod spawn in the same areas in the Baltic, with overlapping spawning periods, however, the spawning strategy and recruitment success of sprat is very different from cod. Typically sprat produces a series of year-classes below average and then one or two very abundant year classes. The limiting environmental factor for reproductive success of sprat appears to be temperature in the intermediate water layer which influences egg mortality. These processes are currently not considered in the management of Baltic cod, but we hypothesize that:

a) different environmental regimes are identifiable,
b) their effects on recruitment are quantifiable and as a result,
c) different fishing strategies based on these regimes may be justifiable.

If critical spawning stock sizes or threshold egg production values are not adapted to long-term variations in the environmental regime, especially the cod population in the Baltic may be at risk of recruitment failure due to unfavourable combinations of biotic and abiotic variables, although being above any minimum level showing still successful recruitment in the historical data set so far.

Objectives:

The objectives of the research project are to:

- Determine stock-recruitment relationships for Baltic cod and sprat in relation to key environmental factors influencing the production of viable spawn and the survival of early life history stages.
- Improve short-term predictions of stock development by integrating recruitment estimates based on the present status of the stock and its biotic and abiotic environment.
- Develop predictive recruitment models for medium- to long-term forecasts of stock development under different environmental and fishery scenarios.
- Estimate biological management reference points, critical stock limits and target spawning stock sizes based on stock-recruitment relationships and stock development simulation models, and considering the precautionary approach for fisheries management.

Research tasks:

The key questions to be answered by the project are: how do environmental factors influence the stock-recruitment relationship for cod and sprat stocks in the Baltic and what are the implications of variations in these factors for the use of biological reference points and critical stock limits in the management of the fisheries. These questions will be addressed by following tasks:

1. Evaluating the accuracy of the spawning stock biomass as a measure of viable egg production by: a) determining the reproductive potential of the stocks in relation to size and structure of the spawning stocks, sex ratios, maturation processes and spatial distribution of the populations; b) determining the viability of the produced eggs in relation to parental growth conditions and contamination with toxic substances.
2. Resolving the direct impact of hydrographic factors on the fertilization and developmental success of cod and sprat eggs and early larvae by field and laboratory experiments.
3. Identifying and describing the hydrographic, oceanographic and behavioural processes influencing growth, survival and distribution of young of the year cod and sprat and determining the component of the spawning stock contributing to recruitment through the examination of survivor characteristics.
4. Developing and employing combined drift and feeding models to ascertain the potential role that interannual hydrographic variability has on survival and growth of eggs and larvae.
5. Determining the impact of predation on early life stages of cod and sprat caused by clupeids. Extending the time series of stock and recruitment estimates of cod and sprat utilizing MSVPA. This includes a dis-aggregation of stock and recruitment estimates into different spawning areas characterized by specific environmental conditions.
6. Integrating the findings of the previous tasks into new recruitment models and thereby assess the utility of such models in management applications, e.g. simulation of medium- to long-term stock development scenarios under different environmental conditions and fishing activities, forecasts of annual recruitment ranges to be used as input in short-term stock predictions, determining SBL´s and biological reference points and their sensitivity to environmental perturbations.

State of progress:

Following activities were performed within the first reporting according to task:

Task 1: Viable egg production for Baltic cod and sprat

- Intensive field programme describing the distribution, abundance and stock structure of cod and sprat within and between different spawning areas in 1999 including hydrography, as well as compilation and analyses of corresponding historic research survey data.

- Updating database on sex specific maturity ogives and sex ratios at age of cod and analysis of spatial and temporal variability, histological validation of visual maturity staging scale; set-up of sampling scheme on sprat sex specific maturity ogives.

- Intensive field programme in 1999 to describe the gonadal maturation and timing of spawning of cod and sprat in relation to size/age and condition, compilation of corresponding data from surveys conducted within the CORE-project (AIR2 94 1226) in 1995-1998.

- Laboratory experiments on the relationship between female cod characteristics and egg and larval size and viability, fertilisation success and sperm quality of individual cod males relation to age/size and condition and cod egg and larval viability in relation to burden of toxicants.

- Compilation of extensive historical data material on weight at size and condition of cod and sprat from commercial fisheries.

- Exploratory analyses on the spatial and temporal variability of cod fecundity and influencing environmental factors as well as compilation of available data on sprat fecundity.

Task 2: Hydrographic factors influencing the developmental success of cod and sprat eggs and early larvae

- Intensive field programme to determine the distribution, abundance and production of cod and sprat eggs and larvae in different spawning areas throughout the spawning season 1999 in relation to hydrographic conditions.

- Compilation of available time series of cod and sprat egg and larval abundance according to stage/size in different spawning areas.

- Test of applicability of a three-dimensional physical oceanographic model to estimate the amount of advective losses out of the ichthyoplankton survey area.

- Laboratory experiments to determine the duration of egg stages and yolk-sac depletion in relation to temperature as well as mortality and survival rates of eggs and larvae in relation to temperature, salinity (sprat) and oxygen (cod).

- Limits for successful development and impact of sub-optimal but not lethal hydrographic conditions for egg and larval survival based on results from field and laboratory experiments.

- Update of time series of seasonally and spatially dis-aggregated reproductive volumes for cod and test alternative measures describing the ambient conditions for successful egg development.

