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Report of the

Study Group on Incorporation of Process Information into Stock Recruitment Models

Lowestoft, UK
14–18 January 2002

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 INTRODUCTION

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1.2 Terms of reference

The **Study Group on Incorporation of Process Information into Stock Recruitment Models** [SGPRISM] (Chair: C. O'Brien, UK) met in Lowestoft, UK from 14–18 January 2002 to:

a) further consider the two case studies (North Sea cod and Bay of Biscay anchovy);

b) further develop the modelling and testing of process and recruitment relationships for incorporation into management procedures;

c) identify the sources of data necessary for the determination of the reproductive potential of fish stocks and specify a protocol for their collection within existing co-ordinated surveys.

SGPRISM will report for the attention of the Oceanography and Resource Management Committees. The report will be brought to the attention of the Working Group on Recruitment Processes.

1.3 Scientific justification for the Study Group

The relationship between spawning stock and recruitment is fundamental to the scientific approach to fisheries management. Considerations of environmental factors can make a difference to how one might manage a stock. Simulation models can play an important role in helping identify whether and where benefits to management are most likely to accrue and therefore where it would be best to focus attention in terms of other (e.g., process) studies. Results from simulation studies should be used to guide biological studies. Short-term focused studies aimed at identifying likely mechanisms are also crucial, but results from such studies can only be put to full use with information from longer-term observations. There is also benefit in long-term studies of the environment and underlying processes so that one is prepared if something unexpected happens. For example, if a process study reveals a strong relationship with some environmental variable, then it would be possible to incorporate this immediately if historic data are already available.

The Study Group has afforded an opportunity for biologists and stock assessment practitioners to meet under a common theme and to begin the much needed process of integrating biological knowledge and stock assessment methods/techniques.

The first meeting of the Study Group (ICES 2000a) had concentrated mainly on environmental issues as drivers of recruitment variability; whilst the second meeting jointly considered possible environmental and biological causes for recruitment fluctuations (ICES 2001a). Whilst the Study Group had addressed its terms of reference at both meetings, it was felt that much work still remained to be undertaken and that a third, and final, meeting should be held.

1.4 Structure of the report

The terms of reference (ToR) are addressed within the four main sections of the report. Specifically, ToR a) is addressed within Sections 2–5 of the report, ToR b) is addressed within Sections 3 and 5, and ToR c) is addressed in Section 2.

For a given level of spawning stock biomass there is often considerable variation in recruitment. This variation is frequently attributed to environment effects on survival. However, there is increasing evidence that the age, size and spatial structure of the spawning stock and the physiological condition of spawners can influence the number of surviving recruits (ICES 2001a). Section 2 of this current report reviews approaches for quantifying the reproductive potential of individuals and stocks; building on the work of a recent NAFO Scientific Council Working Group on Reproductive Potential (BD1).

In Section 3, a limited number of area-based case studies are presented that illustrate a sequential introduction of biological processes into estimates of stock biomass. Recruitment is viewed from both a biological and a stock assessment perspective. Potential impacts of spawning characteristics on reference points for fishery management are reviewed and discussed in the context of the Precautionary Approach (PA). Results from a modelling of the effects of environment variability on North Sea cod are presented in Section 4, together with the investigation of model-diagnostics and a temperature-induced characterisation of the weight-at-age relationship. Data for North Sea plaice were also examined in parallel to investigate systematic changes in condition factor.

The further development of stock assessment software tools, as proposed by the ICES Working Group on Methods on Fish Stock Assessments [WGMG] (ICES 2002c), is discussed in Section 5 in the context of the WGMTERM software for medium-term projections. Time series characterisations of historical weight-at-age are presented for a selection of North Sea stocks, including North Sea cod. A model of spawning-stock structure in Northeast Arctic cod is presented to investigate those components of the spawning population, which have had the greatest influence on subsequent recruitment. The model was applied during this meeting of SGPRISM to North Sea cod and herring, in order to ascertain its general applicability and whether it would be beneficial to use it more widely.

Further work and the relevance of the Study Group to similar activities within ICES and NAFO are discussed in Section 6.

The low accuracy of the environmental indices as recruitment predictors makes it impossible at present to estimate the population abundance one-year in advance (ICES 2000a; ICES 2001a; ICES 2002b). Therefore any use of those indices is postponed so far for the provision of forecast advice to managers until better predictive power of the environmental stock-recruitment models is achieved. At a recent meeting of the SPACC/IOC Study Group on the Use of Environmental Indices in the Management of Pelagic Populations (Cape Town, South Africa, 3–5 September 2001), it was proposed that a simulation analysis be conducted to evaluate the benefits of using environmentally linked recruitment predictors in the management of anchovy stocks. This work will be conducted later in 2002 and the results will be pertinent to ICES.

2 REPRODUCTIVE POTENTIAL

2.1 Introduction

The stock-recruitment (S-R) relationship assumes that spawner biomass (SB) is directly proportional to the reproductive potential of the stock, i.e., that the relative fecundity (number of eggs produced per unit weight) of the stock is constant both temporally and spatially. This assumption has long been recognized as invalid (Oosthuizen and Daan 1974; Ware 1980), however, until recently there has been no concerted effort directed towards replacing SB with more sensitive measures of reproductive potential.

In the case of Atlantic cod processes such as skipped spawning and/or atresia (Kjesbu *et al.* 1991; Witthames and Greer Walker 1995; Ma *et al.* 1998; Marshall *et al.* 1998; Bromley *et al.* 2000; Rideout *et al.* 2000) contribute to the lack of proportionality between total egg production and SB over time. As both responses are observed in poor condition fish, a high degree of interannual variability in food abundance and condition are likely to increase the divergence between reproductive potential and SB. Reproductive potential is also affected by shifts in size composition because large/old spawners have higher relative fecundities than small/young spawners (Marshall *et al.* 1998; Marteinsdottir *et al.* 2000). The progressive loss of large spawners in stocks experiencing sustained high fishing mortalities (Trippel 1999) can therefore reduce the total egg production disproportionately to the reduction in spawner biomass.

As a result of increased knowledge of variability in relative fecundity of individuals and stocks, the S-R relationships for several stocks are being re-evaluated using alternative indices of reproductive potential. The approach taken to re-estimating reproductive potential varies according to the type of data available. A limited number of stocks have fecundity data that is being used to hindcast potential total egg production by the stock (Köster *et al*. 2001d, Marshall *et al*. WD9). Bioenergetic approaches to quantifying the reproductive potential of stocks have also been developed (Painting *et al*. 1998; Henderson *et al*. 2000; Marshall *et al*. 1999, 2000). These take advantage of historical databases derived from industrial sources (e.g., liver condition, oil meal ratios). Long time series describing spawner condition have also been used as proxies for the reproductive potential of individual spawners (Marshall and Frank 1999; Blanchard 2000). Basic demographic data (e.g., numbers-at-age) have been used to construct age diversity indices that can potentially be used as simple proxies for reproductive potential (Lambert 1990; Marteinsdottir and Thorarinsson 1998; Secor 2000).

Stocks span an information gradient in the sense of having variable quantities of biological data that are relevant to estimating stock reproductive potential (Figure 2.1). In the worst case, reproductive potential is quantified by using time-invariant maturity- and weight-at-age values to estimate spawner biomass. These estimates are driven solely by variation in spawner quantity. Incorporating year-specific values for maturity- and weight-at-age increases the sensitivity of spawner biomass to the effect of interannual variation in growth and condition on reproductive potential. Incorporating year-specific fecundity information into estimates of reproductive potential (e.g., total egg production) can also increase the sensitivity of estimates (Armstrong *et al*. WD7). Ongoing research is being undertaken with the goal of incorporating interannual differences in egg quality, egg mortality (e.g., predation) or spatial/temporal origin of eggs.

To provide an overview of available information and data resources the NAFO Working Group on Reproductive Potential is compiling tables summarizing the available data and data sources for selected stocks within NAFO and ICES jurisdictions'. These tables will soon be available, both through the NAFO website and in the *Journal of the Northwest Atlantic Fishery Science*. The tables for Northeast Arctic cod (Appendices A-D) and North Sea cod (Appendices E-H) are included in this report to illustrate the range of data available for data-rich and data-poor stocks, respectively. The analytical assessment is providing basic data about stock size (total abundance) and age/size composition for both stocks. However, the relative scarcity of data pertaining to reproductive potential for the North Sea cod stock is immediately apparent from comparing Appendix A and Appendix E with respect to the number of years having data on sex ratio, maturity, weight, condition and fecundity.

In the case of data-poor stocks alternative indices of reproductive potential are necessarily restricted to proxies that could be derived directly from the analytical assessment (e.g., age diversity indices) or limited time series. The approach taken at this meeting of SGPRISM was to contrast Northeast Arctic cod and North Sea cod in terms of the available data resources, types of indices of reproductive potential that can be estimated, and how the indices can potentially be used in stock management. Given the lack of knowledge, SGPRISM undertook an exploratory exercise for the North Sea cod.

2.2 Northeast Arctic cod

Northeast Arctic cod is an example of a stock having several historical databases that are relevant to estimating reproductive potential (Appendices A-D). A simulation analysis suggested that the dynamic range of SB is less than the range in total egg production (Marshall *et al*. 1999). Consequently several alternative measures of reproductive potential, including total egg production (Marshall *et al*. WD9) and total lipid energy (Marshall *et al*. 2000), are being estimated for the assessment time period (1946-present) and being compared to both SB and recruitment.

2.2.1 Estimating reproductive potential

Until recently, values of SB for Northeast Arctic cod were estimated using knife-edge maturity ogives (1946–1981) and constant weight-at-age values (1946–1982). The resulting S-R relationship (Figure 2.2a) was therefore insensitive to the effect of growth variation on reproductive potential. In 2001, the ICES Arctic Fisheries Working Group [AFWG] compiled historical data from Russian and Norwegian sources and developed new time series for maturity- and weight-at age (ICES 2001b). Replacing the constant values led to a substantial downward revision of SB such that the long-term mean decreased from 577,425 t (1946–1999) to 372,934 t (1946–2000; ICES 2001b). In spite of this major change in the SB time series, the major change to the S-R relationship was a shift of outlying post-war values towards lower SB values (Figure 2.2b).

Concurrent to the revision of the SB time series, preliminary estimates of total egg production were made (Marshall *et al*. WD9). These estimates were calculated using a general fecundity model developed from field observations made during a time period when the condition of Barents Sea cod decreased rapidly due to the collapse of the Barents Sea capelin stock (Kjesbu *et al.* 1998). In the general model the year effect on the fecundity/length relationships was represented using condition. The relationship between total egg production and recruitment shows that the high recruitment values for 1963, 1964 and 1970 are more consistent with the level of egg production (Figure 2.2c) compared to levels of SB (Figure 2.2b). The SB and total egg production time series show major differences with total egg production being higher in the 1970's than in the 1990's while the opposite holds true for SB estimates (Figure 2.3).

Identifying the factors causing discrepancies between SB and total egg production is a high priority for future research. There are several refinements planned for estimates of total egg production that will hopefully increase their sensitivity to true variation in reproductive potential. These include:

- improvements to the year-specific age/length keys used to convert VPA numbers-at-age to numbers-at-length;
- improvements to the general fecundity model to better utilize environmental information, e.g., capelin stock biomass or liver condition index;
- checks on the consistency between time series of growth parameters (maturity, weight and fecundity) used in estimates of SB and total egg production; and
- corrections for size- or condition-dependent effects on egg quality.

2.2.2 Incorporating this information into stock management

The AFWG is currently investigating the appropriateness of the biomass reference points in light of the revised maturity- and weight-at-age times series (Fig 2.2b). However, it should also be recognized that reference points for SB will have a degree of uncertainty resulting from any divergence between SB and total egg production (Figure 2.3). Reference points that are explicit for reproductive potential (e.g., limit and threshold total egg production) will be developed further in future research. Classifications of stock status using these reference points will be compared to the classifications made using B_{pa}. Medium-term stock projections would need modification to take into account reference points for reproductive potential and the resulting stock projections would need to be compared to projections of SB. Inter-sessional work towards this goal is planned for the summer of 2002 through a collaboration between scientists from Aberdeen and Bergen. This work will be presented as a case study at the proposed meeting of the Study Group on Growth, Maturity and Condition Indices in Stock Projections [SGGROMAT] that is planned for December 2002 (see Section 6.1). This work will extend current stock projection methods with existing biological data and models for Northeast Arctic cod.

2.3 North Sea cod

The data available to construct more sensitive measures of reproductive potential for North Sea cod on time scales that are comparable to the assessment were initially thought to be limited (Appendices E-H), particularly when compared to a data-rich stock such as Northeast Arctic cod (Appendices A-D). Closer investigation revealed there to be limited quantities of relevant data. Cod maturity data from the IBTS for 1980–1995 are given in Cook *et al.* (1999). Maturity ogives separated by sex are reported in Rijnsdorp *et al.* (1991) for the 1985–1989 period. A historical comparison of the changes of length-maturity ogives is given in Oosthuizen and Daan (1974) extending from the 1890s to the 1970s. It shows a shift in L_{50} from approximately 75 cm to just above 50 cm in length at maturity over this long-term period (Figure 2.4). Condition data are available for 11 years from English groundfish surveys (see Section 4.3). Fecundity data exist for 1970–1972 (Oosthuizen and Daan 1974) and for 1987–1988 (Heessen, unpublished, reported in Rijnsdorp *et al.* 1991). Mean dry weights of eggs are available from eggs collected from ripe and running females in 1969, 1971, 1972 and 1987 (Rijnsdorp *et al.* 1991). Estimates of egg production have also been made according to egg surveys carried out in the southern Bight during 1970–1974 (Daan 1981).

2.3.1 Estimating reproductive potential

Using the available data this meeting of SGPRISM estimated three alternative indices of reproductive potential (age diversity, female-only biomass and condition) for North Sea cod.

2.3.1.1 Age diversity

Stocks experiencing sustained high fishing mortalities typically exhibit truncated age structure (Trippel 1999). Age diversity indices have been used as an index of reproductive potential for Icelandic cod (Marteinsdottir and Thorarinsson 1998) and striped bass in Chesapeake Bay (Secor 2000). As it is easily estimated from basic demographic data, the utility of this index was examined for North Sea cod. The numbers of mature fish at each age, obtained using the proportion mature as used in the assessments (Table 2.1a), were taken from the 2001 XSA assessment (ICES 2002a). A Shannon diversity index (H) was then estimated to the numbers of mature fish as follows:

$$H = 1/n(\log(n) - \sum_{i=1}^{k} f_i \log(f_i)) \qquad \text{Eq. 1}$$

where k is the number of age groups, n is the total number of mature fish in all age groups and f_i is the number of mature fish in each age group (Shannon 1948). The assessment for North Sea cod used fixed values of proportion mature to estimate spawner biomass. Values of H were estimated using fixed proportions mature and annual estimates of the proportion mature derived from annual surveys (Cook *et al.* 1999, Armstrong *et al.* WD 7, Table 2. 1b).

The age diversity of North Sea cod has shown a long-term decline since 1963 (Figure 2.5). Since 1993, age diversity has been below the long term mean value. Using values of H estimated with variable annual proportions mature suggests a steeper decline although the data series is shorter. In the 1990s fishing pressure was very high on the North Sea cod stocks and there has been an accompanying decline in the SSBs. Hence it is not surprising that the age diversity has declined in recent years.

Age diversity indices estimated using time invariant proportions mature show no relationship with recruitment (Figure 2.5). However, the use of year-specific proportions mature suggests that there is a relationship between age diversity and recruitment (Figure 2.6, $r^2=0.31$). The relationship is stronger than that observed for Icelandic cod ($r^2=0.15$, Marteinsdottir and Thorarinsson 1998). A multiple linear regression of recruitment (R) on age diversity (H) and $\log_e$ SSB gives a weak positive relationship ($r^2=0.44$, $p=0.06$):

$$R = 25.06\text{x}10^6 - 37.60\text{x}10^6\, H - 2.23\text{x}10^6 \log_e SSB + 3.38\ \text{x}10^6 (H*\log_e SSB) \qquad \text{Eq. 2}$$

In terms of assessing reproductive potential, it appears that age diversity is a useful tool for describing major changes in the population age structure that will impact on reproduction (Marteinsdottir and Thorarinsson 1998, Secor 2000). For North Sea cod the correlation between age diversity and recruitment was only significant when the variable proportion mature in the stock were used to estimate H. **Time invariant maturity ogives give an incorrect perception of age diversity as well as other aspects of the stock dynamics**.

Table 2.1.a. Proportion of fish mature time invariant used in the 2001 XSA stock assessments of North Sea cod.

a)

Age	Proportion mature
1	0.01
2	0.05
3	0.23
4	0.62
5	0.86
6	1.00
7	1.00
8	1.00
9	1.00
10	1.00
+ grp	1.00

Table 2.1.b. Survey derived estimates of proportion mature of North Sea cod, both sexes combined (Cook *et al.* 1999).

b)

					Age					
Year	1	2	3	4	5	6	7	8	9	10	+grp
1980	0.01	0.1	0.08	0.56	1	0.88	1	1	1	1	1
1981	0.01	0.04	0.16	0.52	0.85	0.87	1	1	1	1	1
1982	0	0.03	0.17	0.64	0.93	1	1	1	1	1	1
1983	0	0.03	0.2	0.5	0.96	0.99	1	1	1	1	1
1984	0	0.06	0.25	0.42	0.81	0.98	1	1	1	1	1
1985	0	0.04	0.1	0.45	0.56	0.91	1	1	1	1	1
1986	0	0.09	0.18	0.35	0.63	0.9	1	1	1	1	1
1987	0	0.02	0.15	0.6	0.76	0.98	1	1	1	1	1
1988	0	0.05	0.27	0.53	0.9	0.95	1	1	1	1	1
1989	0	0.13	0.24	0.59	0.77	0.97	1	1	1	1	1
1990	0.01	0.19	0.54	0.73	0.93	0.99	1	1	1	1	1
1991	0	0.09	0.39	0.5	0.89	0.98	1	1	1	1	1
1992	0	0.21	0.52	0.85	0.85	1	1	1	1	1	1
1993	0	0.07	0.42	0.7	0.88	0.96	1	1	1	1	1
1994	0	0.14	0.43	0.77	0.98	1	1	1	1	1	1
1995	0.01	0.05	0.3	0.82	1	0.97	1	1	1	1	1

2.3.1.2 Condition

Condition indices reflect the amount of available energy reserves of the fish (Kjesbu *et al.* 1991). Adult female condition affects the quantity (number of eggs produced by individuals) and possibly the quality and survival of offspring (Kjesbu *et al.* 1991, Marteinsdottir and Steinarsson, 1998). Fluctuations in temperature and food can contribute to inter-annual variability in condition. For example, in Northeast Arctic cod, condition is positively correlated to mean annual bottom temperature and, particularly, capelin stock biomass (Kjesbu *et al.* 1998, Yaragina and Marshall 2000).

