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Recruitment Processes

OVERVIEW OF THE EU FAIR PROJECT "STEREO" (STOCK EFFECTS ON RECRUITMENT RELATIONSHIPS)

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ABSTRACT

The overall objective of the STEREO project is to improve the methodology for determining limit reference points for the biomass of exploited fish stocks. Limit reference points set boundaries which are intended to constrain harvesting within safe biological limits, and are integral components of the decision making process in fisheries management. In most cases limits are currently estimated from historical time series data on spawning biomass and recruitment. However, the underlying stock-recruitment relationship is often poorly defined by such data and hence there is considerable uncertainty around many reference limits. This project will produce an operational scheme for refining functional form of stock-recruitment relationships by incorporating biological, spatial and temporal information on the stock structure, with the aim of reducing the uncertainty associated with the derived limits. The methodology will be developed for cod and haddock stocks around Iceland, Norway and in the North Sea as case studies.

BACKGROUND

A consortium of partners (Marine Laboratory Aberdeen; Institute of Marine Research, Bergen; Marine Research Institute, Iceland; and the Danish Institute for Fisheries and Marine Research) conducted a project entitled "Recruitment processes in cod and haddock: Developing new approaches" between 1 January 1996 and 31 December 1997, with funding from the EU FAIR programme (FAIR-CT95-0084). An expanded consortium then submitted a further funding proposal "An operational model of the effects of stock structure and spatio-temporal factors on recruitment", or STEREO ("Stock effects on recruitment relationships"), which commenced in December 1998 (FAIR-CT98-4122). This presentation will give an overview of the outcome of the former (1996-1997) project, and the workplan and objectives of STEREO.

OUTCOME OF THE 1996-1997 PROJECT

Objectives

The overall objective of the 1996-1997 project was to evaluate methodologies for partitioning sources of variability in gadoid recruitment between effects due to spawning stock structure (ie age composition, spatial distribution) and those due to the environment. This represents a significant advance on earlier approaches which have focussed on single classes of processes. The approach to this problem was twofold:

- Develop an environmental survival index, based on sound understanding of processes, so that a more realistic specification of the statistical error distribution about stock recruitment relationships can be provided.
- Establish the importance of the structure of the spawning stock, by accounting for the non-linearity between stock biomass and viable egg production, thereby allowing an examination of the potential value of manipulating stock-structure to reduce the probability of low recruitment.

To achieve this the project has developed a conceptual framework within which the following specific objectives are addressed through a combination of field measurements, studies in mesocosms and the laboratory, and modelling:

- determine the relationship between spawning stock structure and the timing, duration and amplitude of egg production;
- determine the relationship between female age, size and condition and the viability of eggs and larvae;
- determine the relative contribution of the various components of the annual egg production to the surviving population of pelagic juveniles;
- determine the relationship between larval growth rate and survival;
- determine the environmental factors which influence individual growth rate and derive a suite of environmental parameters which could provide an index of their contribution to year-class survival;
- evaluate methodologies for coupling environmental indices of survival to data derived on the effects of stock structure, so that their relative importance can be evaluated.

Introduction and Rationale

Gadoid fish produce very large numbers of eggs per individual, and only a small proportion survive to recruit to the adult stock. In the case of most NE Atlantic gadoid stocks the relationship between the abundance of the spawning stock and subsequent annual recruitment is generally obscured by a combination of factors. These include environmental effects on the survival of eggs and larvae and the use, for lack of alternative information, of spawning stock biomass as an index of the reproductive output of the adult population. Environmental factors exert strong control over the mortality rates of eggs and larvae, possibly through starvation but also through the dynamics of predator populations. At the same time, the survival of larval fish is linked to their growth rate. In general, the survival of fast growing individuals over a growth interval, will be higher than that of slow growing individuals. With regard to the reproductive output from the spawning population, egg production per unit biomass varies with the size, age and condition of the females, and so changes in the population structure associated with exploitation and annual differences in year-class strength are likely to have a major effect on population fecundity. These effects are not taken into account by conventional analyses of stock-recruitment relationships.