Task 3: Identification of abiotic and biotic processes influencing the feeding environment, growth, distribution and survival of larval/juvenile cod and sprat

- Intensive field programme in 1999 directed to cod and sprat larvae and juveniles for otolith microstructure and biochemical analyses to resolve birthdate distributions, growth rates and nutritional conditions.

- Laboratory experiments on coupling of cod early juvenile otolith growth and somatic growth rates to develop a reliable growth model.

- Intensive field programme in 1999 on distribution and abundance of zooplankton suitable as prey of cod and sprat larvae and juveniles as well as temporal and spatial overlap between predator and prey.

- Experiments on egg production of different copepod species at varying environmental conditions.

- Compilation of remote sensing data on sea surface temperature.

- Simulations of within and between years variations in primary and secondary production with the FinEst ecosystem model.

Task 4: Modelling the influences of hydrographic/biological processes on the survival, distribution and growth of fish early life history stages

- Development of a preliminary IBM model on early life history stages of cod and sprat with couplings to adult characteristics and stock structure.

- Coupled IBM to 3-D circulation model and to describe the drift and growth of early life stages relative to abiotic and biotic factors.

- Employ 3-D hydrodynamic eddy-resolving circulation models to describe advective exchange of early life stages between the different Baltic cod stocks.

Task 5: Prey/predator interactions and their impact on the dynamics of cod and sprat populations

- Field programme in 1999 on clupeid predation on early life stages of cod and sprat in relation to prey abundance and predator/prey overlap forced by hydrographic conditions.

- Stomach content analyses of sprat and herring sampled within the CORE-project in 1997-1998 and compilation of corresponding historic data material.

- Cannibalism rates of sprat eggs and larvae in comparison to production and abundance estimates.

- Compilation of cod, sprat and herring catch and weight at age in the catch data according to quarter and Sub-division for years presently not covered in the multispecies database, including a revision of data already included in the database.

- Estimation of individual quarterly consumption rates of cod, considering ambient temperature, distribution of predators and predator weight as additional variables.

- Implementation of a practicable tuning procedure into the MSVPA and testing different suitability sub-models and their impact on recruitment estimates.

- Updated MSVPA run covering the period 1977-1998 providing preliminary recruitment, spawning stock sizes and predation mortalities for modelling approaches under Task 6.

- Evaluation of area dis-aggregated MSVPA runs with respect to the impact of drift of pelagic juveniles and spawning migration of adults on recruitment and spawning stock estimates of cod and sprat in various areas of the Central Baltic.

Task 6: Model the combined effects of environmental variability and fishery on cod and sprat recruitment and evaluate the sensitivity and applicability of critical stock limits and biological reference points for fisheries management

- Preliminary assessment of cod egg and larval viability and environmentally related survival probabilities in dependence of maternal characteristics.

- Applications of 3-D circulation models to verify drift patterns of cod early and juvenile life stages from spawning to nursery areas.

- Description of temporal and spatial variability in environmental conditions conducive for cod egg survival and test of preliminary stock-recruitment relationships of cod incorporating environmental variability and spatial heterogeneity.

- Analysis on the stability and sensitivity of single- and multispecies reference points considering multispecies interactions between cod. sprat and herring as well as feed back of sprat and herring prey availability on growth, maturation and recruitment of cod.

APPENDIX 7 LIFECO

Linking hydrographic Frontal activity and ECOsystem dynamics in the North Sea & Skagerrak: Impact on fish stock recruitment. (LIFECO)

LIFECO is a multidisciplinary research program designed to resolve the influence of tidal mixing and shelf break fronts on the recruitment success of North Sea fish stocks.

Co-ordinator : Danish Institute for Fisheries Research (DIFRES), partners:
Institut für Meereskunde an der Universität Kiel (IFM Kiel)
Centre for Environment, Fisheries and Aquaculture Science (CEFAS)
Universität Hamburg (UNIHH)
Department of Geography, University of Bergen (UNIBER)
Institut für Ostseeforschung (IOW)
Institute of Marine Research (IMR)

The objectives are to:

a) Develop environmentally sensitive recruitment models. To do so, LIFECO integrates results from:

- a 3-D coupled bio-physical model (HAMSOM/NORWECOM),
- remote sensing (SEAWIFS ,AVHRR & ENVISAT) with
- field programs and historic databases utilising GIS to :

b) Test the hypothesis that variations in frontal activity influences recruitment of commercial fish stocks via bottom up and top down processes acting on the young of the year.

c) Resolve the importance of hydrographic processes on spatial distribution and feeding interactions of commercial fish stocks, a result of importance for assessment and management strategies.

d) Identify ecological enclaves which will aid in the development of management strategies based on environmentally sensitive areas.