Condition can be measured using a bioenergetic approach (e.g., lipid analyses, liver condition index) or more simply based on the relationship between weight and length (Lambert and Dutil 1997). There is a high degree of seasonal variation in condition (Yaragina and Marshall 2000). The timing of research surveys may not always be optimal for establishing a representative annual condition measure. Traditionally, weight information has not been collected on the IBTS. Consequently, the data available to describe interannual variation in condition is very limited. Figure 2.7 shows a reconstruction of relative condition factor (Fulton's K = weight/(length)^3) for North Sea cod ages 1–6. The time period 1996–2001 suggests that there is rapid fluctuation that is not synchronous across age-classes. For cod ages 4 and 6 there is some suggestion of condition values being lower in 2001 compared to values for 1979 to 1981. Due to the short, incomplete nature of the time series it is not possible to determine whether there is a correlation with recruitment trends. However, it should be noted that other gadoid stocks show positive associations between condition and recruitment (Blanchard 2000, Marshall *et al.* 1999).

2.3.1.3 Female-only biomass

As a result of dimorphism in growth, mortality and behaviour, sex ratios shift towards a higher proportion of females with increasing size. The loss of large/old spawners affects the number of mature females disproportionately. This could result in losses of reproductive potential that are disproportionate to the loss of spawner biomass. For example, more of the variation in recruitment of Baltic cod can be explained using female-only biomass compared to the biomass of males and females combined. Female-only biomass for North Sea cod was calculated as the product of numbers at age, sex ratio-at-age, female maturity-at-age and weight-at-age. Numbers-at-age of cod were available from the North Sea Demersal Working Group report (ICES 2002a). Female maturity-at-age, sex ratio, and weight-at-age were obtained from the English groundfish surveys carried out in the North Sea during the third quarter. Only ten surveys had sufficiently resolved data. Therefore, estimates of female-only biomass were confined to the years shown in Table 2.2.

Table 2.2. Results of model fitting for North Sea cod.

Year	Female-only SB (metric t)	VPA SB	Recruitment at age 1	Ricker fitted recruitment	Residuals
1979	56962	164268	899522	363008	536514
1980	87145	181869	314766	380027	-65261
1981	101074	195732	618498	391356	227142
1989	47887	90611	133940	253088	-119148
1990	25889	78040	168570	226865	-58295
1996	27339	76358	421717	223165	198552
1997	31428	80187	69536	231519	-161983
1998	11500	71553	139369	212343	-72974
1999	27497	61467	215023	188356	26667

Within this time period there was a weak but insignificant (r^2 = 0.28, p = 0.14, n = 9) linear relationship between female-only SB and recruitment (Figure 2.8b); however, the overall pattern of variation was similar to that observed in the conventional stock-recruitment relationship (Figure 2.8a). It should be noted that the maturity assessment in the third quarter underestimates the SB of the younger first-time spawners. There was no significant (r^2 = 0.09, p = 0.14, n = 9) relationship between female-only SB and the residuals from the S-R relationship.

2.3.2 Incorporating this information into management

The North Sea cod stock was initially considered data-poor in terms of analysis of reproductive potential. However, the analyses undertaken during this meeting of SGPRISM revealed that there were data resources which could be utilized (Section 2.3). The perception that there is no data is not justified! However, existing data often are discontinuous in time or subject to sampling biases. More definitive databases are required to describe the relationship between SB and reproductive potential and between reproductive potential and recruitment conclusively.

There are several considerations when reconstructing historical trends in reproductive potential or collecting new data:

- When reconstructing historical trends in reproductive potential for data-poor stocks, missing data are often extrapolated from another stock in spite of evidence of large inter-stock differences in the fecundity/length relationship (Oosthuizen and Daan 1974). Until more is known about the stock-specific nature of reproductive parameters and the degree of spatial and temporal variation in. sex ratio, maturity, fecundity, and condition, it is inappropriate to extrapolate this information between stocks.
- It is essential to collect time series of reproductive data if reproductive potential is to be successfully incorporated into stock assessment and projections. Emphasis must be given to the quality of surveys and appropriate survey design. Surveys must take place at times relevant to the reproductive process being considered, e.g., maturity should be assessed approaching the spawning period and condition prior to vitellogenesis. Surveys should also account for biases caused by spatial patterns, fish behaviour and sampling strategies such as stratified length sampling.
- In the case of North Sea cod data obtained from market sampling has limited value because gutted fish are landed (e.g., no condition or fecundity information). Consequently, data obtained from surveys are critical to characterizing the dynamics of growth and reproduction (see also Section 4.4.3).
- Maturity data should be collected and reported by sex and be of suitable resolution for the correct interpretation of diverse spawning strategies.
- In the absence of data, simulation approaches may be advantageous to examine the effect of variation of weights and maturities on medium-term stock projections.
- New data on fecundity and egg quality of North Sea cod may become available in the near future (Witthames *et al.* WD2).

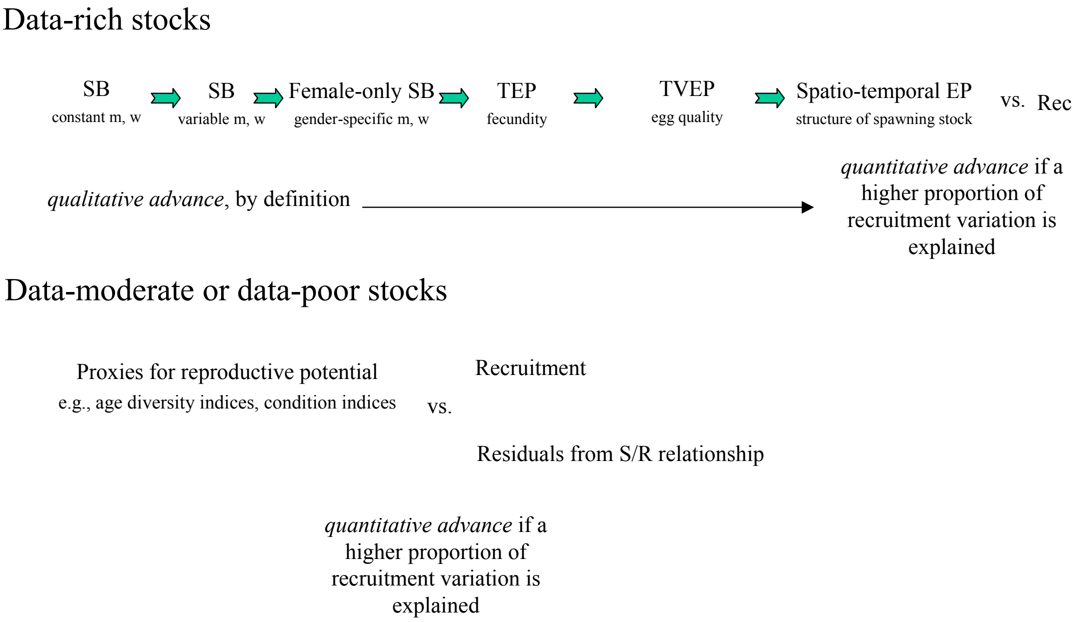


Figure 2.1. Schematic illustrating the differences between qualitative and quantitative advances in quantifying reproductive potential. For data-rich stocks qualitative advances are achieved by replacing spawner biomass (SB) to total egg production (TEP), total viable egg production (TVEP), and spatio-temporally disaggregated egg production (EP) through the addition of more highly resolved information on maturity (m), weight (w), sex ratio, fecundity (f), egg quality, and spatio-temporal distribution of spawners. Quantitative advances result if a higher proportion of recruitment variability is explained by the new index. Data-moderate or date-poor stocks are limited to comparing proxies of reproductive potential either to recruitment or to residuals from the stock-recruitment relationship.

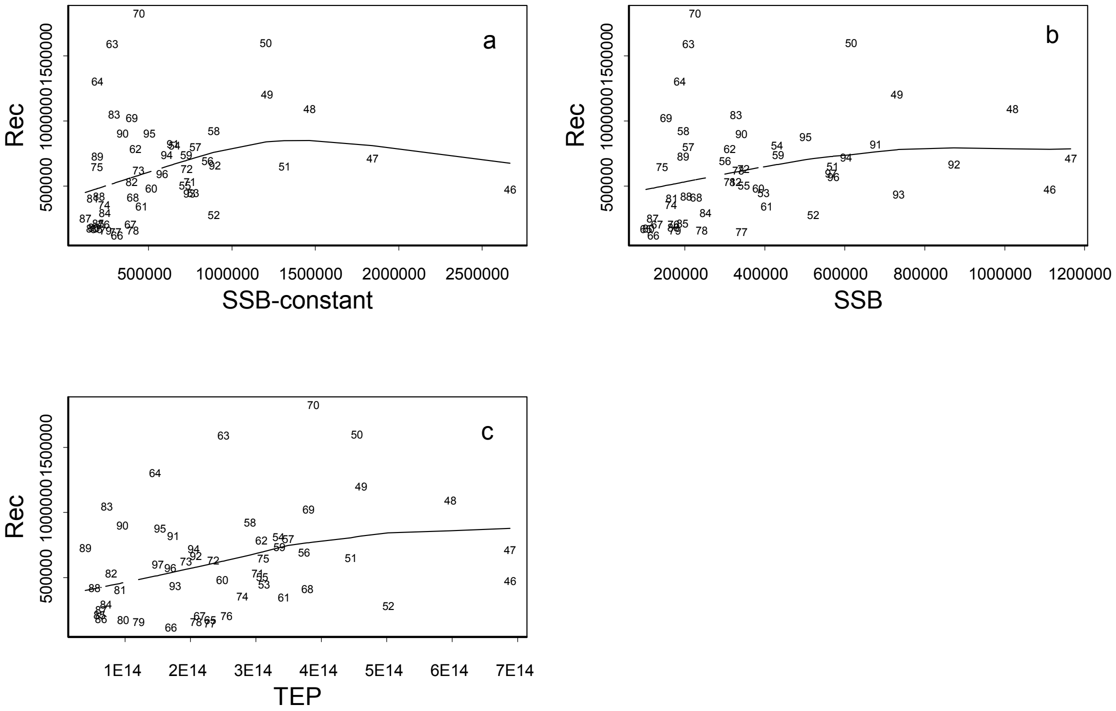


Figure 2.2. The stock/recruit relationship for Northeast Arctic cod using different indices for reproductive potential. **a)** spawner biomass calculated with constant values of proportion mature and weight at age for pre-survey time period (ICES 2001d); **b)** spawner biomass calculated with year-specific values of proportion mature and weight at obtained from Russian and Norwegian historical sources (ICES 2001b); and **c)** total egg production. The recruitment index used is the abundance at age 3. Observations are labelled by year. The loess curve (degree=1, span=1.5) is shown for each.

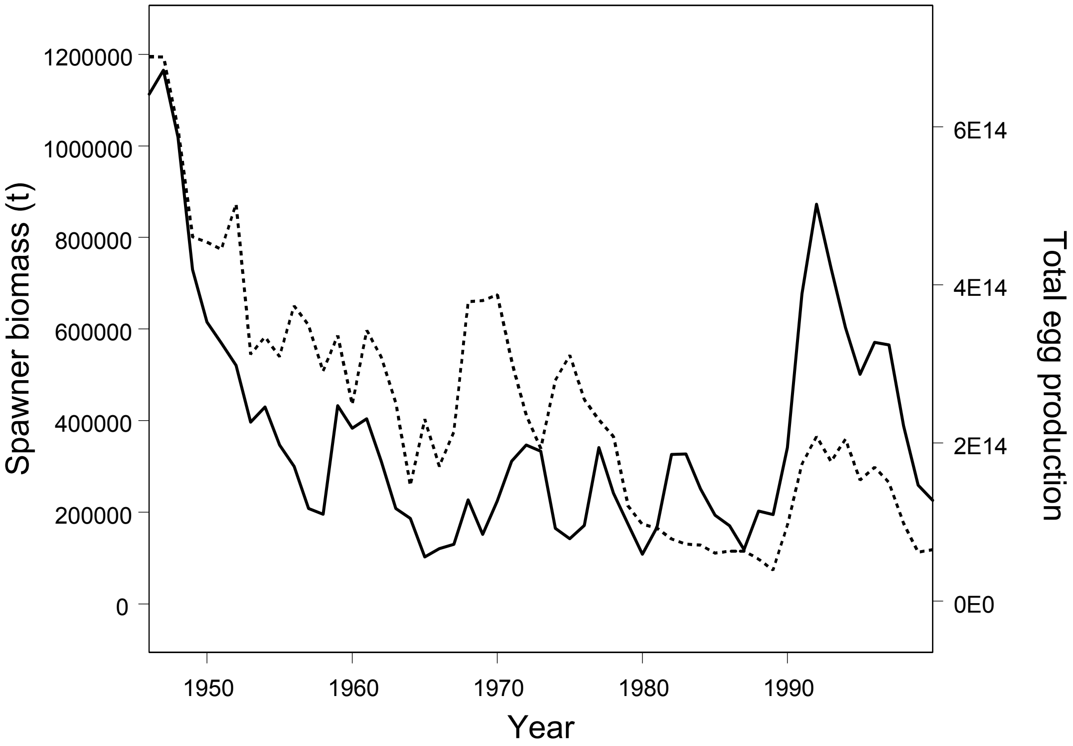


Figure 2.3. Time series of spawner biomass (solid line; from ICES 2001b) and total egg production (dashed line).

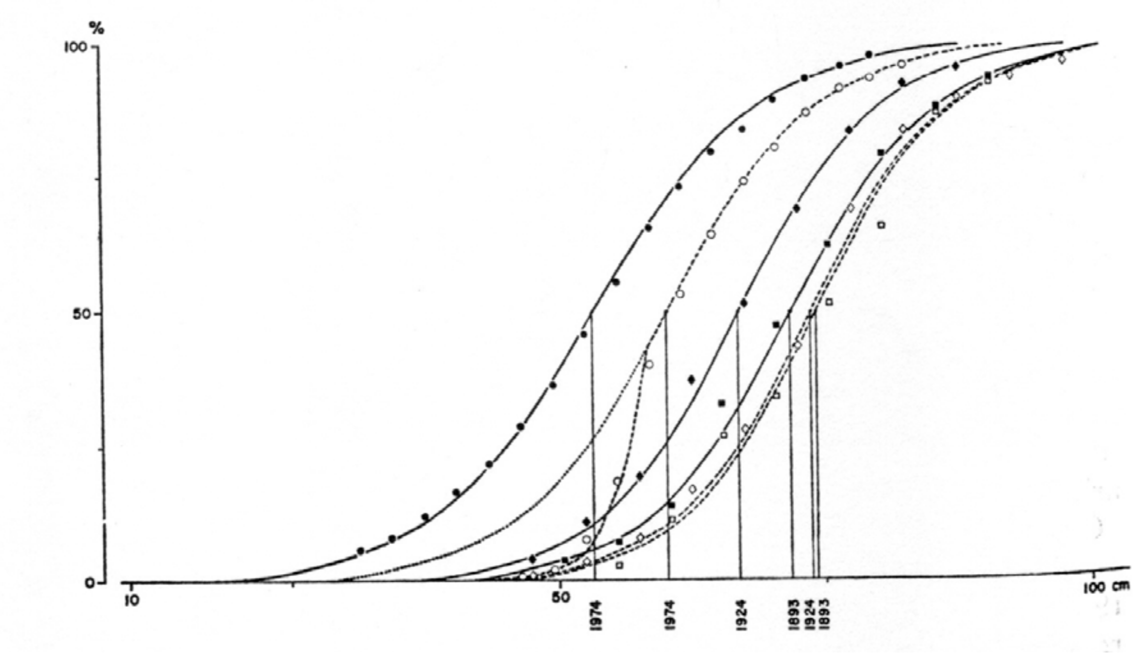


Figure 2.4. Length maturity ogives (estimated from logit transformations) of North Sea cod for males (solid symbols and females (open symbols), according to data by Holt (1893) (squares) Graham (1924) (diamonds) and Oosthuizen and Daan (1974) (circles). L_{50} values indicated by the date.

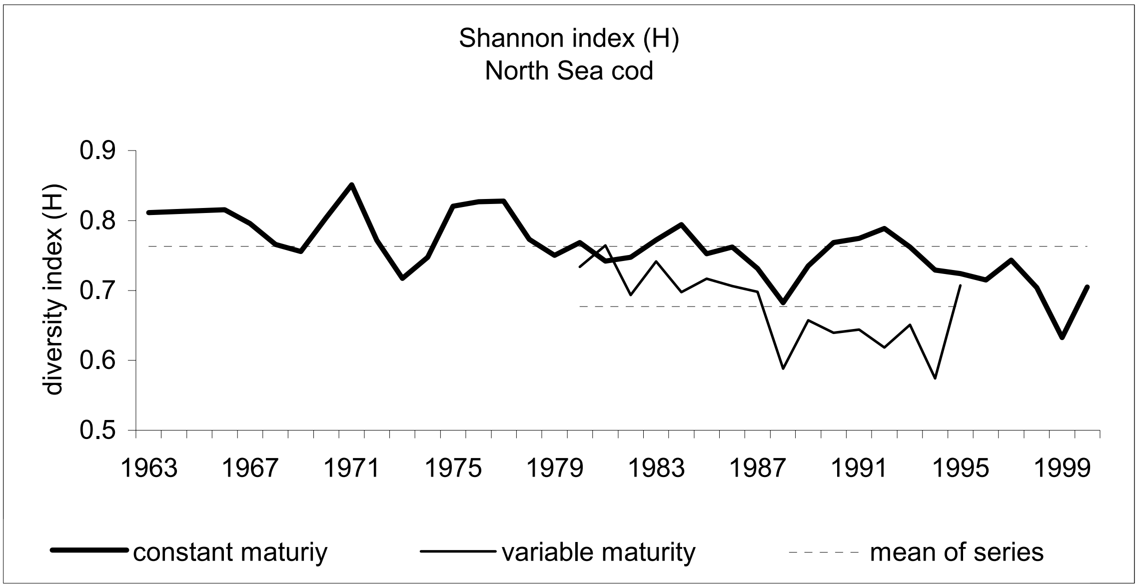


Figure 2.5. Interannual variation of age diversity of cod in the North Sea based on the Shannon diversity index. Dotted lines denote long-term means.