The aim of the project has been to establish the priorities and develop methods for investigating recruitment mechanisms in gadoid species, focussing on Icelandic and Norwegian cod stocks and North Sea haddock. The eventual aim is to be able to disaggregate the effects of changes in spawning stock structure on stock-recruitment relationships, from effects due to the environment. This is an important goal because it has the potential to significantly reduce the uncertainty in the models currently used to assess the sustainability of fisheries.

The key findings of the project are:

- The timing and distribution of spawning activity in both cod and haddock populations studied is strongly related to the age and size composition of the adult stock;
- The size and viability of larvae is strongly related to the size of eggs, which is in turn related to batch number, size and spawning history of the adult females;
- For North Sea haddock, the juvenile fish surviving to the demersal phase in August were not drawn at random from the annual egg production by the adult stock. In 1996, spawnings in early April contributed a disproportionate number of recruits;
- A patch tracking study of larval haddock growth and survival showed that hatch date, rather than short term variations in environmental conditions contributed most to the variability in individual growth rates, and hence to survival. The fastest growing individuals in the study were from spawnings in early April;
- Laboratory experiments showed that signatures of diet composition and feeding rate of reared cod and haddock larvae can be detected in the biochemical composition of individuals. However, there was little relationship between these indices and temporal variations in environmental conditions during the patch tracking study in the North Sea. Larvae appeared to be feeding maximally under the range of conditions encountered during the study;
- Turbulence regimes, representative of those encountered in the field can be generated artifically in mesocosms. Protocols for conducting experiments on the effects of turbulence on larval fish feeding and growth have been developed. However, simulation modelling indicates that current theory is not sufficiently robust to predict the consequences of such experiments;
- Strategic modelling of the interaction of growth and mortality rates for the composition of larval fish populations shows that short-term variability in growth rates can significantly modify, and in some cases mask, the outcome. These results were partly confirmed by rearing experiments in mesocosms. No relationship between growth and mortality rates could be detected in the results from the patch tracking study on larval haddock;
- Modelling predictions of the most favourable hatch-sites for subsequent growth of larval cod and haddock in the North Sea matched closely with the observed distributions of eggs of the two species;
- The project has deveoped a strategy for integrating models of egg production by cod and haddock spawning stocks with bio-physical models of egg and larval dispersal and survival, to produce a system capable of evaluating the relative contributions of stock structure and environmental effects on recruitment.

Summary of results

Maternal Effects and Egg Production

Samples of cod were obtained from four areas in Icelandic waters (two offshore and two inshore) and of haddock from two areas in the North Sea. Potential fecundity and the incidence of pre-ovulatory atresia were measured by a variety of methods. Data on atresia allow estimation of the proportion of potential egg production which is resorbed by the ovaries rather than being shed.

This study provides the first estimates of potential fecundity in Icelandic cod since 1967. The new estimates are significantly higher than those from the earlier period for fish of equivalent size and age, possibly reflecting unfavourable environmental conditions and presumably low food levels during the late 1960's. This is especially true for the older fish in the population. Relative fecundity was shown to increase with age and size of cod and to be influenced by liver condition. This study has also been the first to estimate the realised fecundity of haddock, ie the number of eggs that are actually spawned as opposed to the number of oocytes present in the ovaries of the female stock. Age, size and spatial differences were demonstrated for the North Sea populations.

The study indicates that size and age-specific differences in reproductive development are important for protracted spawning. Results from the comparison of size and age of mature females suggested that in both cod and haddock the largest females begin spawning first. In haddock, but not in cod, the age of females also seems to be related to the onset of spawning, the older females tending to begin spawning earlier than young ones. The duration of spawning also appears to be related to size and age. In Iceland, the size of eggs produced by the spawning population decreased as the season progressed. This effect was most pronounced in the larger females in the population. In addition, female body size and egg diameter were directly related.