The program consists of 9 Work Packages:

WP1: Advancement of Hydrodynamic Models: Resolution of frontal variability and key forcing processes
WP2: Coupled Bio Physical Modelling: Simulation of lower trophic level dynamics
WP3: Remote Sensing of Frontal Regimes
WP4: Distribution and abundance of plankton and fish relative frontal processes
WP5: Effects of frontal processes in the plankton: resource controls and trophic interactions
WP6: Predatory interaction between fish species and top-down control of zooplankton relative to frontal processes
WP 7: Data Base Assembly
WP 8: GIS and Spatial Data Analysis
WP 9: Synthesis, Scenario and Hypothesis Testing

APPENDIX 8 GLOBAL COMPARISONS OF RECRUITMENT VARIABILITY:

These studies involve comparative and meta-analyses of fish recruitment and ecosystem carrying capacity. Studies include multi-species and multi-population statistical analyses of recruit production across stocks, species and ecosystems. The methods being employed include regression analyses, mixed models and Bayesian approaches. One of the objectives is to compare recruitment variability among stocks and species to identify the relative roles of stock size and environmental variability on recruitment. A second objective is to investigate statistical methodologies for improving parameter estimates in poorly-fitted stock-recruitment relationships. The collaborations involve Prof. Ransom Myers, Killam Chair of Ocean Studies, Dalhousie University, Halifax, Nova Scotia, Canada.

APPENDIX 9 RECRUITMENT VARIABILITY OF FISH AND SHRIMP STOCKS OFF WEST GREENLAND.

This project/programme aim at increasing our understanding of the reproduction and larval ecology of the major fish and shrimp stocks in the area off West Greenland (between 64N and 69N).

In the area of investigation we observe marked frontal zones between major currents running along the shelf slope, and assemblages of fish and crustacean offspring are found in the vicinity of these fronts.

The objectives of the project are to:

1. Describe linkages between frontal hydrography and the plankton/nekton drift and migration

2. Ascertain larval growth and mortality in relation to prey and predator abundances.

3. Evaluate the importance of hydrographic variability on the planktonic ecosystem in general and specifically on the recruitment to commercially important fish and shrimp stocks.

The project is co-ordinated between research institutes in Greenland and Denmark, and is supplemented with international co-operation on specific topics.

APPENDIX 10 REFERENCE GROWTH CURVES

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[1] Department of Marine Biology and Fishieries, University of Bergen, Bergen, Norway

Folkvord presented the updated results on the work on reference growth curves (see ICES CM 1999/C:2 report for further details).

An individual-based model of growth processes (encounter rates, ingestion, assimilation and metabolism) in herring larvae has been developed. The model consolidates existing models on single processes and new experimental results on how temperature and food supply influence growth and survival (starvation) in this species. Environmental forces like wind (small-scale turbulence), light, turbidity, temperature, prey-density and -size structure, and intrinsic biological variables like larval size, ontogeny (prey capture- and visual capabilities) and starvation (point of no return) are all included in the model. A period just after yolk absorption is recognised when the larvae are particularly vulnerable to reduced food concentrations. Lack of food during this period may limit the development of the visual system and thereby the ability to detect and catch prey. Both experimental results and the simulations demonstrate the integrated effects of prey density, larval development and seasonal progression on growth processes. The growth difference between spring- and autumn- spawned larvae is suggested to be a result of seasonal variations in irradiance. Sensitivity analyses of parameters and submodels are performed.

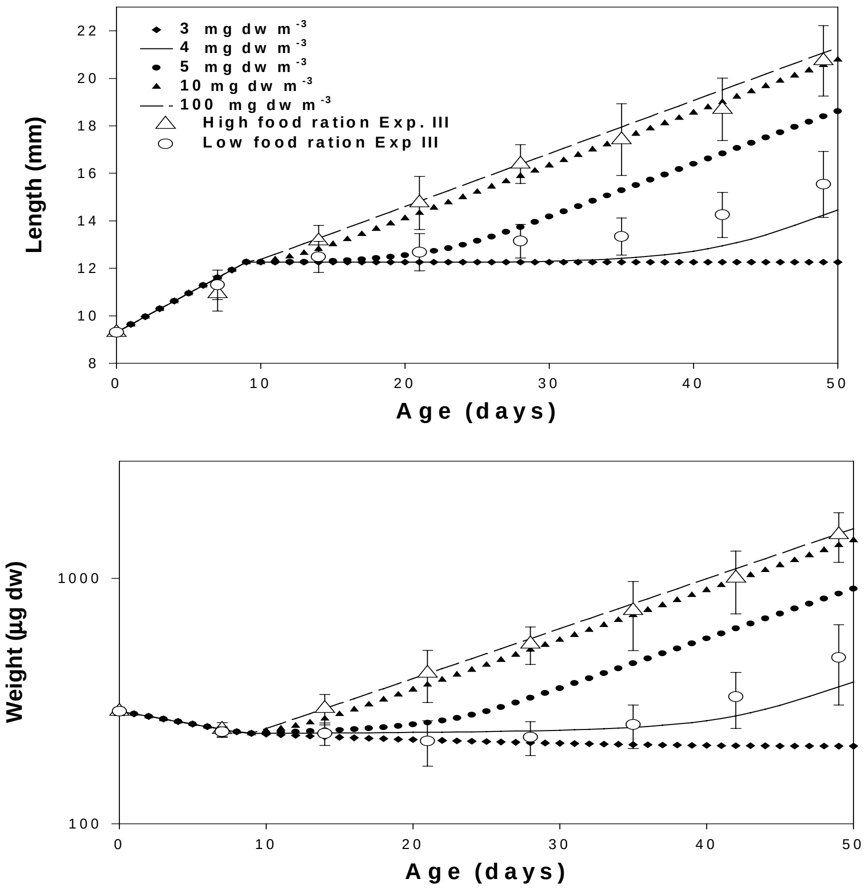

Figure 1. Simulations of growth (upper panel: length; lower panel: weight) of herring larvae at 6 ºC, in a range of food densities (3 – 100 mg dw m^{-3}). The data from Exp. III are included in the plots. The simulations are made at 10 m depth, starting at day of the year = 105, which correspond in time with the experiments

References

Fiksen, Ø. and Folkvord, A. 1999. Modelling growth and ingestion processes in herring larvae (*Clupea harengus* L.) . Marine Ecology Progress Series, 184:273-289.