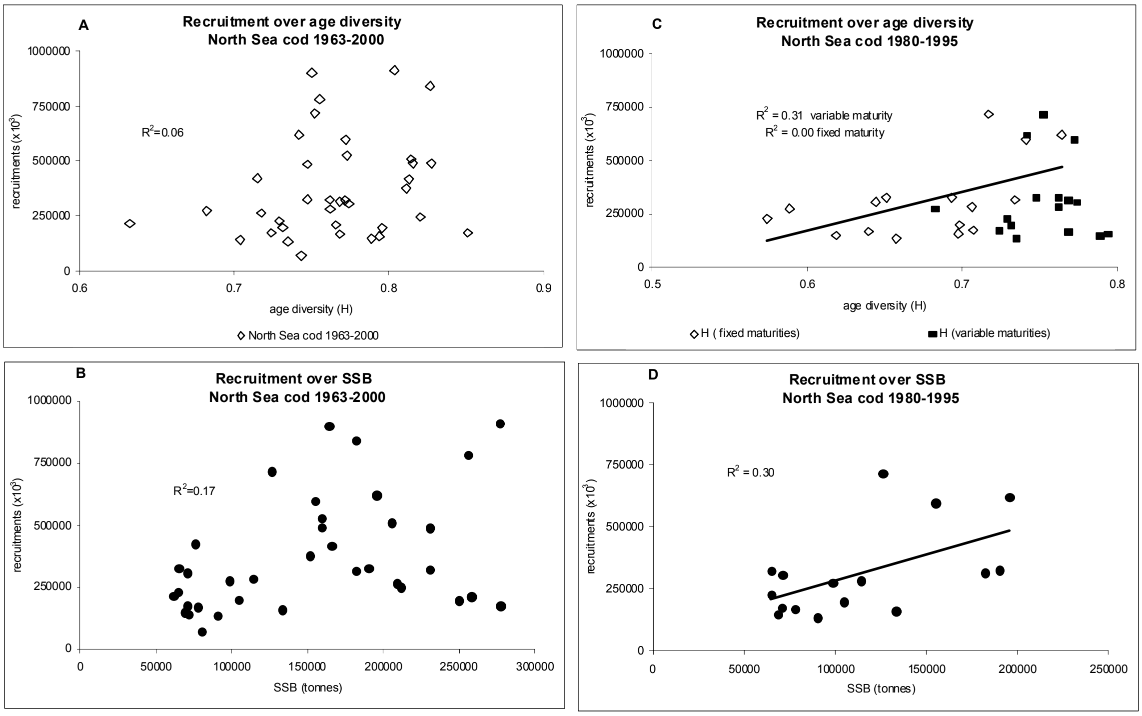


Figure 2.6. Recruitment in North Sea cod (age 1). **A)** against age diversity H (time invariant proportion mature); **B)** against SB in tonnes (1963–2000); **C)** against age diversity H (with variable proportion mature, open diamonds and fixed proportion mature, closed squares) (1980–1995, Cook *et al.* 1999, ICES 2002a); and **D)** against SB in tonnes (1980–1995). Linear relationships shown where applicable.

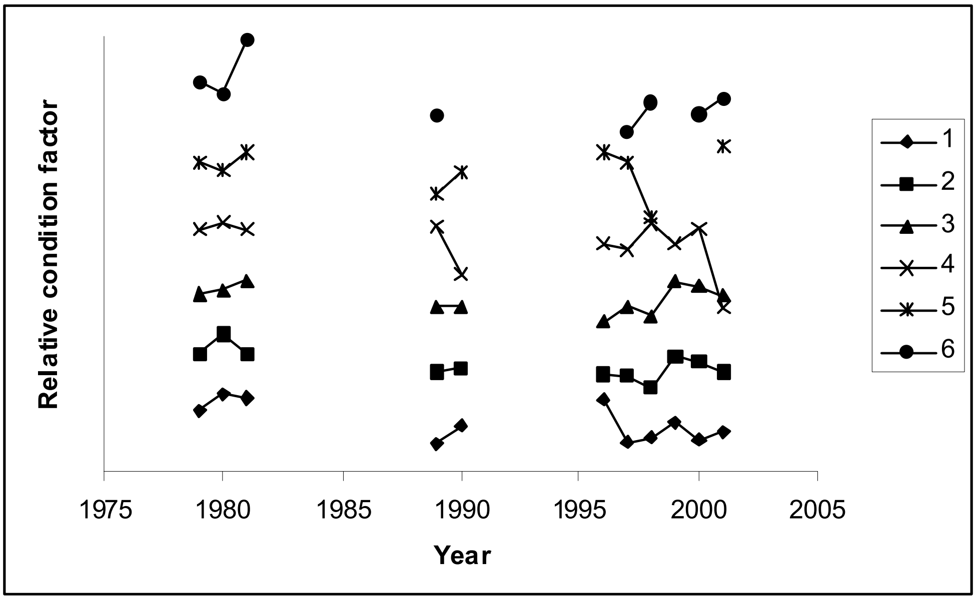


Figure 2.7. The time series of relative condition factor at ages 1 to 6 for the North Sea cod (combined sexes) calculated from the English groundfish survey data sets. The values are scaled in order to separate the time series so that the year effects can be distinguished.

A)

B)

Figure 2.8. A) The relationship between SB of North Sea cod and recruitment at age 1. Labels denote year; and **B)** the relationship between female-only SB and recruitment at age 1. Labels denote year.

3 FISHERIES AND BIOLOGY: PROCESS STUDIES IN ASSESSMENT AND ADVICE

3.1 Introduction

This section is intended to provide a brief summary of process studies in selected areas, touching on the potential for using the results from these studies in management advice. This is followed by a discussion focussing on general aspects of the use of process studies in this context.

3.2 Area case studies

The areas covered here represent the interests of members of this meeting of SGPRISM. They are also notable for the differing extents to which the areas have been covered by process studies, ranging from highly detailed and systematic coverage (the Baltic) to much sparser coverage (the North Sea).

3.2.1 Baltic Sea

The processes affecting recruitment to stocks in the Baltic Sea have been the subject of extensive studies under the EU CORE and STORE programmes. A general introduction to these programmes is given by MacKenzie and Köster (2001), and the following summary of progress in the STORE project, with particular reference to cod recruitment, is adapted from Schnack and Köster (2001).

The objectives of the STORE project are the following:

a) 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.

b) 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.

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

d) 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.

On the basis of extensive retrospective data compilation and verification, simple correlation analysis have first been made between SSB and stage I egg production derived from ichthyoplankton surveys and between 4 successive developmental stages of cod and sprat (Table 3.2.1). When concentrating on those sub-areas which were best sampled for the respective species, for cod there is a significant correlation between the abundance of larvae and 0-group stage but not between any of the earlier stages. This indicates that variations in spawning stock structure and in environmental conditions during egg to larval development are critical for recruitment success of Baltic cod, whereas the larval to juvenile development appears to be more stable. In sprat the main regulation seems to take place in the larval to juvenile phase. In the following only cod is further considered with a focus on the critical early stages.

Table 3.2.1. Correlation coefficients for successive early life stages of cod in Sub-division 25 and sprat in Sub-division 26

Variable 1	Variable 2	Cod SD 25	Sprat SD 26
SSB$^{1)}$	Egg production stage 1	0,19	**0,66***
Egg production stage 1	Egg production stage 3	0,51	**0,82***
Egg production stage 3	Laval abundance	0,36	**0,81***
Laval abundance	0-group abundance	**0,80***	0,32

* correlation coefficients significant at p<0.01

$^{1)}$ based on maturity ogives invariate over time

In Table 3.2.1, SSB is based on constant maturity ogives as used previously in standard stock assessment. When including the actual fluctuation in maturity ogives and using only the mature female stock component, this is already significantly correlated to stage I egg production. Moreover, relative fecundity changes over the years, with an obvious general trend to higher values in more recent years (Kraus *et al.* 2000). On population level, this fecundity appears to be clearly related to the food supply (Kraus *et al.* 2001), expressed as suitable clupeid (sprat age-groups 1+ and herring 1–2) biomass per predator weight. Temperature had an additional but very minor effect. SSB, thus, appears to be too coarse a measure of the potential egg production; information on maturity and fecundity has to be considered in addition.

When calculating the potential seasonal egg production, based on area specific mature female stock components and relative fecundity values, predicted from food availability, this leads to a significant relationship with the observed daily egg production as obtained from egg surveys during peak spawning time. A corresponding relationship is obtained also with the observed total seasonal egg production, but can be based on a rather limited data set only.

Turning now to the second phase in the correlation scheme, which addresses the variability in egg mortality, for cod this phase is assumed to be largely depending on the oxygen conditions in the deep-water layers. To consider this factor the *Recruitment Volume* (RV) has been defined by Plikshs *et al.* (1993), which identifies the pelagic habitat volume in the depth range with sufficient salinity for fertilization success and floating of cod eggs, and with an oxygen level above the minimum required for egg development. This RV has frequently been utilized in stock-recruitment considerations, but unfortunately it explains only a limited part of the variation in egg mortality (Köster *et al.* 2001a). This can be related to the following problems: When using the total RV in the Baltic, combined for the different spawning areas, as a measure of oxygen related survival, a large and varying amount of the total egg production is placed in areas with no RV present, and also large and varying portions of the total RV may be available in areas with no egg production. Thus, individual spawning areas have to be considered separately. In addition, the proportion of the total egg production placed within the vertical range of the RV varies according to the varying salinity profile, and the survival of these *well placed* eggs is largely depending on the widely varying oxygen profile within the limits of the RV. So this vertical information has to be utilized as well.

From experimental work, the relative viable hatch has been related to oxygen and this relationship been utilized to define an improved *oxygen related survival index* (OES). This index is based on the observed oxygen profile and the predicted vertical egg distribution, derived from the salinity profile (Köster *et al.* 2001b). This new survival index follows the variation in RV only in the very general trend; for specific years or periods there are substantial differences. Predicted egg survival, based on the OES, is significantly related to observed daily egg survival as derived from successive egg surveys during peak spawning; and also when applying OES on the estimated potential egg production, then the predicted surviving seasonal egg production explains a significant part of the variation in the observed seasonal production of stage III eggs. This could not be achieved with the RV. The remaining variance is still high though, but this is not surprising as the variance between potential and realized egg production is still included and other factors, especially predation, are effective in addition to oxygen.

Quantitative estimates of predation on early life stages are difficult to obtain (Bailey and Houde, 1989). The predation by sprat is rather high in the early years of this time series but is much reduced in the more recent years, whereas predation by herring has increased, and in total the relative importance of predation has decreased. This shift in the importance of the two clupeid species can be explained by the shift in the peak spawning time of Baltic cod from spring into summer period. Sprat leave the central parts of the basins after spawning and feed in more shallow waters, and herring having spawned in the coastal areas return back into the central parts.

In addition to these changes in the horizontal overlap of predator and prey, variation is also observed in the vertical overlap, depending on the salinity and oxygen profiles. When combining predator abundance and vertical overlap of predator and prey, the results indicate an especially high predation on cod eggs in the second half of the 1980s and much lower levels in the years before and in recent years.

In the early larval phase, predation appears to be much less important (Köster and Möllmann 1997), but during this stage the food supply may be more relevant, especially when considering changes in the zooplankton composition, described by Möllmann *et al.* (2000, 2001). According to light conditions, visual performance and vertical distribution of the larvae, the food supply in the depth range of 25–50 m should be most critical, as described by Grønkjær and Wieland (1997). The seasonal distribution of abundance of nauplii has been modelled for the Bornholm basin (Hinrichsen *et al.* 2001a) and presented as average concentration in dependence of the total water depth. When all species are considered, then the concentration of nauplii is not substantially different between deep and shallow areas and a marked seasonal maximum is showing up in May-June. Excluding *Pseudocalanus elongatus*, a species which has reduced in abundance in more recent years (e.g., Mölmann *et al.* 2000), then the seasonal maximum of nauplii is shifted to the autumn and concentrations are much lower in the deeper parts of the basin, where the early larvae are mainly placed, as compared to the more shallow areas. This result shows the potential relevance of the observed changes in species composition of zooplankton in recent year for cod larvae survival.

For the larval to juvenile phase, mortality was indicated to be not as variable as for eggs (Table 3.2.1). Nevertheless, two factors appear to be of importance: the drift of the pelagic stages and the mortality due to cannibalism.

In the drift pattern of larvae, yearly differences may be quite striking as derived from hydrodynamic modelling (Hinrichsen *et al.* 2001b). The drift into shallow areas appears to be essential for the settlement of the early juvenile stages and successful further development. Accordingly a larval transport index has been developed, based on the wind conditions, to be included into the cod recruitment model.

The second factor, cannibalism, is indicated by MSVPA to be a major potential source of pre-recruit mortality (e.g., Neuenfeldt and Köster 2000). However, large differences were obtained in the suitability coefficients of 0-group cod as prey obtained from MSVPA runs based on sub-sets of stomach content data covering different time periods. These differences were obvious only for predators above age 4, related obviously to a decline in spatial overlap with the juvenile stages at decreasing adult stock size (Uzars and Plikshs 2000). Thus, a substantial variability in pre-recruit mortality due to cannibalism is to be expected only if substantial amounts of older age classes are present in the stock.

Those factors identified as significant in the different spawning areas have been included into statistical stock-recruitment models, built up for each of the three major spawning areas separately. The effects were then combined for the Central Baltic in total. Factors that have been considered are: potential egg production, clupeid egg predation, oxygen content in the reproductive volume and larval transport index (the latter in Sub-division 25 only).

The combined model describes fairly well at least the general trends in recruitment variability as obtained from MSVPA. However, differences may still be substantial for individual years, e.g., 1979. In order to test its predictive power, the model was refitted again to the time series of data, excluding alternatively the first or the last 4 years. The models derived this way could reasonably well predict the recruitment success in these excluded years, again with exception of year 1979. Also for the most recent years after 1995, not included in any of the fitting procedures, the predictions compare well with the VPA estimates. This, however, is a less rigid test, as only minor changes occurred in stock size and recruitment during this last period.

In conclusion, the basis for prediction of Baltic cod recruitment has obviously been improved, but the model so far utilized is still a conventional statistical approach. The improvements have been achieved by using more of the available information and including newly provided results, which allow for instance to estimate the potential egg production more reliably as compared to using SSB as a too coarse proxy only. To a large extend improvements are related to a better spatial resolution of information: i.e., individual spawning areas have been handled separately, predator-prey overlap, larval transport and the distribution of eggs within the oxygen profile including consequences for survival have been considered. The remaining variance in the recruitment model may be due especially to parental effects on early life stages (Vallin and Nissling 2000) and to the prey availability for larvae (Hinrichsen *et al.* 2001a). Both factors have not yet been considered in the model but are a focus of study in the STORE project.

In addition to the spatial aspects, further improvement of resolution in time will be essential. So far, average environmental conditions in the main spawning times and areas have been considered. However, these may not always be the most relevant ones. Backtracking of actual survivors to their birth dates and places, based on age analysis and drift modelling, shows that they can be originated to a large and varying extend from outside the spatial and temporal centers of egg production (St. John *et al.* 2000).

Thus, describing characteristics of survivors and identifying those environmental conditions on adequate scales, relevant for growth and survival, is a main focus of the project. On the modelling side, purely statistical models, assuming linear though multifactorial relationships, do not seem to be satisfactory for predicting purpose. Thus, the construction of Individual Based Models (IBM) is attempted in order to follow the developmental success on the basis of a number of functional relationships and non-linear responses to environmental conditions. This is done in combination with hydrodynamic and also some food web modelling to provide the relevant environmental input data to the IBM. This approach introduces a better resolution in time and allows to study the sequential effects for changing conditions, which may be different from effects of constant average conditions. Also, it allows to include the variance in the performance of individuals within a cohort and its relation to characteristics of the parental stock.

Potential use of process information in assessments for Baltic cod

As the above summary notes, the STORE project includes the intention to incorporate information obtained on recruitment processes into medium-term projections and reference points for cod and sprat. WD12 summarised some preliminary investigations into this for Baltic cod. This noted that most of the existing studies on stock and recruitment used multiple regression models, which were not suitable for direct use in stock projections. This was partly because regression models are not appropriate for use with values outside the range of observations, and partly because the studies summarised above have used multi-species assessments which differ in age range and area coverage to the stock units used in the routine assessments. However, these studies have highlighted that potential egg production and reproductive volume are important determinants of recruitment, and future work will focus on the incorporation of these effects into stock projections.

3.2.2 Barents Sea

General

It is believed that the state of the Barents Sea ecosystem to a large extent will be revealed through the state of the stocks of Northeast Arctic cod, Barents Sea capelin and Norwegian Spring-Spawning herring (Hamre 1994). Both total fish production in the Norwegian-Barents Sea area (including Norwegian coastal waters), and also other aspects of the total ecosystem, are believed to be closely linked to the development of these stocks. Cod prey on capelin, herring and young cod (Bogstad and Mehl 1997), while herring is an important predator on capelin larvae (Huse and Toresen 2000). Cod growth is also affected by prey (especially capelin) abundance (Mehl and Sunnanå 1991). All three stocks show large variations in recruitment.

In the present case study on including process information in stock-recruitment models for fish species in the Barents Sea, we will thus only consider these three species. Appropriate modelling of other processes (growth, maturation, predation/species interactions) are also important both for short-term and medium/long-term stock prognosis for these three stocks. However, in this context we will focus on how to incorporate process information in stock-recruitment models for these three species.

Cod

The recruitment of Northeast Arctic cod is quite variable, and several processes and variables have been suggested as explanation: Spawning stock biomass, egg production, temperature in the spawning/larvae period, NAO, cod cannibalism, prey abundance, wind and currents etc. (see e.g., Marshall *et al.* (2001,WD 9), Ottersen and Sundby, 1995; Ottersen and Stenseth, 2001; Bogstad *et al.*, 1994). The issue of replacing spawning stock biomass with other measures (e.g., total egg production) of reproductive potential has been elaborated on in Section 2.

For this stock, there is a need for predicting year-classes, which have been spawned but have not yet entered the fishery, in order to improve short-term predictions. Also, there is a need for incorporating process information to improve medium- and long-term predictions. These two issues will be addressed separately below.