Detailed laboratory and mesocosm studies on the characteristics of eggs and larvae in relation to female attributes found initial batches of eggs from repeat spawners were larger than those from recruit spawners, but eggs in the final batches were the same size. The dry weight of larvae decreased with batch number, and was independent of previous spawning experience. Viability and swimming activity of larvae decreased with batch number for recruit spawners but not for repeat spawners, but feeding incidence and growth rates of larvae were not related to batch number.

Field and Laboratory Studies of Larval Growth and Survival

The range of birth dates estimated by back calculation from otolith ring counts of both pelagic and demersal juvenile haddock sampled in the North Sea showed temporal differences in survivorship with most of the surviving demersal juveniles in August originating from spawning in early April. The environmental basis for variability in the survival rate of gadoid larvae was investigated during a drift tracking study of a patch of larval North Sea haddock to the east of the Shetland Islands during May 1996. The patch of larvae was tracked for around 10 days during which sampling was carried out on a 6 h schedule. A wide range of meteorological conditions were encountered during the study, which coincided with the onset of the spring phytoplankton bloom. Analysis of the microstructure of otoliths removed from larvae failed to show a consistent relationship between individual daily growth rates and short term (day-to-day) variability in environmental factors such as food concentration and turbulence. However, there was strong relationship between individual growth rate and birthdate, with later spawned individuals in the tracked patch having higher growth rates. Time series data on the vertical distribution of haddock larvae showed a strong tendency for the larvae to aggregate in mid-water (25-50 m depth). During daylight there was a slight movement of the population towards the surface, whilst the population was distributed deeper in the water column at night. For the largest size groups of larvae, this behaviour was modified by wind induced turbulence. During calm periods the larvae ascended closer to the surface during daylight than during windy periods.

A range of individual-based biochemical parameters were measured on haddock larvae collected during the drift study, and laboratory calibrations of these parameters were carried out on reared cod and haddock larvae. The laboratory studies showed that differences in food abundance have a significant effect on lipid-based condition indices in early larval haddock. However, free fatty acid levels in larval cod were found to be insensitive to short-term variations in food abundance, rendering them unsuitable for application as short-term indicators of food consumption. Tryptic enzyme activities and gut fullness indices for haddock larvae captured during the field programme showed that feeding incidence was generally high but varied strongly according to a diel cycle. Day-to-day variations in tryptic enzyme activity were only weakly related to prey concentration and turbulent dissipation rates. Similarly, RNA/DNA ratios suggested that growth rates were generally not, or only weakly, related to either food concentration or turbulence during the 48 h prior to capture. However there were large variations in RNA, protein and lipid content between individual haddock larvae of the same length, indicating wide variability within the population in growth, condition and the ability to survive stressful conditions (eg low food abundance, attack by predators). Some of this variability can be attributed to the diet composition of the larvae since those individuals having a high proportion of lipids characteristic of diatom dominated food chains were in better condition (more lipid per body mass) than those with a high proportion of dinoflagellate tracer lipids. Overall, it seems that the growth of the haddock larvae in the patch was in general not limited by food, which was available in excess in the water column. Thus, short-term variations in turbulence and plankton concentration were not strongly reflected in otolith growth or the biochemical indices of growth.

Modelling

The modelling aspects of the project have been on two levels. Firstly, strategic individual based modelling was used to explore the interaction between growth-dependent mortality and short term variability in the growth rate of larvae, and the effects of turbulence on prey capture. Secondly, a spatially resolved individual based model of the dispersal and growth of cod and haddock larvae was developed for the North Sea.

The strategic modelling of growth-dependent mortality showed that linkage between growth rate and mortality rate has the power to substantially affect the composition of the surviving population. However, some conditions of fluctuating environmental conditions, leading to fluctuating growth rates, could mask these effects. Data to test the conclusions were obtained during mesocosm experiments on cod larvae carried out in Norway. Replicate mesocosms were maintained under different feeding regimes and the otolith microstructure of the surviving populations analysed at various stages. The results show that under high ration regimes the survivors in the population are drawn from the fastest growing components of the initial population. However, under low ration conditions the surviving population appeared to be drawn at random (with respect to daily growth rate) from the initial population.