Otterlei, E.; Nyhammer, G.; Folkvord, A., and Stefansson, S. O. 1999. Temperature and size dependent growth of larval and juvenile cod (*Gadus morhua* L.) - a comparative study between Norwegian coastal cod and Northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences, 56:2099-2111.

APPENDIX 11 PRELIMINARY INVESTIGATIONS INTO THE GROWTH RATES OF 3 MONTH OLD WHITING IN THE IRISH SEA IN 1997 AND 1998

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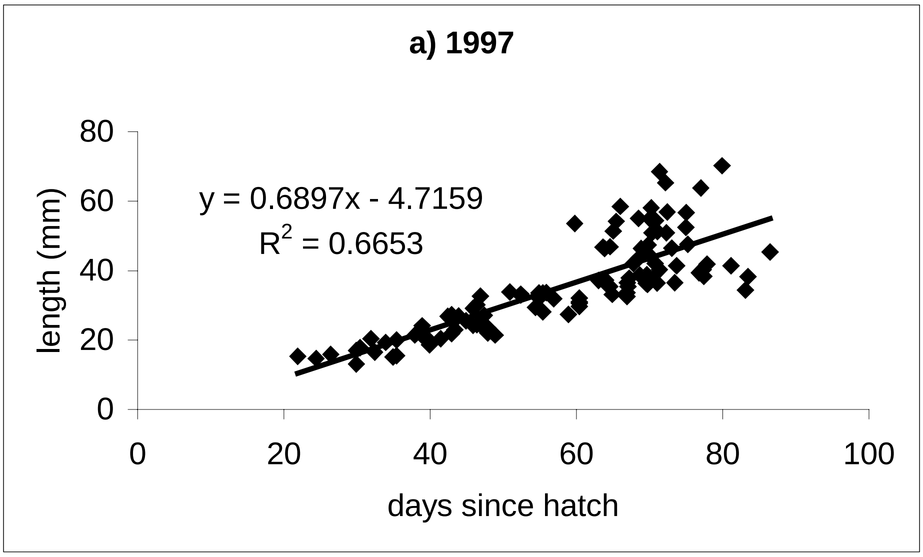
[1] DANI, Belfast, Northern Ireland

Preliminary investigations into the growth rates of 3 month old whiting in the Irish Sea in 1997 and 1998.

The Department of Agriculture and Rural Development (NI) carries out surveys of the abundance and size of pelagic juvenile gadoids in the western Irish Sea every summer. The most common gadoids in the samples are whiting. A study was instigated into the interannual difference in growth rate of pelagic juvenile whiting (*Merlangius merlangus* L.).

Studies on laboratory reared larvae showed that whiting, up to 40 days old, generally deposit one primary increment per day. Counts of increments from whiting caught in 1997 and 1998 showed that the juveniles were growing at approximately 0.7mm per day (Figure 11.1). There was no significant difference between the growth rates in the two years. However the level of scatter in size at age appeared to increase in whiting over 60 days old (Figure 11.1). The sample sizes of the study were really too low to investigate birth date distributions, but most of the fish caught seemed to have hatched in the first three weeks of April (Figure 11.2). The low sample sizes were due to problems in reading otoliths from some of the wild caught whiting. Further work is proposed to address this problem.



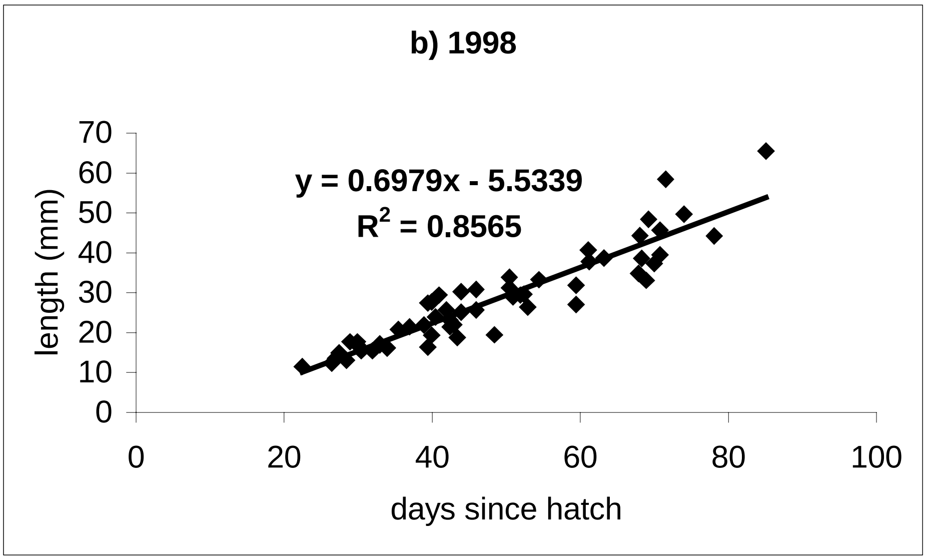


Figure 11.1. Length at age of western Irish Sea whiting. Samples collected in 1997 and 1998.