Northeast arctic cod enters the fishery at age 3. The ICES Arctic Fisheries WG has for many years (since 1987) used the ICES computer program RCT3 (formerly RCRTINX2) (Shepherd, 1997) to predict the strength of recruiting year classes at age 3. This is a simple calibration and regression method, which combines multiple time series of recruitment indices and VPA estimates of year-class strength at the age of recruitment to the fishery. It does not take into account at which life stage an index is measured. Also, RCT3 does not allow for including information on environmental conditions, cod cannibalism and other processes, which are important in determining recruitment of this cod stock. A model that predicts the abundance of NEA cod of a cohort of age 3 based on available information about the abundance at earlier life stages, as well as process information, should be constructed. Tretyak (1999) constructed a model of the mortality from ages 0–3 which is of this kind, but there is a need for a model incorporating both Norwegian and Russian data sources and recent knowledge on process information (see WD 5 for a summary of some recent studies).

For medium- and long-term predictions, a population model for cod where the recruitment is modelled accounting for fecundity information and cannibalism could be a reasonable first step to aim for. Thereafter, the biological realism of the predictions could probably easier be improved by using a cod-capelin-herring model rather than by including more process information in the stock-recruitment model for cod. Cod cannibalism is inversely related to capelin abundance (ICES 2001b), which could be accounted for using a multispecies model.

For this stock, it is also important to model the length of the age 3 recruits, as this has been observed to vary from 28 to 41 cm, according to Norwegian survey data (ICES 2001b).

Herring

Norwegian spring-spawning herring spawn along the Norwegian coast, but abundant year-classes are generally found in the Barents Sea approximately from age 6 months until age 3. Year-class strength seem to be determined in first half year of life; the larval survey in April is a good indicator of spawning stock size but useless for predicting recruitment, while the 0-group survey in August-September is a reasonable predictor of recruitment. Temperature variations are also an important factor affecting recruitment, but according to Toresen and Østvedt (2000) it was heavy fishing pressure and not environmental variability which was the main cause of the collapse of this stock in the late 1960s.

The recruitment model used by WGNPBW (ICES, 2001c) is a traditional Beverton-Holt recruitment model where the parameters are estimated on a log scale. However, the recruitment is highly dynamic with a few outstanding year classes. To better adapt the model to this stock 10% of the highest recruitments are excluded from the regression. When a draw from the recruitment model is made these year classes are selected with a 10% probability and a draw with equal probability is made. If the highest recruitments are not selected the recruitment is given as the exponentiation of the logarithm of the Beverton-Holt model with a random draw from the residuals added. This relationship does not contain any process information.

As for cod, there is a need for including process information in prediction of herring year-classes that already have been spawned (from age 0 to age 3 at which the fishery starts). However, much less survey information is available for age 0–3 herring than what is the case for cod.

Capelin

Predation by juvenile herring on capelin larvae seems to have a strong impact on the recruitment to the Barents Sea capelin stock. Hamre (1985) was the first author to suggest that the decline in the capelin stock could possibly be associated with the presence of young herring in the nursery area of the capelin larvae. In years with high abundance of juvenile herring in the Barents Sea, capelin recruitment is severely hampered (Gjøsæter and Bogstad 1998).

Capelin spawn approximately 1 April. In ‘herring’ years the abundance of capelin larvae, as measured during a larval survey in June, seems to be adequate for securing recruitment. However, in these years nearly all 0-group capelin disappear between this June survey and the 0-group survey (Anon. 1997) in August-September (WD 1). Predation by herring on capelin larvae has also been observed (Huse and Toresen 2000). The effect of herring on capelin recruitment also seems to be linked to the overlap between juvenile herring and 0-group capelin (Gjøsæter and Bogstad 1998).

Gjøsæter and Bogstad (1998) fitted the following curve to the stock-recruitment data for capelin and abundance data for young herring:

$R = \frac{758SSB}{SSB + 74 + 2797H_{1+}}$, where H_{1+} is the biomass (million tonnes) of one year and older herring in the Barents Sea from the acoustic young herring surveys in the Barents Sea during May-June. This model explains 87% of the variation in recruitment at age 1. The relationship should be revised based on new data on herring abundance and capelin spawning stock biomass, but is formulated in such a way that it can be utilised for short- and medium-term predictions of the capelin stock. The abundance of young (1+) herring in the Barents Sea can be predicted reasonably well one year ahead, based on survey data.

Barents Sea capelin has almost total spawning mortality, and is managed by a target escapement strategy (Gjøsæter *et al*., 2002). The management is based on an acoustic survey in September, which is considered to give an absolute abundance estimate of the abundance of 1+ capelin. A length-dependent maturation model is then used to determine the maturing stock, which is predicted half a year ahead based on a multispecies model where predation by cod is taken into account. The fishery is conducted in January-April, mainly on the spawning stock. It has been discussed in the Northern Pelagic and Blue Whiting Fisheries Working Group (ICES, 2001c; Anon., 2001a) how the target escapement strategy could be made dependent on the expected abundance of young herring in the Barents Sea in the year of spawning, but no method to do this has yet been found.

Prediction models which could be used

The multispecies model Bifrost (Anon., 2001a) could be used for making predictions for the cod-capelin-herring system in the Barents Sea. This model is an age-structured multi-species model where predation, growth, recruitment and fishery are modelled. It is presently used for investigating harvest control rules for Barents Sea capelin.

One way of including the process information on reproductive potential (Section 2) is to use a population model with an age and length structure. For Northeast Arctic cod, such a tool is available – Fleksibest (Frøysa *et al*., 2002). Fleksibest is a single-species application to Northeast Arctic cod of the multi-area, multi-fleet, multi-species age-length structured model framework Gadget (formerly BORMICON) (Anon., 2001b). Here, the population dynamics processes growth, maturation, predation and fishing are modelled as length-dependent processes. A stock can be divided into a mature and an immature part, as is done in Fleksibest. It is easy to include also information on sex ratio and on fecundity, as well as letting the condition factor influence the processes in addition to the length. Gadget currently lacks a stock-recruitment module (recruitment is estimated or read from file), but there are plans to include such a module. Using such a flexible framework allows for studies of the effect of changes in growth, exploitation rate, and selection pattern on stock development.

3.2.3 North Sea

The only species to be examined for the North Sea by the Study Group was herring (*Clupea harengus*) (WD6). The basis of the work presented was an interest in exploring life history trajectories in an attempt to understand the factors that determine year class strength in fish populations. In general, there are very few species where there is sufficient information to undertake relatively detailed analyses of the different life history stages.

One exception is the long series of survey indices for North Sea herring. Fishery independent data are available on the age, length, mean weight, fecundity and abundance of the adults, larvae, O-ringer pelagic stage, 1-ringers and 2-ringers. Thus providing information on estimated number of eggs and abundance at spawning, 0–3 months, 3–6 months, 1 year and 2 years within the life of a cohort. The data used in this study are generated from survey data and are assumed to be linearly related to the abundance of the life stage measured. Since there are no estimates of absolute abundance the relationships between life stages can only be considered as relative.

There is an effect of age structure of the adult population on the numbers of eggs produced. There are relationships between egg production and the numbers of larvae but there is a suggestion that the relationship has shifted over time (a regime shift in the North Sea during the late 1980s (Reid *et al*. 2001)). In general the numbers of early juveniles are positively correlated with the numbers of larvae, however, there are some notable exceptions. There are a series of three years (1988–1990) plus 1997 when there was poor survival from larvae to early juveniles and one year (1986) when survival appeared particularly good. In the next transition from early juveniles to 1-ringers there was a good correlation between years with one exception (1995). This was a particularly strong year class. In the transition from 1 to 2-ringers there was again correlations between successive years, however, there appeared to be a shift in survivorship for the periods pre and post 1990. These data are visualised in the form of Paulik diagrams (Paulik 1973), four panel graphs (Figure 3.2.3.1, note that neither the estimated egg production nor 2-ring abundance are shown in this figure) that highlight where in the life history changes in correlations between years in each year-class occur.

It is apparent that good or bad year classes are formulated at different time periods within life history. Variation in abundance of potential predators and/or competitors were examined in conjunction with the abundance of herring at the different life history stages but these did not shed any light on why there are apparent shifts in survivorship. Without detailed studies on the predator/prey relationships for herring it is not possible to try and determine the processes, which are determining year class strength.

In reviewing stocks within the North Sea it became very apparent that there are no other stocks with sufficient information through the life history to undertake studies such as these. In the same vein there was not sufficient information on North Sea cod to undertake similar studies to those undertaken on Baltic cod and sprat or Barents Sea cod and capelin. Part of this may stem from the more complicated species interactions seen in the North Sea compared with either the Baltic or Barents Seas.

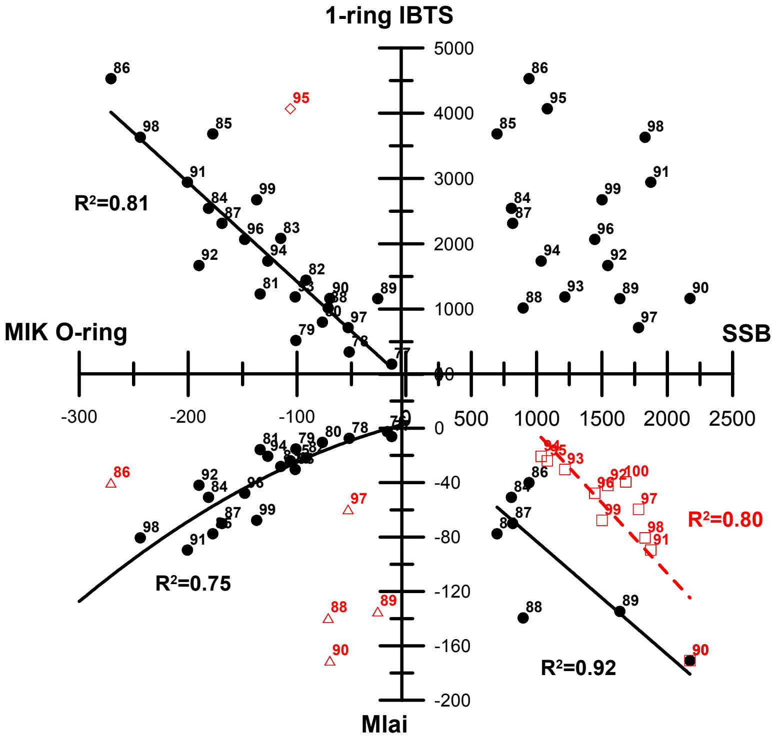


Figure 3.2.3.1. Paulik diagram for North Sea herring using survey data. Axes show the units for each index and are not absolute values. SSB estimated from acoustic surveys, Mlai (Multiplicative Larvae abundance Index), MIK 0-ring (Methot-Isaacs Kidd 0-ring index) and 1-ring IBTS (1-ring index from the International Bottom Trawl Surveys). The SSB/Mlai panel has data divided into pre and post North Sea 'regime shift' (see Reid *et al.* 2001). In the Mlai/MIK panel the years shown as triangles have been removed from the regression. In the MIK/1-ring panel the 1995 data point (open diamond) has been removed from the regression.

3.3 The management context for process information

Management advice for an ICES stock will typically be based on an age-based assessment which estimates the current state of the stock, which is then compared with pre-determined reference points. A short-term catch forecast will be used to present catch options for the forthcoming year for a range of possible levels of fishing mortality, and medium-term projections will be used to make a statement about the probability of a given management objective being achieved as a result of the various management options which are presented. In the absence of explicit management objectives for most stocks, these statements are usually framed around the probability of returning or maintaining the stock above specified biomass reference points.

This system presents two areas where process information might be incorporated: in the determination of reference points, and in the projections used to estimate the probability that the management targets are achieved in the medium-term.

3.3.1 Precautionary Approach reference points

The precautionary approach to fishery management provides the framework for the fishery management advice provided by the ICES Advisory Committee on Fishery Management [ACFM] (ICES, 2000b). This states that reference points will be stated in terms of biomass and fishing mortality rate. These two indicators can be divided into one describing an attribute of the resource (biomass) and one describing an attribute of the fishing fleet (fishing mortality). While the two indicators are related, it is clear that process information is most relevant to the resource indicator. The use of the two indicator scales is summarised in the following extract from the ACFM advice:

In order for stocks and fisheries exploiting them to be within safe biological limits, there should be a high probability that 1) the spawning stock biomass is above the threshold where recruitment is impaired, and 2) the fishing mortality is below that which will drive the spawning stock to the biomass threshold, which must be avoided. The biomass threshold is defined as B_{lim} *(*$_{lim}$ *stands for limit) and the fishing mortality threshold as* F_{lim}*.*

From this extract, it can be inferred that the ICES implementation of the precautionary approach is framed around a rather simple model of stock dynamics, i.e., that there is a specific value of spawning biomass below which recruitment is impaired, and that fishing mortality is the only external factor which influences the size of the spawning stock. Such a simple approach is open to criticism, particularly in view of the information becoming available from process studies. Before elaborating on these criticisms however, it should be noted that the simplicity of this conceptual model has a number of advantages from a management perspective. Firstly, the two indicators, SSB and mean fishing mortality, are readily available from age-based stock assessments, so their estimation does not require data or modelling beyond what is already routine. Secondly, the simplicity also implies a correspondingly simple control rule for management action, e.g., 'If $B < B_{lim}$, then Take Action'. Thirdly, the implication that SSB is influenced only by fishing mortality is often not far from the truth for heavily exploited stocks, with the added justification that fishing mortality is usually the only factor influencing SSB which fishery managers can seek to manage.

As noted above, the results from various process studies imply a number of potential criticisms of the conceptual model underlying the ICES implementation of the precautionary approach. Firstly there is the implicit assumption that SSB is an adequate measure of the stock's reproductive potential, when there is an increasing amount of evidence to indicate that this is not the case – see Section 2. Secondly, there is the assumption that there is a fixed level of SSB (or reproductive potential) below which recruitment is impaired. This in turn implies that recruitment is determined only by reproductive potential; another point which is not consistent with the results of process studies. These points also have implications for the effectiveness of fleet reference points as in cases where stock size is not the only important influence on recruitment, a greater reduction in fishing mortality may be required to ensure a given probability of stock recovery. This in turn implies that process studies have implications for both resource (biomass) reference points, and fleet (fishing mortality) reference points.

Within the context of the current ICES implementation of the precautionary approach, a number of approaches based on use of process information may be possible, for example:

- Use resource reference points which incorporate more biological complexity than SSB. At its simplest this could be no more than specifying a higher minimum SSB in cases where a high proportion of the spawning stock consisted of first time spawners. More complex measures, perhaps even incorporating environmental information might also be possible.
- Set reference points more conservatively in cases where effects other than fishing have a strong influence on the stock, in order that the additional uncertainty due to these other components is accounted for

Although they do not incorporate process information, it is useful to note that the segmented-regression models used by O'Brien and Maxwell (WD3 & WD4) are an objective means of fitting a model which corresponds to the conceptual model behind the ICES implementation of the precautionary approach

3.3.2 Medium-term projections

A key feature of current medium-term projections is the use of a stock-recruitment model to estimate future recruitment. Fitting a stock-recruitment model in this way treats the other factors contributing to recruitment variation (apart from SSB) as residual variation, which is assumed to be random, and using such a model in a projection implicitly assumes that this variation will continue to be purely random. A process study will, by nature, seek to identify other components of this variation. Hence the contribution that a process study may make to medium-term projections will be to increase the proportion of variance allocated to modelled effects and hence to reduce the residual variance. This will not reduce the variance around the projected recruitment estimates unless the additional factors are readily predictable. This applies whether the additional factors are biological, (e.g., fecundity), or environmental, (e.g., temperature). The uncertainty around projections may actually be increased by explicitly accounting for the variation of these additional parameters but this may actually be more realistic as current medium-term projection methods have been shown to under-estimate the uncertainty around stock projections (Patterson *et al*., 2000).

The reallocation of variance through the incorporation of process information represents a potential improvement to the procedure as it makes the assumptions about future variation of the additional factors explicit rather than implicit. This would allow presentation of medium-term projections for a number of scenarios; for example environmental change, as well as improvement of estimation of uncertainty, and thus also in the quality of probabilistic statements which are based on the medium-term projections. This point was addressed in the Report of the first meeting of this Study Group (ICES, 2000a), and some progress in these areas is described in Sections 5.1 and 6.1.

3.3.3 Practical implications of the incorporation of process information in assessment and advice

Process studies can give us the ability to understand why a stock produces a certain level of recruitment for a given number of individuals in that stock and how the stock will behave over space and time. The implication is that more realistic population models and stock projection models can be formulated.

In the context of stock and recruitment the process studies provide information and relationships, often relatively complex, on the factors that influence production and survival. In essence there is a possibility of providing new relationships between stock and recruitment that have a basis in biological processes.

The general problem is that at present very few process studies have been directly undertaken with the intention of input to the assessment and management process. By nature process studies are aimed at understanding what has happened in the past, and hence the models they use are detailed and descriptive, and are often based on multiple-regression-type approaches. These models are not usually suitable for use in projections, partly because of the need to forecast a large number of variables, and partly because of undesirable properties such as the possibility of generating negative recruitment or of generating a finite recruitment at zero stock size. Other drawbacks of these approaches are discussed in ICES (2000a).

The fact that process studies tend not to produce recruitment models which can be used directly within projections means that additional work is required to develop recruitment models for projections using the results from process studies. How this is done depends on the nature and results of the process study, but in general such work might involve identifying a small number of major factors, and considering how these might be incorporated in a recruitment model of an appropriate functional form, and how they might be projected forward. Similar considerations also apply to how external factors might influence such processes as growth and fecundity.

3.3.4 Consequences of incorporation of process information in management advice

As noted above (Section 3.3.1), the current ICES implementation of the precautionary approach assumes that SSB is an adequate measure of the reproductive potential of a stock, and that fishing mortality is the major factor influencing SSB. Under this model, stock recovery is assured if managers can reduce fishing mortality and hence allow SSB to return to above the biomass reference point. The simplicity of this conceptual model has advantages as it is readily understood by other stakeholders in the fishery. Introducing additional biological realism to the management advice would remove this advantage but would hopefully improve the quality and credibility of the advice by more explicit acknowledgement of the influences of effects other than fishing.