The prey capture modelling showed that whilst turbulence in the water column can enhance the rate of encounter between larvae and their prey, the same factor can have a detrimental effect on the success of capture. Conclusions as to the response of larvae to turbulence are critically dependent on assumptions about the prey capture process, and to the representation of turbulent velocity structure in the model. The latter aspect was investigated during a series of mesocosm experiments during the project, in which the statistical structure of turbulence generated in enclosed systems was measured by various instruments.

The spatially resolved modelling concentrated on the population dynamics of cod and haddock larvae in the North Sea. A particle tracking scheme, with water flow and temperature inputs from a hydrodynamic model of the NE Atlantic, was coupled to a simple representation of individual growth in the larvae. The objective was to determine the hatching origin of larvae with the highest probability of survival under climatological mean conditions. The results showed that haddock larvae hatched on the outer continental shelf early in the season (late March) had a higher probability of survival than those hatched in the North Sea. However, as the season progressed through to May, the distribution of favourable hatch sites moved into the North Sea. A similar seasonal shift in the distribution of most favourable spawning areas occurred for cod. Comparison of the modelled distributions of favourable hatch sites showed a strong correlation with both the spatial and temporal distributions of spawning activity by haddock and cod stocks.

Overall conclusions

At the simplest level, the project has exposed the complexity underlying the relationship between spawning stock biomass and recruitment. This has long been recognised, but uniquely, this project has simultaneously addressed the problem both from the perspective of the adult stock and the survival of larvae. Usually, such projects focus only on environmental considerations. The scope for recruitment variability due to the age and size composition and condition of the maternal stock seems greater than has previously been appreciated.

The integration of observational, experimental and modelling skills in the project has been particularly fruitful. An important development has been a framework for modelling the annual egg production by a fish stock, from routine assessment data supplemented with measurements of key biological parameters. The rationale for this model effectively synthesises the understanding of cod and haddock reproductive biology accumulated during the project. However, the key development has been the realisation that the surviving juvenile population at recruitment is not drawn at random from the initial egg stock. This has been clearly demonstrated by the field programme on North Sea haddock, where the survivors originated mainly from a restricted temporal component of the annual egg production. It is clear from this work, and from the modelling studies, that spatial, temporal and maternal factors can all confer enhanced survival probability on eggs and larvae. As a result, the surviving juveniles can potentially originate from distinct subsets of the spawning distribution under given climatic and stock composition scenarios. This conclusion has major implications for the way in which the sustainability of fisheries is evaluated, and for the implementation of conservation measures. The developments produced by the project should provide a platform for incorporating these concepts into future fisheries management.

OVERVIEW OF THE STEREO PROJECT

Summary

The overall objective of the STEREO project is to improve the methodology for determining limit reference points for the biomass of exploited fish stocks. Limit reference points set boundaries which are intended to constrain harvesting within safe biological limits, and are integral components of the decision making process in fisheries management. In most cases limits are currently estimated from historical time series data on spawning biomass and recruitment. However, the underlying stock-recruitment relationship is often poorly defined by such data and hence there is considerable uncertainty around many reference limits. This project will produce an operational scheme for refining the functional form of stock-recruitment relationships 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 is being developed for cod and haddock stocks around Iceland, Norway and in the North Sea as case studies.

The approach is 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.

Demonstration and testing of the operational system is to be accomplished by hindcasting the histories of effective reproductive output for cod and/or haddock stocks in the northern North Sea and at Iceland. These derived data will be used as substitutes for the spawning biomass term in stock-recruitment relationships. Confidence intervals around reference limits based on the new relationships will be then be compared with those based on the conventional analysis of stock-recruitment data.

Work Content

The objective is to build a 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 system is being developed for application to cod and haddock stocks, but must in principle be sufficiently generic to permit tailoring to other species.

The structure of the system comprises 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 system 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 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 seven 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.

<u>Model development</u> 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 parameteriesed 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.

<u>Supporting initiatives</u> 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.

<u>Data assimilation</u> 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.

<u>Regional implementations</u> 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.

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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.