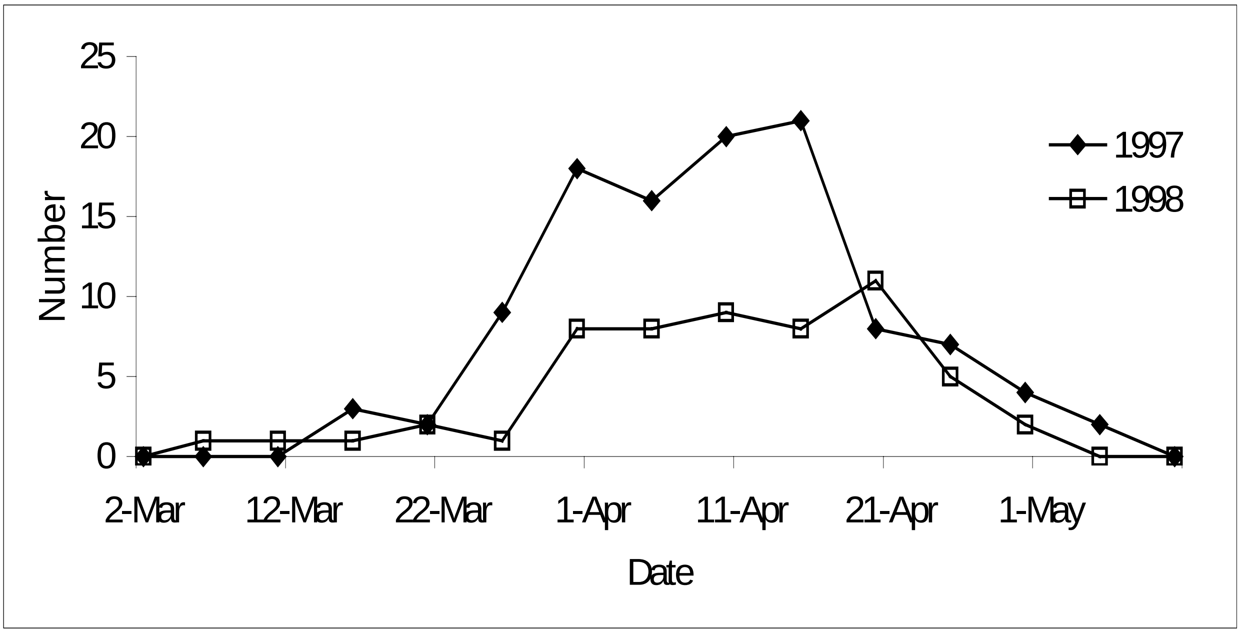


Figure 11.2. Hatch date distributions whiting caught in May and June of 1997 and 1998 in the western Irish Sea.

APPENDIX 12 THE ROLE OF MEASUREMENT ERROR IN THE INTERPRETATION OF GROWTH INCREMENTS FROM OTOLITHS

P. Pepin
Northwest Atlantic Fisheries Centre, St. John's, Canada

We investigated the patterns of variation in otolith increment widths in larvae of radiated shanny (*Ulvaria subbifurcata*) to establish how measurement error contributes to the general distribution of observations; how measurement error influences our ability to detect variations within and among individuals; and how an individual's history affects our ability to detect the influence of changes in the environment that can influence growth rates.

Increments of radiated shanny are approximately 1 Φm in width for the first 10 days after hatch after which their average size increases with age (Figure 12.1). There is considerable scatter among individuals which tends to increase in direct proportion to the mean resulting in a constant coefficient of variation in increment width with age (Figure 12.1). Measurement error of increment widths was not independent of age (Figure 12.2) Although the mean difference between first and second measurements was not substantially different from zero, the variance in absolute error was relatively constant until the 15^{th} increment after which it increased due to decreasing sample size.

Increments widths within an individual radiated shanny larva are not independent. The level of serial autocorrelation in increment widths is not independent of age (Figure 12.3). When viewed relative to the maximum expected correlation, the pattern of serial autocorrelation changes substantially (Figure 12.4). First, it is not possible to detect any external influence on increment widths for about three days because growth patterns appear to be regulated by internal dynamics which reflect the history of an individual larva. Second, the level of residual autocorrelation is substantially greater than observed if measurement error is not taken into account. However the pattern of age dependence still remains with early increment widths being less correlated with subsequent ones than in older ages (Figure 12.4).