4 EFFECTS OF ENVIRONMENTAL VARIABILITY ON FISH STOCKS

4.1 Introduction

It is now well accepted that changes in the environment do impact fish population dynamics. This is evidenced both by the spatial scales over which recruitment appears synchronised for several stocks (Myers *et al*., 1995; Myers *et al*., 1997) and by apparent correlations between recruitment and environmental variables (Ottersen and Sundby, 1995; Myers, 1998; Planque and Frédou, 1999; Fox *et al*., 2000). A significant problem with advancing this work is that variables such as temperature are correlated with many other environmental variables which also affect fish at the individual (and by inference) at the population level. For example, sea surface temperatures in NE Atlantic during the first six months of the year are correlated with atmospheric conditions (NAO) and thus with wind stress and average direction. Wind stress in turn can affect primary productivity through water column processes whilst varying levels of turbulence have been linked with changes in feeding success of fish larvae (Alcaraz, 1997; Dower *et al*., 1997; Fiksen *et al*., 1998). Environment also affects the growth of adult fish both directly and through links with prey availability (Brown *et al*., 1989; Brander, 1995; Dutil *et al*., 1999; Ottersen and Loeng, 2000; Purchase and Brown, 2001). For mature fish, feeding conditions affect condition and the amount of energy which can be put into reproduction. Potentially, combined with whether the fish are first-time or repeat spawners, this could affect subsequent recruitment success (Marshall and Frank, 1999; Marshall *et al*., 1998). Changes in environmental variables such as temperature can also directly affect fish distribution and may lead to changes in spatial overlap with prey (Sparholt *et al*., 1991; deYoung and Rose, 1993; Heessen, 1993; Swain and Wade, 1993; Ottersen *et al*., 1998).

Models developed to explore such relationships vary from simple statistical approaches (examples above) through single species population dynamics models to complex, coupled hydrodynamic-biological models. To date the last category have tended to focus on the biology of early life history stages (Hermann *et al*., 1996; Leising and Franks, 1999). Their complexity and subsequent computer resource requirements currently prevent their application over multiple years which is a requirement for extended time-series population dynamics modelling (Hermann *et al*., 2001). Similarly it can prove prohibitive to undertake multiple model runs for sensitivity testing although applications of engineering simulation theory can help in this respect (Megrey and Hinckley, 2001). Extended time-series population dynamics modelling has thus tended to use simpler, single species population dynamics models but representations of at least some biological processes can be included. The problem is usually knowing how much biological realism it is necessary to include to generate realistic results. The most useful aspect of such models is that they allow explorations of the sensitivity of the population dynamics to changes in rates and processes at different life history stages over several decades of simulated time (Quinlan and Crowder, 1999). Modern computers allow large numbers of model runs to be made producing the scope to explore the effects of stochastic variability. The challenge for the future appears to be in producing models capable of bridging these extremes.

In this section of the working group report we firstly consider some results from a simple, single species population dynamics model for cod. This model is used to explore how North Sea cod population dynamics might be affected by sea temperature. The model is used to assess the relative impacts of temperature on stock dynamics through affects on recruitment (early life history stages) and adult growth. The working question addressed is whether reduced recruitment linked with increased sea temperatures can be compensated for by increases in adult growth rates? One assumption of the model used is that condition (i.e., the relation between length and weight) is constant. In the second section we examine survey based and market sampling data available for North Sea cod and plaice for changes in adult condition factors. We then conduct a simple exploratory analysis to assess whether changes in such factors could be modelled using simple environmental indices as co-variates.

4.2 Modelling the effects of environmental change on North Sea cod

4.2.1 Introduction

Interannual changes in North Sea cod recruitment have been shown to be related to changes in sea surface temperature (SST) (Brander, 1996; Planque and Fox, 1998; Planque and Frédou, 1999; O'Brien *et al*., 2000). The relationship is negative with increased February to June SSTs resulting in reduced recruitment to the stock. Fluctuations in water temperature also have a secondary, continuous effect on cod individuals, through their influence of growth rates and hence weight at age. Cod stocks located in regions with low water temperatures (e.g., Labrador) generally have reduced rates of growth and reach a larger maximum size compared to fish stocks located in warmer waters (e.g., Celtic Sea) (Taylor, 1956; Brander, 1995)

Given this, the expected changes in climate and sea temperatures over future decades will ultimately influence the abundance and biomass of cod stocks. However, although increased temperatures may result in a reduced level of recruitment, this may be offset through higher rates of growth leading to higher Spawning Stock Biomass. We present the results of a study which investigates the combined effects of temperature on recruitment and weight at age, through the use of a self-generating model of North Sea cod.

4.2.2 Model functioning

Overview

The model is a self-generating cod model (similar to WGMTERM (Reeves and Cook, 1994)), but with sea surface temperatures (SST) influencing the interannual changes in the numbers of recruits each January and bottom temperature influencing the changes in the mean length and weight of each age class (Figure 4.1). Abundances of new recruits (at age 1) are calculated using a combined Ricker-temperature stock-recruitment function which incorporates the previous Feb-May SST, and the previous years SSB. For each year, the abundance of age classes 2 to 15 are calculated by considering the levels of fishing and natural mortality (which for 1963 to 2000 were set at ICES 2001 WGNSSK values (ICES, 2002a)). Each month the average increments in length of each year-class are computed using a temperature dependent growth equation. These lengths are then converted into weight using a constant length: weight conversion (currently taken from FISHBASE), multiplied by maturity ogives (currently taken from ICES 2001 WGNSSK) and summated to give SSB of each age class are calculated. The main functional relationships in the model are as follows:

Ricker-Temperature stock-recruitment function

This is an adaptation of the standard Ricker stock-recruitment function with temperature as an added parameter:

$$R = SSB.e^{(\mathrm{a\text{-}b.SSB})}e^{(c.SS\,\mathrm{T})}$$

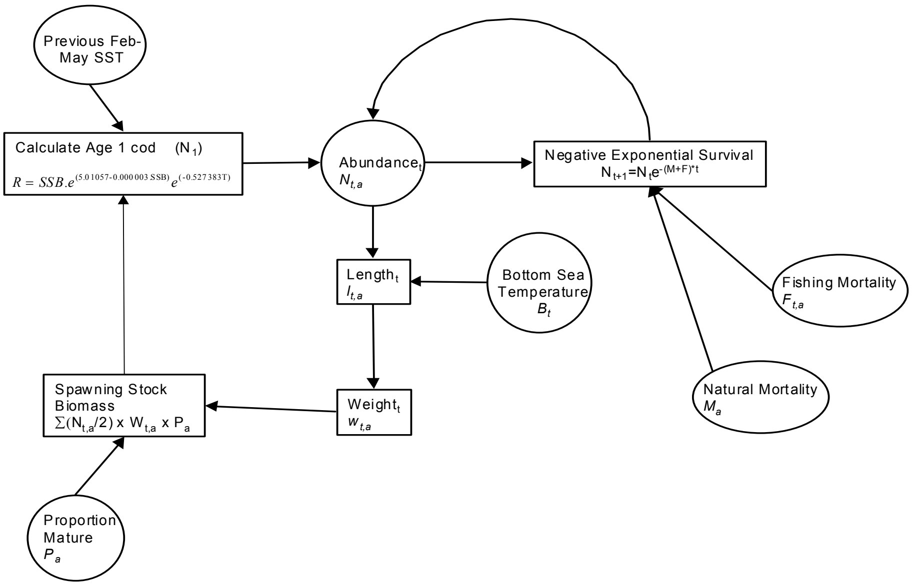


Figure 4.1: Model interrelationships.

where R = the abundance of new recruits, SSB = Spawning Stock Biomass, SST = Sea Surface Temperature. Constants are statistically fitted parameters calculated using data from the 1963–2000 period (a= 5.27542,b= 0.00000355342,c= -0.560823).

Negative Exponential Survival

This function calculates the number of survivors relative to the previous month given the natural and fishing mortality

$$N_t = N_{t-1}e^{-(M+F)t}$$

pressure upon the stock.

where N_t = abundance of fish during that particular month, N_{t-1} = abundance of fish during the previous month. M = instantaneous natural mortality rate. F = instantaneous fishing mortality rate. t = change in time in years (i.e., as monthly t=1/12).

Temperature influenced von Bertalanffy size at age function

The mean length of a particular age class may be calculated using the standard von Bertalanffy function given below:

$$L_a = L_\infty(1 - e^{-K(a-tzero)})$$

where L_a = length at age, L_∞ = asymptotic length (set at 119cm), K = growth parameter, a = age, tzero =age where model registers that length is zero.

Work by Taylor (1956) examining differences in growth rates of cod stocks across the North Atlantic observed that temperature was related to both the rate of growth (K) and the maximum length (L_∞). Thus, K may be calculated as follows:

$$Log_{10}K = 1.22(Log_{10}T) - 1.72$$

where K = growth parameter, T = Bottom temperature.

Taylor (1956) obtained his parameters by relating the growth rates of many North Atlantic cod stocks with the mean water temperatures that these different stocks inhabit (similar models have been formulated by Brander (1995). However, here we are trying to relate relatively small changes in growth rates to similarly small changes in temperature over the 1963 to 2000 period. As such, the parameters in the above equation have been tuned *ad hoc* from those given in the Taylor paper, so that the model will produce weights with a similar mean to that observed over the 1963 to 2000 (see Figure 4.2.3.1.). Taylor (1956) also related differences in L_{inf} to water temperature. However, it has been considered that this is not appropriate for this study when we are only dealing with changes in a single stock (hence L_{inf} is set at 119 cm (Gulland, 1977)).

For the calculation of the length of age 1 cod, the von Bertalanffy equation is used, with the mean annual bottom temperature (obtained from ICES) experienced during the first year of growth used to calculate K. For the length at ages 2+ the differential form of the von Bertalanffy growth equation is used, which calculates the monthly change in length according to age & K, and adds this to the previous length (Gamito, 1998):

$$\frac{\partial l}{\partial t} = \frac{K}{12}(L_{\infty}.1 - K.L_{t-1})$$

where L_{t-1} is the length at the previous time step (in this case the previous month).

4.2.3 Evaluation of model performance and diagnostics

Comparison of observed and modelled cod recruitment and SSB

The fit of the model was evaluated by producing output for the 1963 to 2000 period both incorporating and omitting the influence of temperature on the calculation of recruitment and SSB according to the following scenarios:

1) Ricker. Standard growth
2) Ricker + SST. Standard growth
3) Ricker. Temperature growth
4) Ricker + SST. Temperature growth

The output from each of the scenarios was then compared visually (Figures 4.2 to 4.5) and statistically (Table 4.1) against those values of recruitment and SSB for the 1963 to 2000 period given in the ICES WGNSSK 2001 report.

In order to enable the identification of how well the calculations of recruitment and growth perform separately within the model, two additional scenarios involved the replacement of modelled recruitment and growth with observed values taken from the ICES WGNSSK 2001 report as follows:

5) Observed recruitment. Standard growth
6) Observed recruitment. Temperature growth

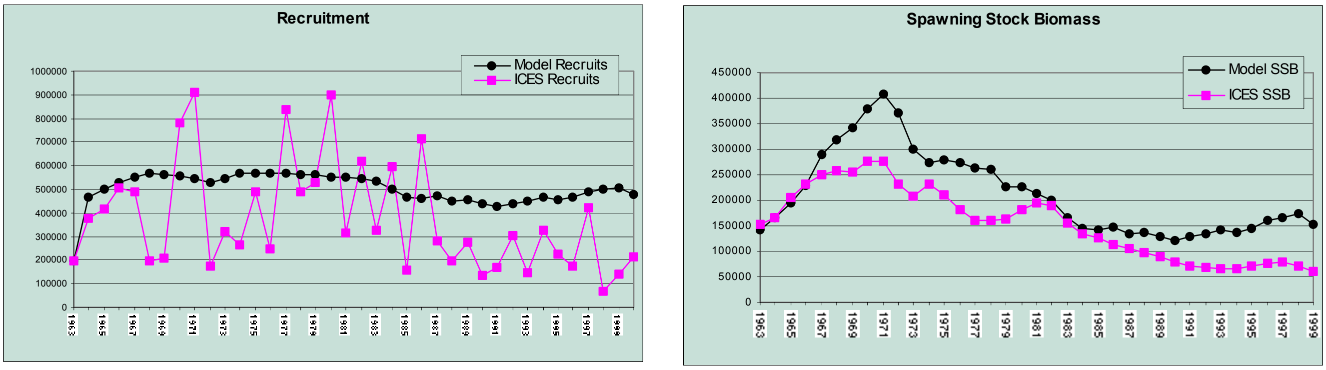
Table 4.1. Sum of squares error (x 10^{-8}) between the observed and modelled recruitment and SSB.

Model run	Recruitment	SSB
Observed recruits, Standard growth	0.00	116.65
Observed recruits, Temperature growth model	0.00	185.07
Ricker, observed weight at age	22763.36	1736.60
Ricker, Standard growth model	20295.30	1211.87
Ricker, Temperature growth model	20193.57	799.69
Ricker + SST, observed weight at age	10384.32	790.86
Ricker + SST, Standard growth model	10916.53	1266.19
Ricker + SST, Temperature growth model	10309.60	415.64

The inclusion of SST in the calculation of the abundance of recruits notably improves the fit of the model to predict the abundance of recruits (Figures 4.2 to 4.5, Table 4.1). However, the additional inclusion of temperature information in the calculation of length (and thus weight) at age produces little additional improvement in the prediction of recruitment (c.f. Figure 4.2 with 4.4, and Figure 4.3 with 4.5), due to the negligible effect that changes in SSB (over the range of values considered here) are predicted to have on recruitment i.e., over this range of SSB the Ricker function is almost flat.

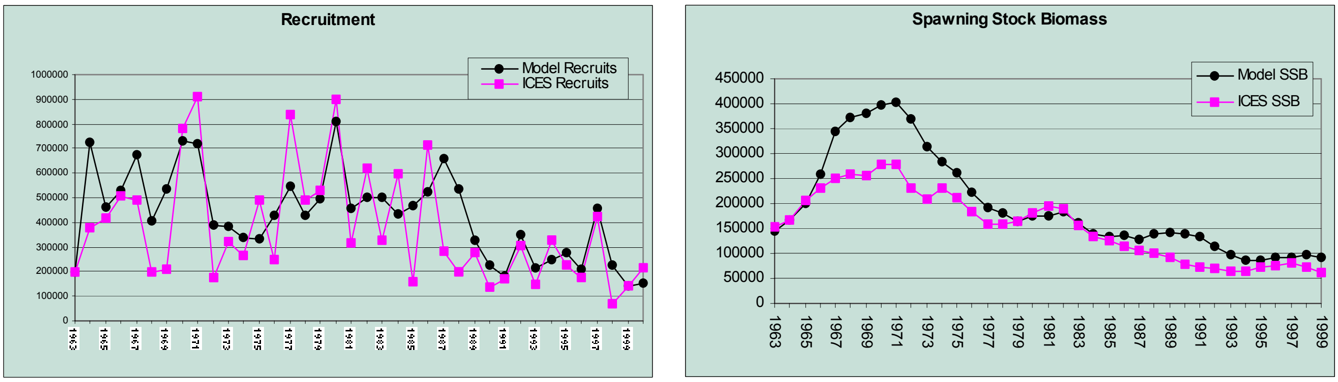
A greater improvement is observed when temperature information is incorporated into the prediction of SSB, as omitting the temperature information causes the model to overestimate the SSB. However, not too much credence can be placed on this, as the equation of Taylor (1956) has been tuned to mimic the observed weights at age. Unsurprisingly therefore, there is a reasonable similarity between the modelled and observed mean weights at age. Figure 4.6 shows the median modelled weight at age is too low for age 1, slightly below the observed for ages 2, 5, 6, 7, 9 and similar for ages 3, 4, 8, 10, 11. The variation in weight is reasonably captured by the model for ages 1 to 5. However, older age classes have increasing inter-annual variation in weight which the model does not reproduce.

The greater variation in observed weight at age relative to modelled weight at age may be seen in Figure 4.6 (left hand plot). A comparison of the weight at age by year using correlation analysis (Table 4.3) shows evidence of similar trends in modelled and observed weight for age classes 1 and 2. However, it is proposed that in the near future, the weight at age portion of the model will be more thoroughly reviewed and re-parameterised (see below).


Recruitment

Spawning Stock Biomass

Figure 4.2. Comparison of model output produced using the standard Ricker function and standard von Bertalanffy growth curve, with ICES values.


Recruitment

Spawning Stock Biomass

Figure 4.3. Comparison of model output produced using the temperature-Ricker function and standard von Bertalanffy growth curve, with ICES values.

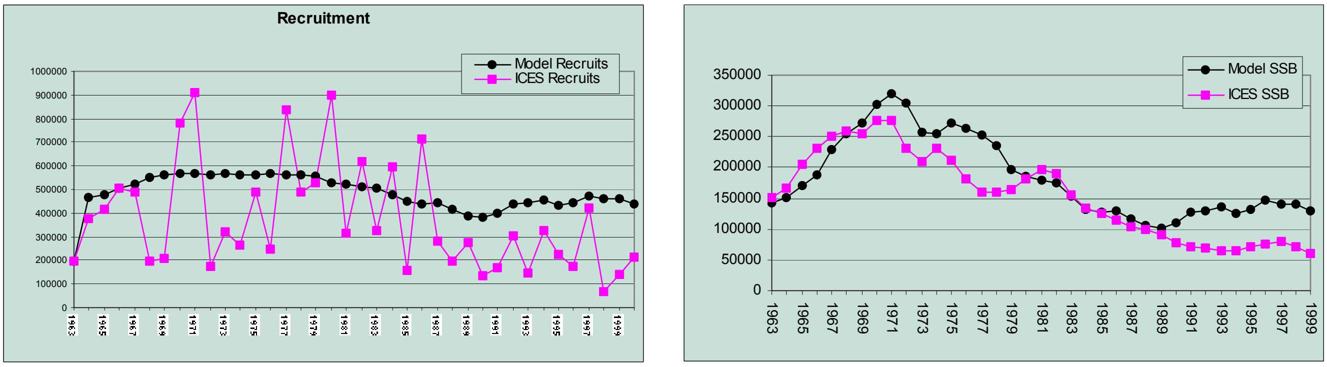

Recruitment

Figure 4.4. Comparison of model output produced using the standard Ricker function and temperature influenced growth function, with ICES values

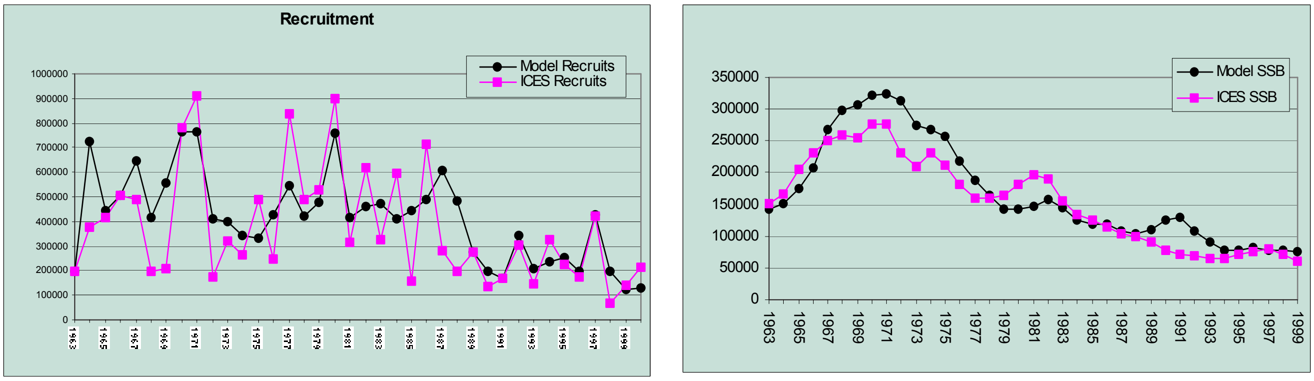

Recruitment

Figure 4.5. Comparison of model output produced using the temperature-Ricker function and temperature influenced growth function, with ICES values.

The distributions of observed and modelled weights at age were compared over the 1963 to 1997 period (Figure 4.6). A second comparison involved evaluating the observed changes in weight at age with time against the modelled weight at age with time (Figure 4.6).

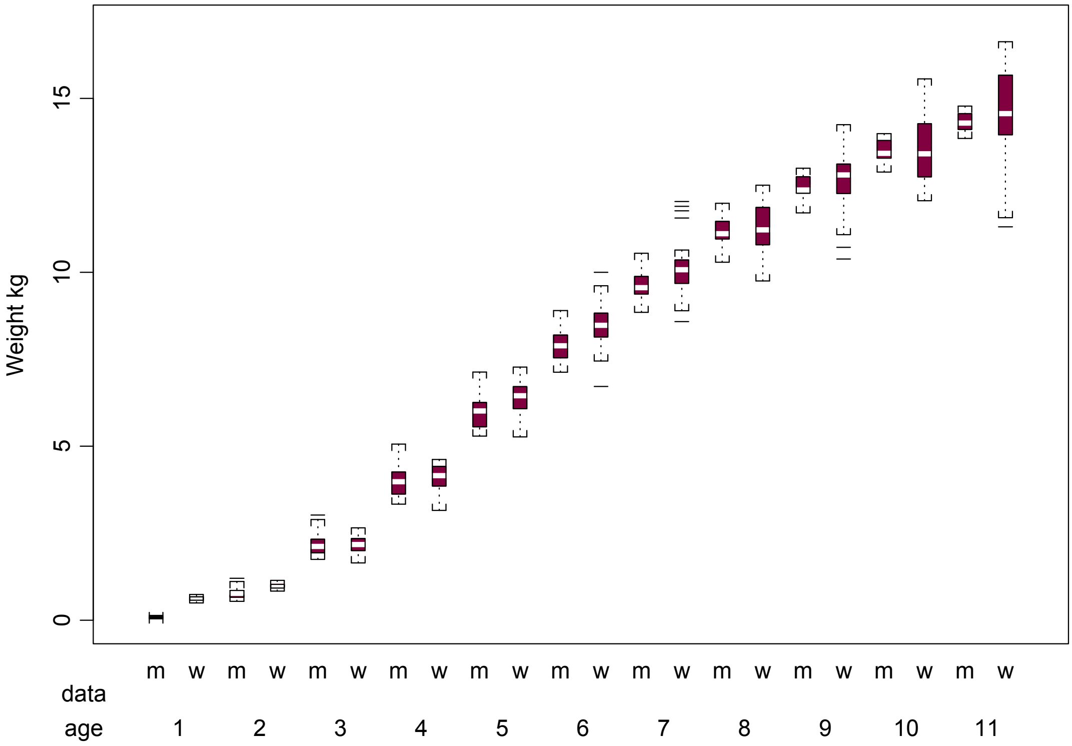
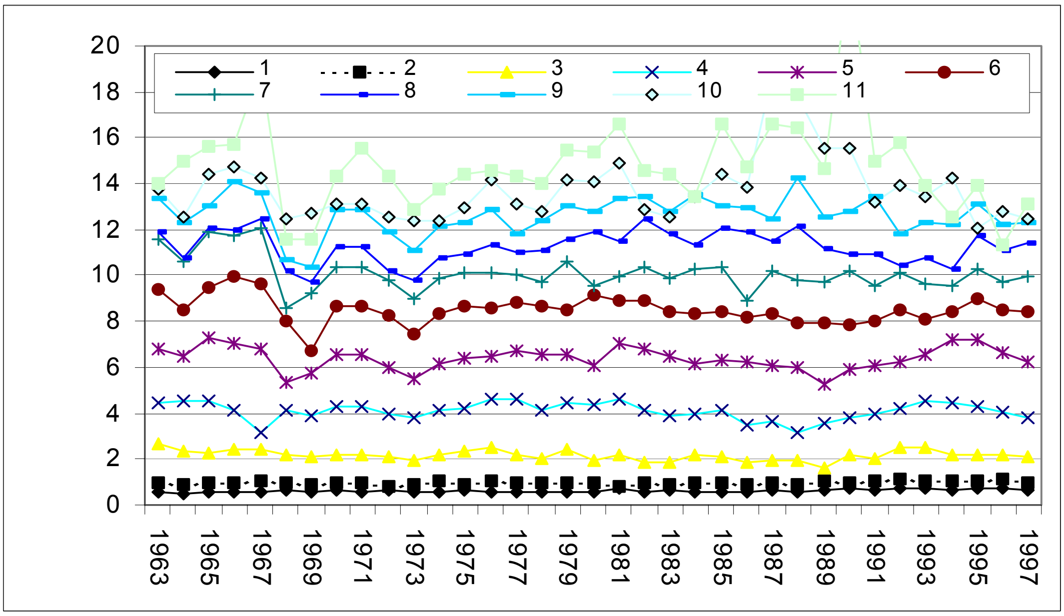


Figure 4.6. Comparison of modelled (m) weights at age with observed values from working group report (w). Solid block part of bar represents 25th to 75th percentile, white horizontal bar the median.

The greater variation in observed weight at age relative to modelled weight at age may be seen in Figure 4.7 (upper plot). A comparison of the weight at age by year using correlation analysis (Table 4.2) shows evidence of similar trends in modelled and observed weight for age classes 1 and 2.



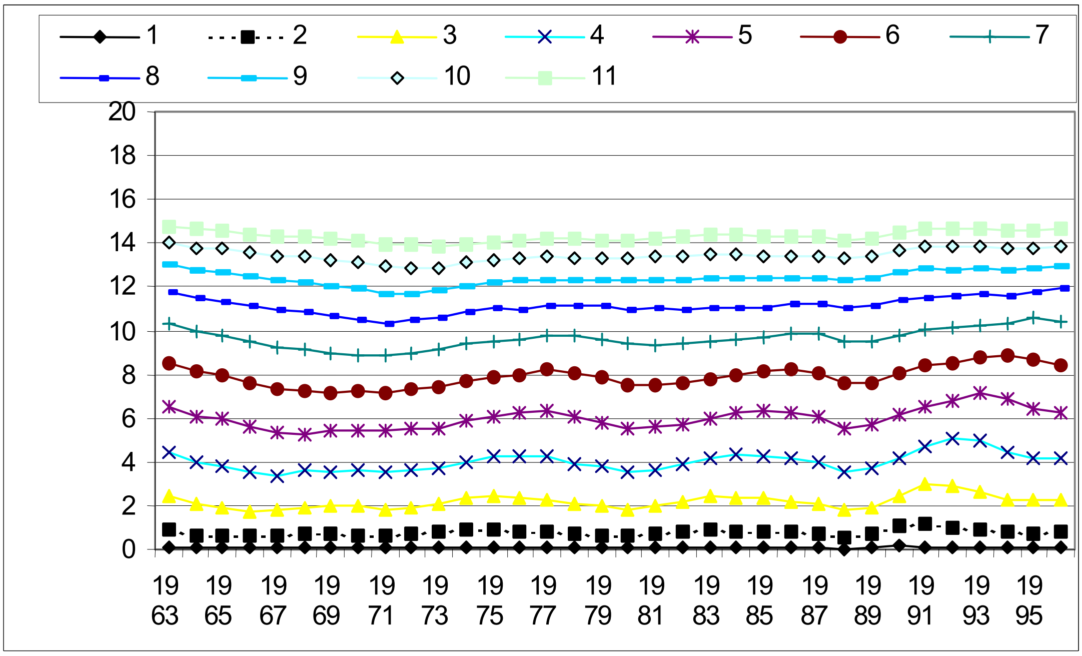


Figure 4.7. Comparison of observed weight-at-age 1963–1997 (upper plot), with modelled weight-at-age (lower plot) 1963–2000.

Table 4.2. Results of correlation analysis between observed and modelled interannual fluctuations in weight.

Age class	r	p
1	**0.536**	**0.001**
2	**0.384**	**0.023**
3	0.209	0.228
4	0.326	0.056
5	0.307	0.073
6	0.122	0.484
7	0.086	0.625
8	0.153	0.38
9	0.203	0.241
10	0.037	0.833
11	0.016	0.927

Examination of bias in modelled SSB

An examination of Figures 4.2 to 4.3 show that there is a bias in the modelled SSB, with the observed SSB being lower than the modelled SSB over the late 1960s/early 1970s. This is despite the model underestimating the weights at age (see above). In order to ensure that this bias was not caused by an inherent error in the calculation of recruits, residuals obtained from the modelled and observed recruits and SSB were plotted. In addition, a comparison of the stock-recruitment functions fitted to the data, with that used in the ICES WGNSSK report was made.

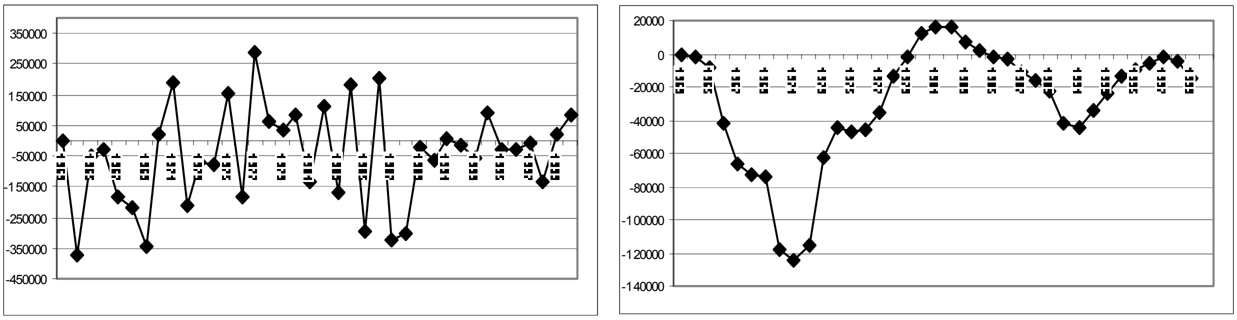


Figure 4.8. Residuals from modelled recruitment (left) and SSB (right) calculated using the temperature Ricker function.

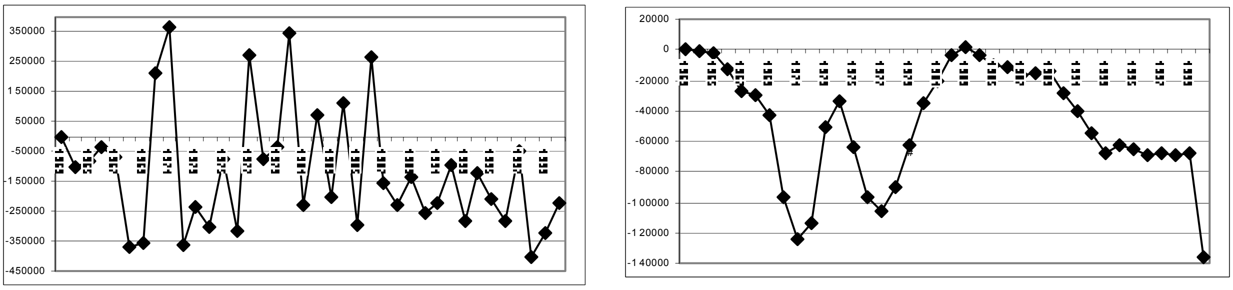


Figure 4.9. Residuals from modelled recruitment (left) and SSB (right) calculated using the standard-Ricker function.

The residual plots (Figures 4.8 and 4.9), taken together with Figures 4.2 to 4.5 suggest that any bias in the SSB is simply due to the different abundances obtained in the calculation of the abundances of recruits. For example, the observed overestimation of recruitment in both the standard and temperature models from 1963 to 1970, and the resulting increased cod abundances resulting from this for the next few years, is the cause of the later bias in SSB during the late 1960s/early 1970s.

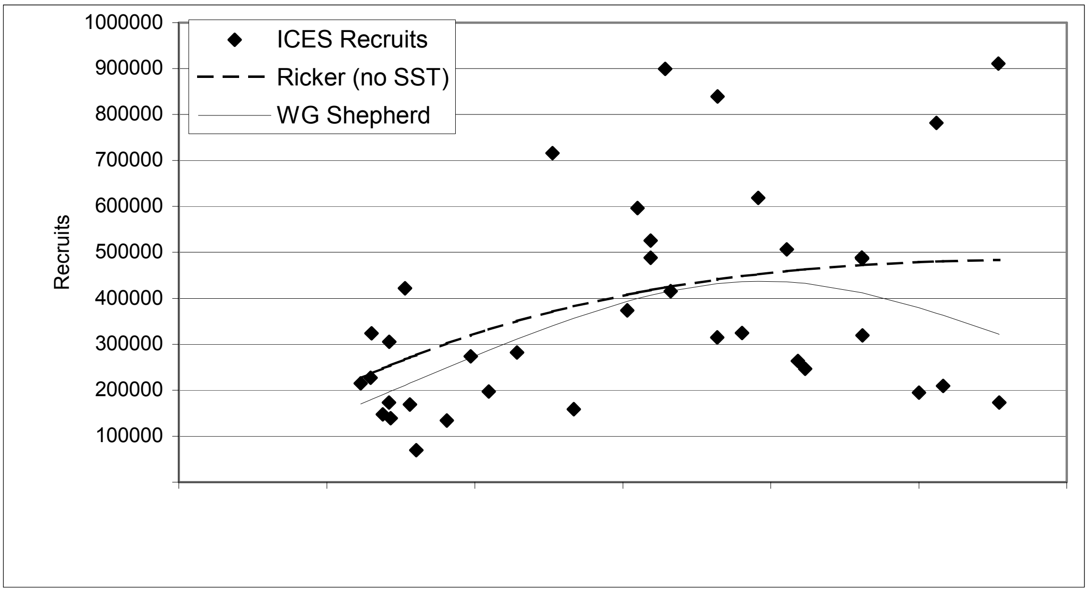


Figure 4.10. Comparison of fitted stock-recruitment functions from the model (Ricker (no SST) and Ricker + SST with that in the ICES WGNSSK report (WG Shepherd). Note that the functions have not been bias corrected.

A final examination of the modelled stock-recruitment functions (Figure 4.10) suggests that there is little difference between the Ricker (no SST) and the WG Shepherd fits, except at the higher values of spawning stock biomass.

4.2.4 Conclusions

Models of this type can be used for examining the relative impacts of changes in environmental variables such as temperature on different life history stages of fish population dynamics. The model described above will be used in conjunction with sea temperature projections from coupled ocean-atmosphere circulation models to examine possible impacts of climate change on cod.

4.3 Modelling variation in North Sea cod condition factors

Weight and length at age data for individual fish are available from the English third quarter groundfish survey for the years 1979–1981, 1989, 1990, and 1996–2001. In addition, for each observation the position at which it was caught (latitude, longitude), the sex and age of the fish were available. Due to the scarcity of data for older ages and age 0, only data for ages 1–5 was used in the fitting of the linear models.

In order to examine the variation in Fulton’s condition factor (weight/(length)^3), taken to be a proxy for the quality of the spawning potential of the fish, a log weight – log length linear model was fitted to the data and the effects of explanatory variables on the variability about this relationship examined. The form of the fitted model was:

$$\text{Log (weight)} = \alpha + \beta \text{ Log (length)} + \delta \text{ A} + \varepsilon \text{ B} + \gamma \text{ C}$$

where $\beta,\delta,\varepsilon,\gamma$ are the regression coefficients for explanatory variables A, B and C. In addition to the main explanatory variables effects, and where the sampling design permitted, the interactions between explanatory variables were examined. The parameter α equates to Fulton’s condition factor.

The analysis of variance tables for the linear models is presented in Table 4.3. In each case an analysis of variance was used to compare model structures. Latitude and sex were found to be non-significant effects within all models in which they were fitted. Year effects were found to have a significant influence on model fit as both a main effects and within interaction terms with the coefficient of Log length. This indicates variation in the power relationship between length and weight within years. When age and year class effects were fitted within the model, they were found to be significant effects only if the interaction between the coefficient of Log length and the year of sampling was omitted from the model.

The final fitted model is listed in Table 4.3 as model 13. It included main effects for longitude Log length and a year effect with and interaction between year and Log length. Plots of the residual from the fitted model, model predictions and observed values are presented in Figures 4.11. Longitude has a strongly significant effect with fish collected in the Western North Sea having higher condition factors (Figure 4.12). The year effects in condition show that weight at length has been declining throughout the time period for which data is available (Fig 4.13). Recent values appear to have been more stable.

Excluding 2001, annual average bottom temperature data were available for each of the years in which the samples were taken. In order to examine correlation between the temperature signal and condition factor a model that included only Log length and the temperature time series as a linear term. The model diagnostics show that temperature has a significant effect on the fit of the model to the observations. Table 4.4. The coefficient is negative indicating a decrease in weight per unit length with increasing temperature (Figure 4.14). However, the reduction in the variance of the model fit was not as great as that achieved when fitting individual year effects to the condition factor time series. If year effects were fitted within the model the temperature effect is not significant. Table 4.4 also shows that there is a significant effect of an interaction between temperature and age on the fit of a length weight model. This suggests that there is a different effect of temperature at each age.