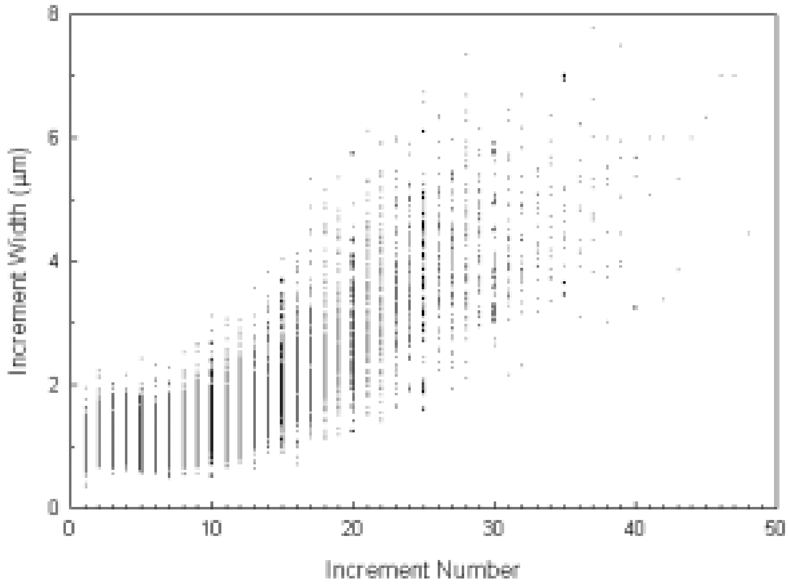


Figure 12.1 Increment width in relation to increment number of larval *Ulvaria subbifurcata.*

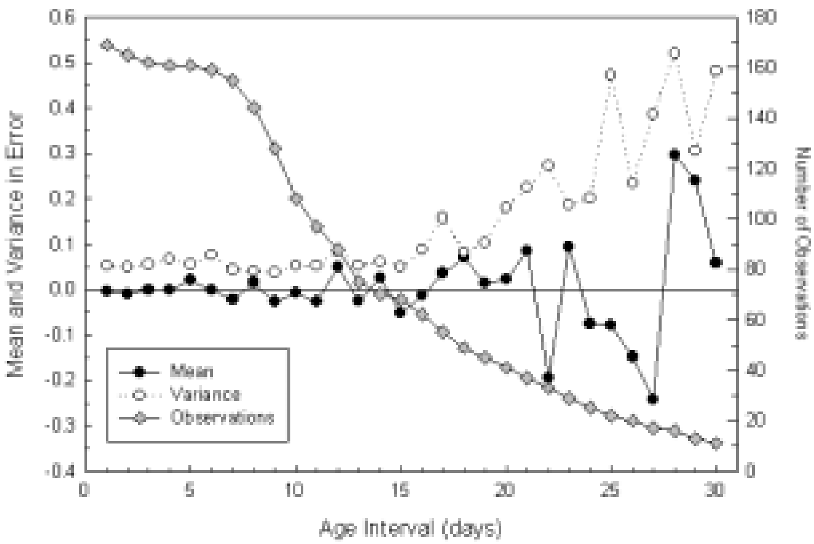


Figure 12.2 Measurement error, variance and number of observations, based on repeated observations by a single reader.

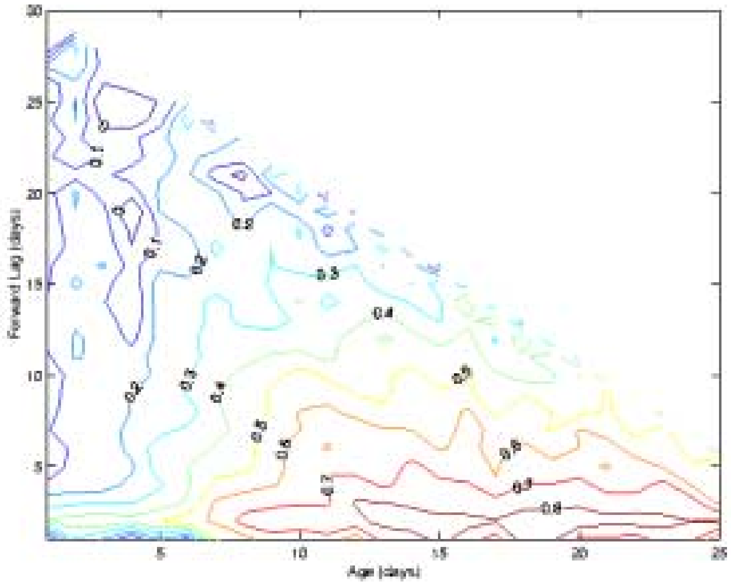


Figure 12.3 Contour diagram of serial forward correlation (Pearson product moment) of increment width in relation to age for larval *Ulvaria subbifurcata*.