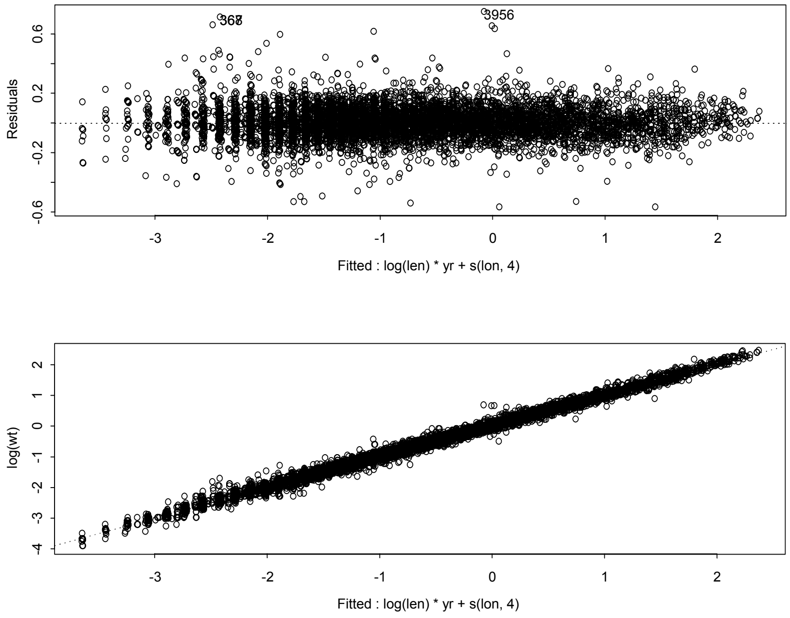
The results of this analysis are preliminary, no causal mechanism has been suggested and the fit is to average annual temperature. It would be expected that a temperature series recorded prior to the capture of the fish and from the location in which the fish was captured would have a dominant effect on an individual's condition.

Table 4.3. The analysis of deviance table used to fit the log weight log length generalised linear and additive models to the English groundfish survey data for North Sea cod.

Terms	Resid. Df	RSS	Test	Df	Sum of Sq	F Value	Pr(F)	Model
log(len)	7712	90.59865						
log(len) + lat	7711	90.59803	+lat	1	0.000619	0.0527	0.81840	1
log(len) + lon	7711	90.56313	+lon	1	0.035518	3.0242	0.08207	2
log(len) + factor(sex)	7710	90.58079	+factor(sex)	2	0.017863	0.7602	0.46759	3
log(len) + factor(yr)	7702	83.75453	+factor(yr)	10	6.844125	62.938	0	4
log(len) + factor(yc)	7690	84.19453	+factor(yc)	22	6.404122	26.588	0	5
log(len) + factor(age)	7708	90.39423	+factor(age)	4	0.204425	4.3579	0.00161	6
log(len) + factor(yr)	7702	83.75453						
log(len) * factor(yr)	7692	82.21828	+log(len):factor(yr)	10	1.536242	14.372	0	7
log(len) * factor(yr)	7692	82.21828						
log(len) * factor(yr) + factor(sex)	7690	82.20466	+factor(sex)	2	0.013627	0.6374	0.5287	8
log(len) * factor(yr) + lat	7691	82.21718	+lat	1	0.001108	0.1037	0.7475	9
log(len) * factor(yr) + lon	7691	82.08083	+lon	1	0.137456	12.880	0.0003	10
log(len) * factor(yr) + factor(age)	7688	82.16372	+factor(age)	4	0.054566	1.2764	0.2767	11
log(len) * factor(yr)	7692	82.21828						
log(len) * factor(yc)	7668	82.72291	1 vs. 2	24	-0.50462	1.9490	0.0036	12
log(len) * factor(yr) + lon	7691	82.08083						
log(len) * factor(yr) + s(lon, 4)	7687	81.31790	1 vs. 2	3.0	0.762924	24.037	1.776357e-015	13

Table 4.4. The analysis of deviance table used to examine the effect of temperature on the fit of the log weight log length for the English groundfish survey data for North Sea cod.

Terms	Resid. Df	RSS	Test	Df	Sum of Sq	F Value	Pr(F)	Model
log(len)	7295	87.41872						
log(len) + temp	7294	86.73512	+temp	1	0.6835991	57.48734	3.819167e-014	14
log(len) + temp	7294	86.73512	+temp	1	0.6835991	57.48734	3.819167e-014	
log(len) + temp+factor(age):temp	7290	86.52371	+factor(age):temp	4	0.2114185	4.453234	0.001354111	15



Figures 4.11a and 4.11b. The residual vs model prediction and observed value vs model prediction plots for a linear model of Log weight against Log length with covariates for the North Sea cod.

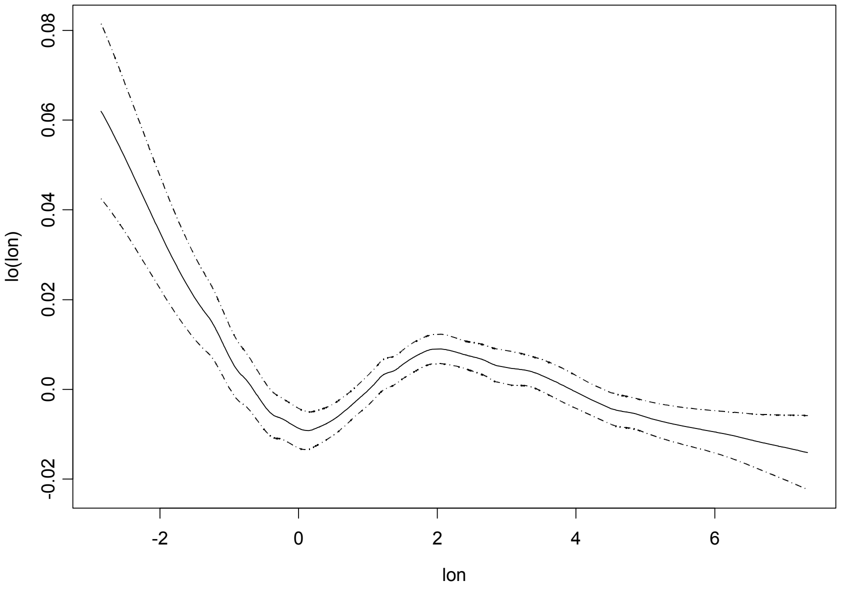


Figure 4.12. The response effect for the weight of North Sea cod to the position from which the English groundfish survey samples were taken. Lon – Longitude, negative values represent degrees west of the Meridian.

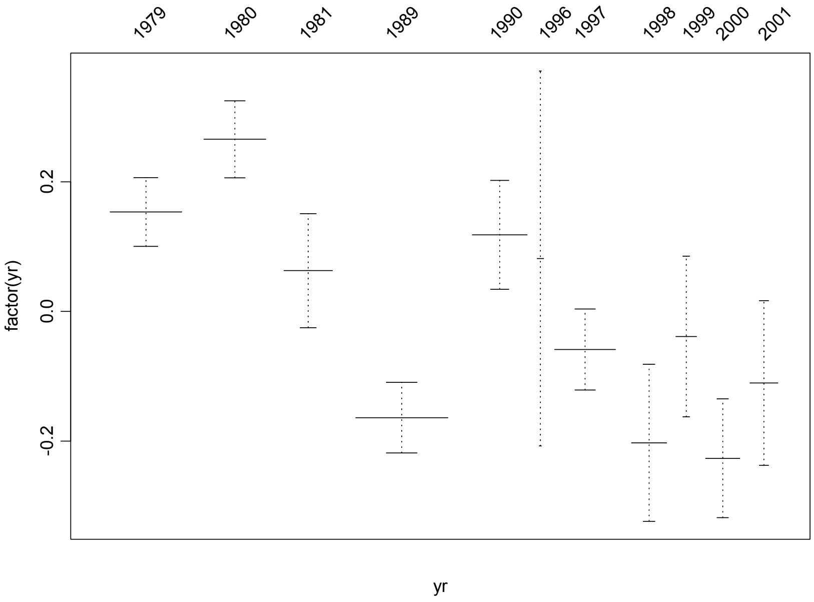


Figure 4.13. The response effect for the weight of North Sea cod to the year in which the English groundfish survey samples were taken.

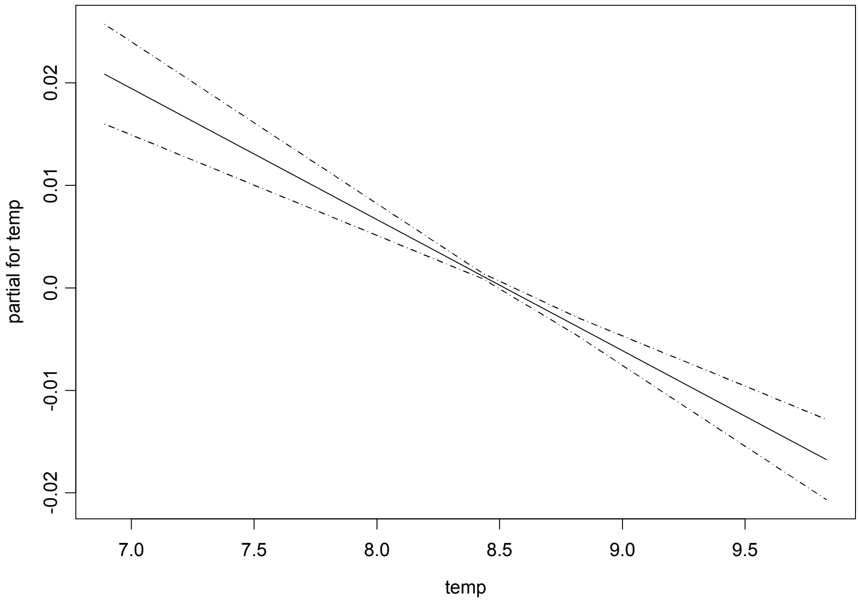


Figure 4.14. The response effect for the weight of North Sea cod to the average annual temperature of the year in which the English groundfish survey samples were taken.

4.4 Changes in North Sea plaice condition

4.4.1 Methods and results

Data for this analysis are available both from research surveys and from market sampling, principally from the port of Lowestoft over the period 1983 to 1999. The data were extracted from the biological sampling database held at CEFAS, Lowestoft. A breakdown is given in Table 4.4. The complete dataset contains 50,000 records from market sampling and 11,654 from ground-fish surveys. Survey derived data were not considered in further analyses since the fishing gear used in the North Sea is not designed to sample plaice. For most years from 1983 onwards, the market sampling consists of between 100–300 records per month. The origin of the fish is described in (Bromley, 2000) and are principally form the central North Sea. In general individual parameters of age (from otolith analyses), length, gutted weight, sex, maturity stage have been recorded (note that plaice caught during the ground-fish survey are weighed complete). The data have been analysed by (Bromley, 2000). Plaice sexual maturation was shown to be affected by body weight, age and geographical location and was subject to annual and seasonal variation. A clear annual cycle of changes in weight at age for mature fish was demonstrated with weight increasing in the months prior to the onset of spawning (June-Dec) followed by a rapid decrease. Male fish showed a similar, though less extreme cyclical pattern. Of interest to the present working group are whether there are identifiable patterns in change of weight at length (condition) in the dataset. This was not analysed by (Bromley, 2000). Condition was computed as

$$\text{Condition} = (\text{weight}/(\text{length})^3)*100 \qquad (1)$$

Figure 4.15 shows the cycles in median condition with age averaged. A clear difference between male and female fish is apparent with the males reaching a peak in condition a month or two before the female fish.

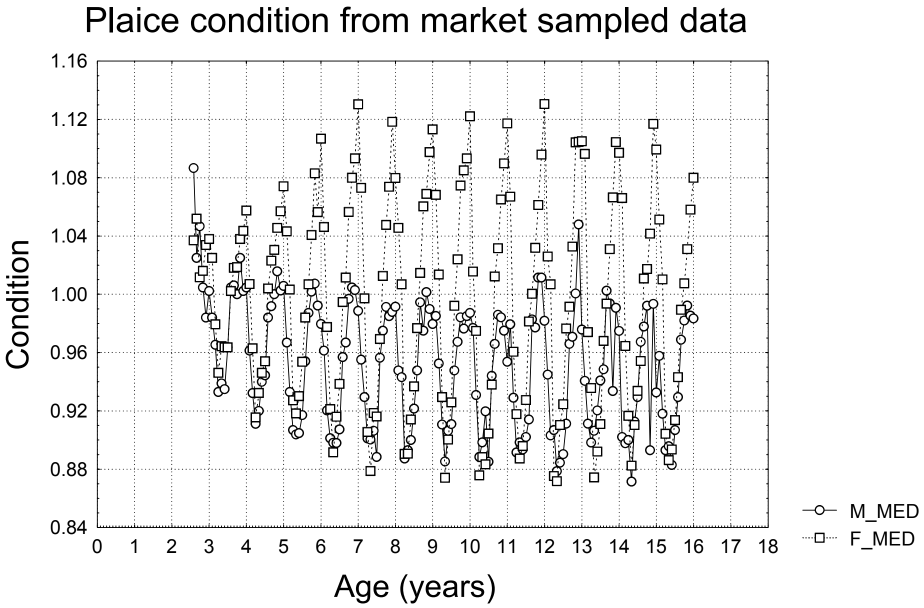


Figure 4.15. Changes in condition of male and female fish with age averaged over all years.

Figures 4.16 and 4.17 show annual cycles in median condition for all male and female fish. There are indications of periods when peak condition appeared to be lower than average (e.g., 1991–1994 for female fish).

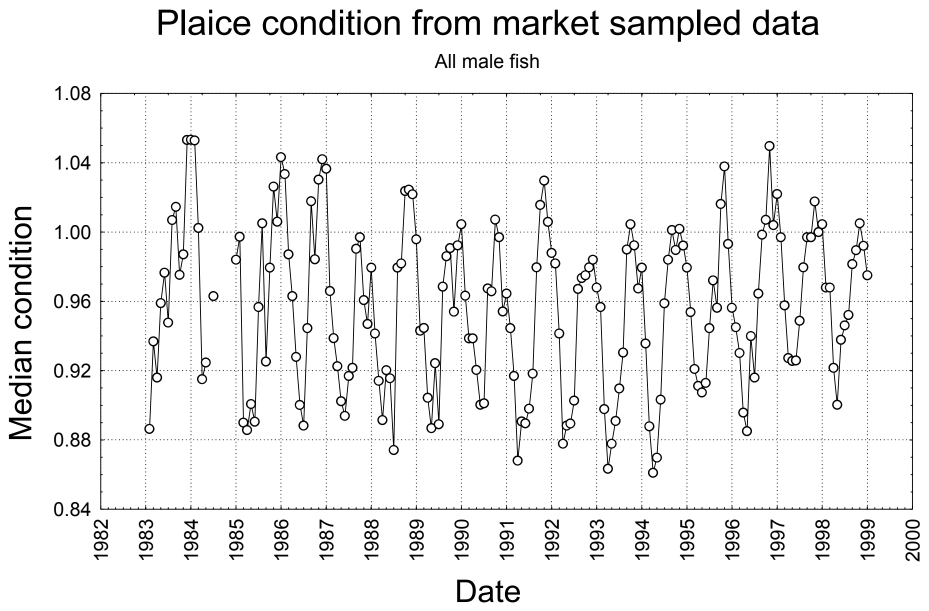


Figure 4.16. Annual cycles in median condition for male plaice.

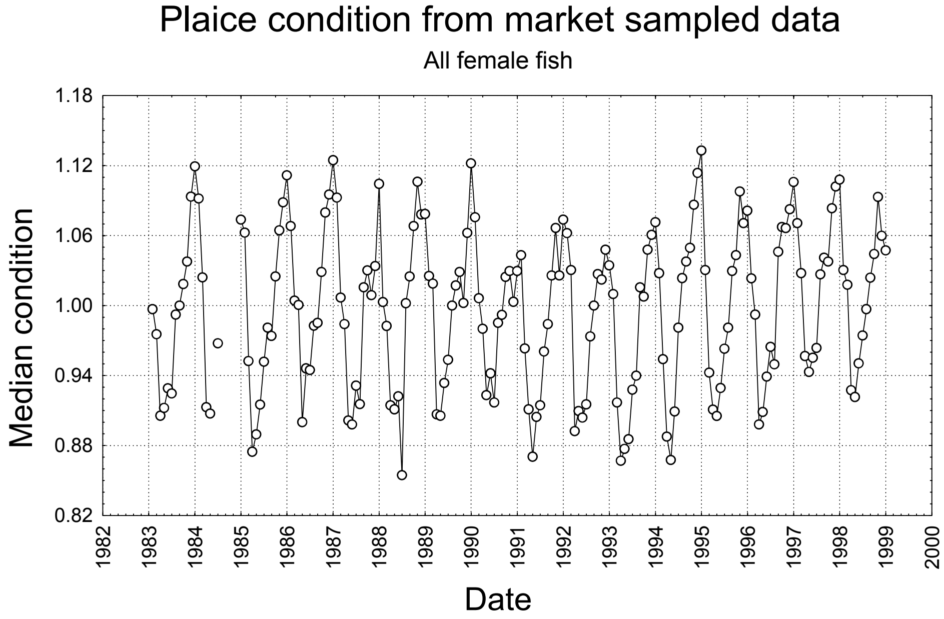


Figure 4.17. Annual cycles in median condition for female plaice.

Exploratory plots were made to evaluate whether there was any connection between peak female condition and peak North Sea bottom temperatures. Figure 4.18 shows that there does not appear to be any obvious relationship but it must be emphasised that this is a very preliminary and crude analysis, for example the bottom temperature data are averaged for the whole southern North Sea and not targeted from regions where plaice feed during the summer. Condition is likely affected by many other factors than temperature and this would require further exploration.

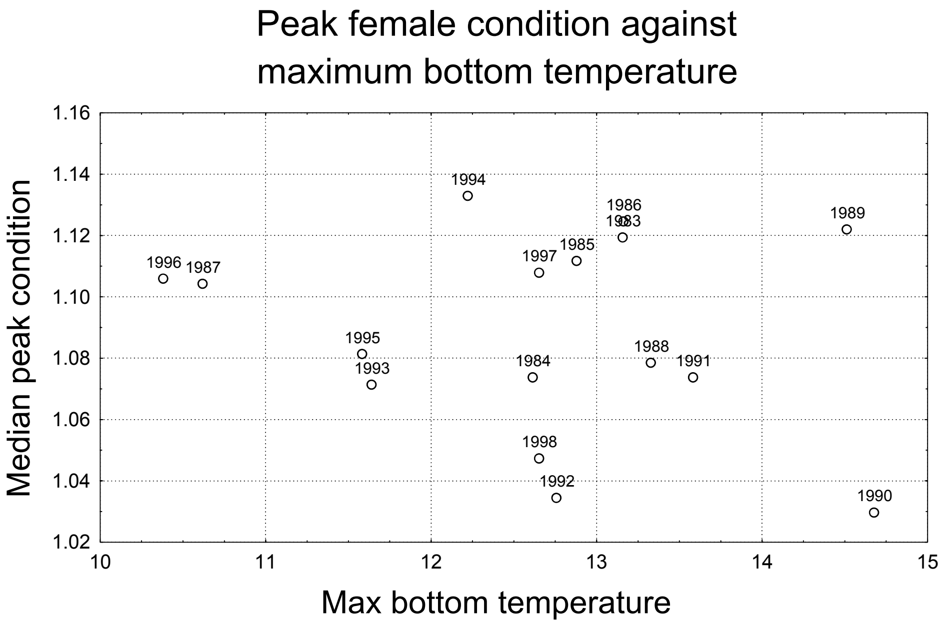


Figure 4.18. Peak female condition against peak monthly mean bottom water temperature for whole North Sea.