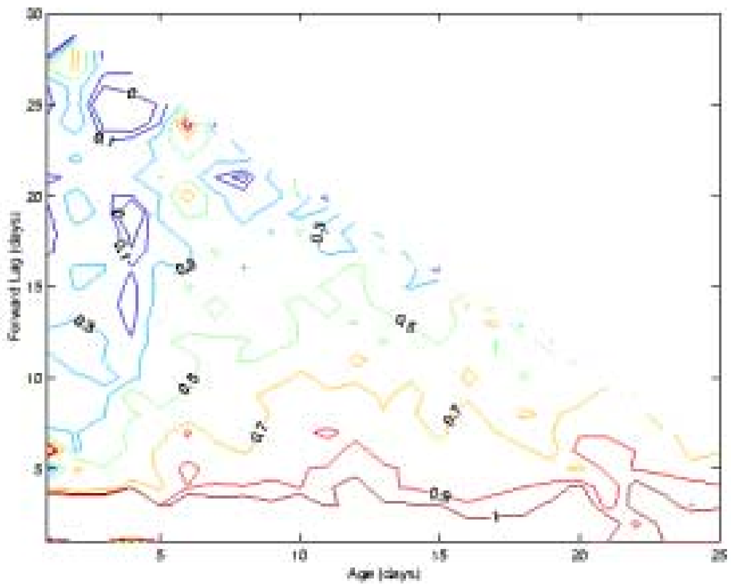


Figure 12.4 Contour diagram of the ratio of serial forward correlation if increment width relative to the expected maximum correlation after taking into account the variance attributable to measurement error.

APPENDIX 13 FEEDING BY A LARVAL FISH COMMUNITY: IMPACT ON ZOOPLANKTON

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[1] Northwest Atlantic Fisheries Centre, St. John's, Canada

This study estimated the seasonal pattern of daily consumption of zooplankton by an ichthyoplankton community consisting of 11 species of larval fish. Data from a previous study is used to take into account size- and species-dependent prey selection patterns (Pepin & Penney 1997). Fish larvae and zooplankton was sampled fortnightly from late May until late September in 1985 and 1986. Sampling was conducted to cover the entire diurnal feeding cycle although logistic constraints prevented us from covering a complete diurnal cycle during a single sample day. We therefore combine all samples from different sampling dates to estimate the diurnal feeding pattern.

The distribution of stomach contents showed a skewed distribution, approaching a log-normal, at all times and for all species. The gut fullness index (*GFI*) varied diurnally, with gut fullness showing a marked increase late in the afternoon or in the early evening in 10 of 11 species and reaching a peak around midnight. Using a gut evacuation rate of 0.5 h^{-1}, our estimates of weight-specific ingestion rates indicate that despite decreases in *GFI* during the day (opposite in *T. adspersus*) feeding by the larval fish population continues throughout the day to some degree (median~1-2% of body weight per hour) (Figure 1). When integrated over a complete diurnal cycle, the average larva ingests between 15 and 150% of its body weight, depending on the species (Figure 5). Most species ingest 30-70% of their body weight daily whereas *Clupea harengus* and *Mallotus villosus* ingest an average of 15% of their body weight. *Pleuronectes americanus* ingests approximately ten times that amount. Sensitivity analysis revealed that estimated consumption rates of each species increased by about 50% if the evacuation time was reduced to 3 hours (k = 0.99 h^{-1}), and decreased by 27% if evacuation times were increased to 8 hours (k = 0.37 h^{-1}).

There was relatively little change in the size distribution of available prey for fish larvae from May to September although larger size categories were somewhat less abundant in May (Figure 2). The overall impact of the ichthyoplankton community on zooplankton abundance was negligible: generally less than 0.1% of the zooplankton, of any size category, was consumed by the entire larval fish community on any given day (Figure 2). The seasonal pattern in total prey consumption mimics the seasonal changes in overall biomass of larval fish. There was a seasonal progression in the size category of microzooplankton which was most heavily preyed upon by the larval fish community, moving from 100 µm in May to 200 µm in September. There was almost no impact on size categories of zooplankton greater than 350 µm in width until July, when larger fish larvae begin to appear in the community.

References

Pepin P, Penney R W (1997) Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? J Fish Biol 51 (Suppl. A): 84–100.

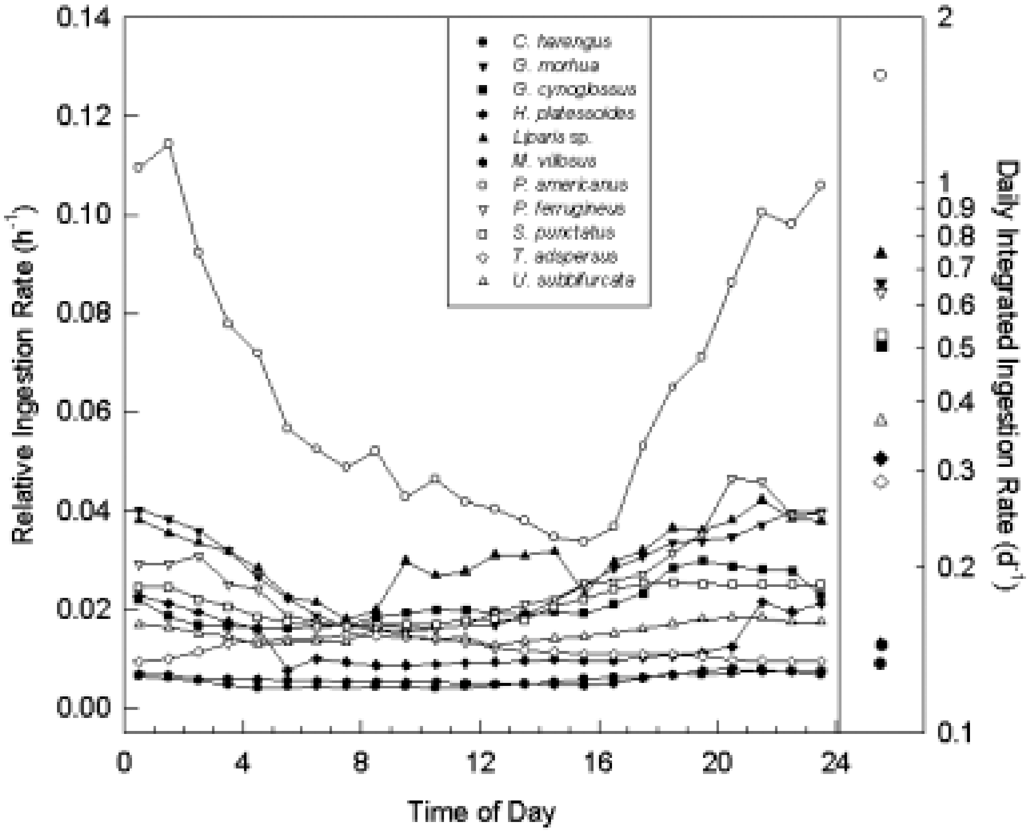

Figure. 1. Median relative hourly weight-specific ingestion rate for the 11 species of fish larvae. The scale is shown on the left-hand axis. Points at the extreme right of the graph show is the integrated daily median weight-specific ingestion for the 11 species. The scale for this information is shown on the right-hand axis.

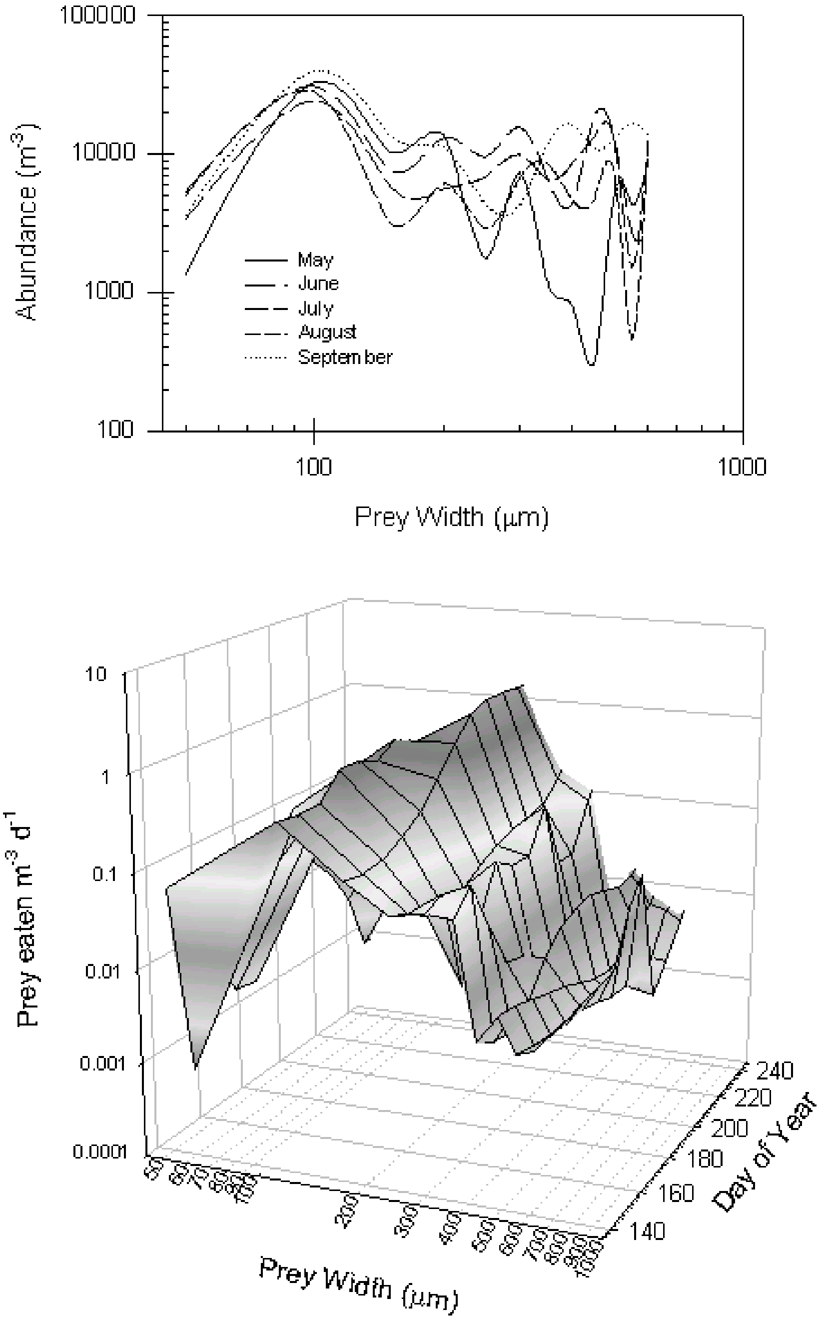

Figure 2. Monthly pattern of abundance of the dominant groups of microzooplankton prey available to fish larvae in relation to their width (upper panel) and the cumulated daily impact of the larval fish community (lower panel).