Table 4.4. Summary of southern North Sea plaice data available from surveys and market sampling.

	From groundfish survey	From market sampling
1977 Female	404	0
1977 Male	296	0
1978 F	458	0
1978 M	354	0
1979 F	463	0
1979 M	367	0
1980 F	390	0
1980 M	259	0
1981 F	411	0
1981 M	300	0
1982 F	221	0
1982 M	170	0
1983 F	211	2326
1983 M	177	1117
1984 F	270	2285
1984 M	207	1051
1985 F	266	2263
1985 M	187	1128
1986 F	331	2221
1986 M	252	993
1987 F	276	2357
1987 M	225	1021
1988 F	419	2274
1988 M	316	800
1989 F	395	2379
1989 M	314	841
1990 F	464	1833
1990 M	353	1036
1991 F	567	1719

	From ground-fish survey	From market sampling
1991 M	434	973
1992 F	210	1746
1992 M	157	986
1993 F	152	1614
1993 M	107	953
1994 F	0	1484
1994 M	0	902
1995 F	0	1505
1995 M	0	938
1996 F	247	1753
1996 M	144	982
1997 F	374	1922
1997 M	264	966
1998 F	56	1851
1998 M	53	1031
1999 F	72	1772
1999 M	61	978
Total number of observations	11654	50000

A preliminary exploratory analysis was undertaken to investigate the relationship between condition factor and the sexual maturity of female North Sea plaice. The maturity data were derived from the Lowestoft fish market during the period 1983–1999 and the English summer ground-fish surveys of the North Sea from 1977–1998. Data from the market sampling for months August to December (6,500 fish) and from the surveys for the same months (3,100 fish) were analysed. Market sampled fish are gutted at sea, but the gonads were left *in situ*. The stage of sexual maturity was ascertained for length-stratified samples of up to 200 fish (mixed sexes) per month, based on visual inspection of the exposed anterior region of the gonad. For this analysis, ovaries were classed as immature or maturing/mature. Plaice maturity was also sampled on the annual English, summer (August/September) North Sea groundfish surveys from 1977–1998, which covered the whole North Sea. The fish were caught in a Granton trawl with a 20 mm stretched-mesh liner in the cod end to retain smaller plaice than are landed commercially. Sampling was length stratified on a regional basis, with the fish being measured and weighed at sea.

Regression analysis was used to summarise the data to ascertain the general trends in maturity in relation on to year, age and condition factor. The form of the model was:

$$\text{Logit}(E[y]) = I + \beta_1 Y_i + \beta_2 A_i + \beta_3 C_i$$

In the model the maturity of each individual fish was input in binary form, taking the value 0 if the gonad was immature and 1 if the gonad was maturing. The estimated maturity level (E[y]) predicted by the model was the number of maturing and mature fish expressed as a proportion of the total number of fish, where I = intercept, Y= year, A = age in years and C = Condition factor (100*Weight/Length^3). The exploratory analysis was undertaken for female fish only.

The results from market sampling (Table 4.5 and Figure 4.19) show the proportion of maturing/mature fish increased markedly with the age of the fish as expected. However, there also appears to be an effect of condition with young fish needing to reach a higher condition factor before starting to mature. Within year classes there is variability in maturity, which appears to be related to year effects and the month of sampling. It is clear that when condition factor is high, a greater proportion of fish are likely to mature, thereby increasing the spawning stock biomass estimates. Similar results are apparent in the analysis of ground-fish survey data (Table 4.6 and Figure 4.20). The shape of the relationship is slightly different probably reflecting the more restricted time over which the fish are sampled (August-September as opposed to August-December). The conclusions from the ground-fish survey data are in accord with those reached based upon market-sampled data.

Table 4.5. Logistic modelling of plaice maturity data derived from English market sampling.

Logit(MATURITY) = -72.11 + 0.031 YEAR + 1.22 AGE + 6.21 CONDITION

Analysis of Deviance

Source	DF	Deviance	Deviance / DF	Scaled Dev	Pr>
Model	3	2298.8963	766.2988	2298.8963	<.0001
Error	6556	3243.5765	0.4947	3243.5765	
C Total	6559	5542.4728			

Type III (Wald) Tests

Source	DF	ChiSq	Pr > ChiSq
YEAR	1	9.0273	0.0027
AGE	1	686.5551	<.0001
COND	1	219.2528	<.0001

Parameter Estimates

Variable	DF	Estimate	Std Error	ChiSq	Pr > ChiSq
Intercept	1	-72.1103	20.7523	12.0743	0.0005
YEAR	1	0.0313	0.0104	9.0273	0.0027
AGE	1	1.1791	0.0450	686.5551	<.0001
COND	1	6.2050	0.4191	219.2528	<.0001

Table 4.6. Logistic modelling of plaice maturity data derived from English ground-fish survey.

Logit(MATURITY)= - 26.17 + 0.010 YEAR + 1.04 AGE + 2.22 CONDITION

Analysis of Deviance

Source	DF	Deviance	Deviance / DF	Scaled Dev	Pr>
Model	3	1164.4013	388.1338	1164.4013	<.0001
Error	3139	2839.9536	0.9047	2839.9536	
C Total	3142	4004.3550			

Type III (Wald) Tests

		Pr >	
Source	DF	ChiSq	ChiSq
YEAR	1	2.0946	0.1478
AGE	1	516.5365	<.0001
COND	1	39.6058	<.0001

Parameter Estimates

			Pr >		
Variable	DF	Estimate	Std Error	ChiSq	ChiSq
Intercept	1	-26.1746	14.4988	3.2591	0.0710
YEAR	1	0.0105	0.0072	2.0946	0.1478
AGE	1	1.0457	0.0460	516.5365	<.0001
COND	1	2.2233	0.3533	39.6058	<.0001

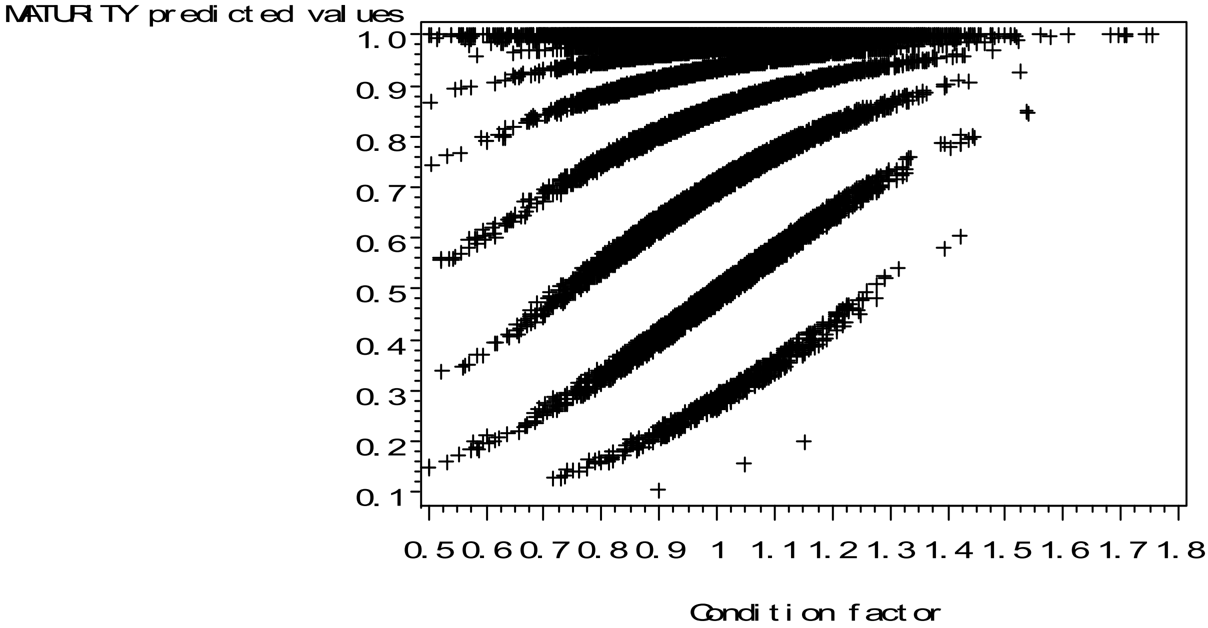


Figure 4.19. English market sampling of North Sea plaice.

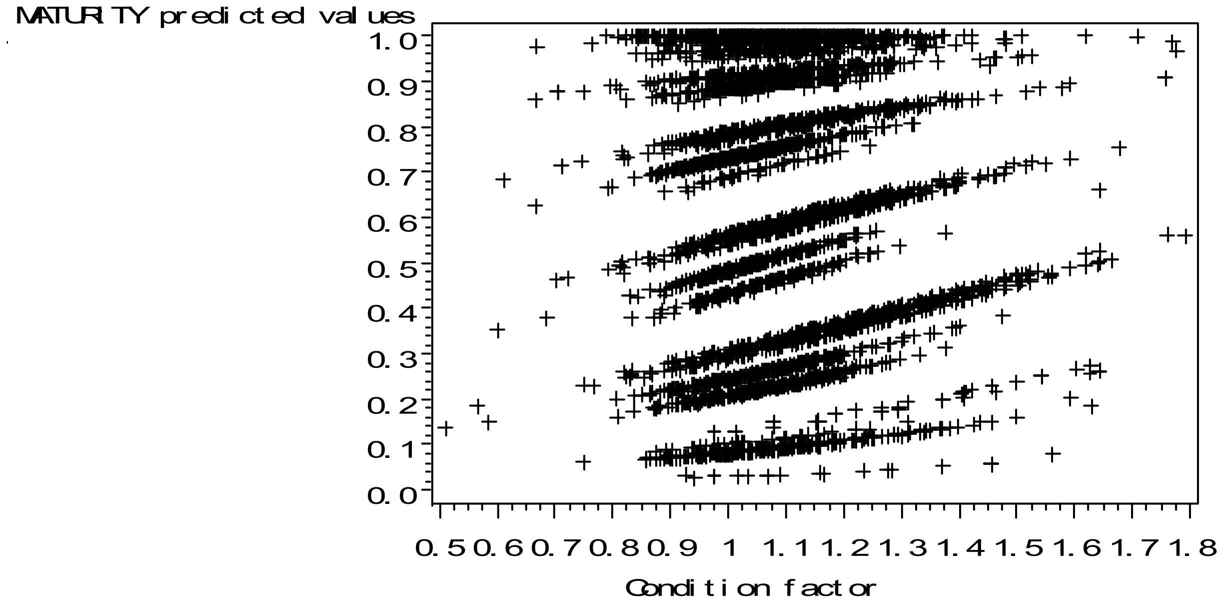


Figure 4.20. English ground fish sampling of North Sea plaice

4.4.2 Conclusions

The allometric weight length relationship expressed as a simple condition index for plaice in the central North Sea shows clear annual cycles related to maturation and spawning. The peak of condition is reached in December for female fish and in October or November for male fish. As well as the month of sampling, condition is influenced by the sex and age of the fish as indicated by (Bromley, 2000). Statistical modelling also indicates that there is a significant year effect and there is some preliminary indication that periods of lower than average or higher than average peak condition may persist for several years. For any age group, higher condition during August – December is linked to an increased probability of ovaries maturing. The data suggest that maturity ogives used in the assessment could potentially be tuned using fish condition data. The level of condition reached in any year is presumably related to the overall feeding success of the maturing fish balanced against metabolic demands. Since temperature might be expected to affect growth and possibly levels of prey availability we undertook a crude analysis using North Sea bottom temperature data. However, this variable alone does not appear to explain inter-annual changes in peak female condition. It must be cautioned that the analysis was extremely crude and could be extended to include more direct measures of potential growth regulating factors on the feeding grounds such as prey availability or temperature data selected from the known summer feeding areas of plaice in the North Sea. Excepting temperature, the likely limit on these analyses will be the availability of time-series data for variables such as prey availability for non-coastal regions of the North Sea. The data described were derived from the English plaice fishery which takes place in the central North Sea. Similar market sampling data have also been collected from the Dutch fishery and work is currently being undertaken to jointly analyse the two data-sets (P. Bromley pers. comm.). This analysis has been complicated by differences in the maturity scales used by the two countries. Future joint studies would be greatly facilitated by the adoption of common protocols and scales for assessing maturity within ICES member countries.

4.4.3 Recommendations

Further work on developing the cod growth and recruitment model will focus on reconstructing the weight-at-age component. It is considered that the higher variation in observed weights in the older age classes may be partly driven by more uncertainty in their estimation, and also through additional factors influencing the weight-at-age. As such, the way that temperature influences the weight at age will be reassessed. In addition, comparing modelled and observed lengths at age will show if differences in observed and modelled weight are due to lack of fit in the growth model or varying condition factors. A possible development in the model is to allow variable condition factors, as these may be able to capture some of the year to year variation in weight at age.

The model will be used in the near future in conjunction with sea temperature projections derived from the Hadley3 coupled atmosphere-ocean model to assess possible impacts of climate change on North Sea cod over the next 50 years. This work falls within the context of longer-term scenario simulations. At present the results cannot be passed directly into medium-term projections for this stock because of the relative uncertainty in the underlying relationships included in the model.

Finally, such models could be re-parameterised for cod stocks in contrasting regions such as the Barents Sea. A comparison of stocks at the northern and southern limits of the species range could be informative.

The rationale for consideration of maternal effects (age, condition and whether fish are first-time or repeat spawners) is that these factors are very probably linked to egg quality and size and thus survivability of early life history stages. Much of the understanding of maternal factors has come from aquaculture studies. Recent mesocosm studies in Norway have attempted to extend this understanding by rearing larvae from known parental stock in mixed populations. Genetic identification was used to identify the parentage of surviving larvae. Published results from this particular study indicated that differences in environmental conditions between replicate mesocosms appeared to have a stronger effect on survival than parentage. **We recommend support for further experimental studies on larval growth and survival in relation to maternal factors and also suggest that the ICES Working Group on Recruitment Processes [WGRP] might review current understanding on this subject.**

Market sampling and fisheries survey observations which include measurements of condition (in whichever form is appropriate for each species) along with assessments of maturity can provide valuable insights into changes in fisheries population reproductive potential. But, such analyses must be based upon rigorously collected data. In particular for market sampled observations care must be taken to understand possible changes in selectivity of the commercial fishery. For both sources of data there needs to be unified protocols and scales for the assessment of maturity in order to ensure that data-sets from differing countries can be combined for analysis. There is a temptation to merge maturity stages to achieve this but maturity scales need to be sufficiently detailed such that patterns in maturity and spawning can still be resolved. **Co-ordination of maturity assessment on national market sampling needs to be considered within ICES.**

5 POPULATION FORECASTING

5.1 Medium-term projections

During the two previous meetings of SGPRISM (ICES 2000a, 2001a), work was initiated on the improvement of the prevailing ICES medium-term projection methodology, currently available as WGMTERM (Reeves and Cook, 1994) or ICP (Patterson, pers. comm.) These methods differ somewhat, but share the underlying theme of using bootstrapped recruitment residuals to drive stochastic population forecasts, with such variables as weights-at-age and proportion mature-at-age being held constant over time. The improvements proposed under the remit of SGPRISM related to the statistical appropriateness or otherwise of the bootstrap resampling approach, and the possibility of incorporating aspects of biological process modelling.

Studies have continued intersessionally, and are now pursued under the aegis of SGPRISM, the Methods Working Group (ICES 2002c) and the UK CFRD Working Group on Recruitment Processes. The development of the method is recorded in Needle *et al.* (2000, 2001, in press). Attention has focussed on time-series characterisations of recruitment, weights-at-age and proportion mature-at-age, because of problems caused by the way these variables are modelled in WGMTERM and its ilk. For example, the assumption of constant weights-at-age in short- and medium-term catch forecasts can result in significant estimation bias. Darby (BD4, BD5: see also ICES 2002c) has shown that for the majority of the North Sea stocks, trends in catch weights-at-age through time could have resulted in estimation bias in the total catch of up to 50%. During the past five years, North Sea cod landings could have been over-estimated by 5–25%, a bias that is consistent with the deficit between the total catch landed by the fishery and the final agreed TAC. If the recent landings information is “reliable”, the magnitude of the bias is such that it could have removed the pressure of TAC regulation from the fishery. Darby (BD4, BD5) showed further that there appear to be systematic changes in weights-at-age that could be modelled using time series and/or cohort effect models. Removal of the bias from the short and medium-term forecasts will require modelling of such temporal changes in weight-at-age. At the current meeting of SGPRISM, two presentations were made relating to this topic (in addition to Darby, BD4 and BD5).

Projection development work plan

The first presentation (Needle, BD6) was a summary of a paper first discussed at the recent ICES Working Group on Methods on Fish Stock Assessments [WGMG], detailing progress to date and outlining a work plan for future methodological development. Briefly, this work plan is as follows:

- Recruitment residuals will be modelled using ARMA time-series (where a significant ARMA fit is found). However, the efficacy of using only a subsample of the historical stock-recruitment pairs for each projection will be investigated. Under this scheme, several different model formulations would be fitted to these data, and the best fitting one used to generate projections. Thus, uncertainty about the form of the recruitment model would be modelled, as well as variation about it.
- The VARMA method presented in Needle (BD6) for characterising weights-at-age models incorporated cohort effects in weights, but not year effects. For stocks such as cod, cohort effects appear to be more important (Darby BD4, BD5), and in this context the VARMA model is likely to be sufficient. However, for other stocks, year effects may be more important. To account for this, an alternative has been proposed in which weights at age 1 would still be projected as residuals to a function of stock density, but subsequent ages would be modelled in terms of increments down cohorts. This would have the additional benefit of avoiding the problem in the VARMA method of ignoring data from incomplete cohorts.
- Maturity could be modelled in several ways. A single ogive could be fitted with weights as the independent variable (thus ignoring age), or use could be made of empirical nonparametric kernel distributions. Examples of these two approaches are given in Figure 5.1.1. Ultimately, deriving maturity as a function of weight will always be an approximation, and it is intended that alternative methods involving length-driven fecundity estimates will be pursued in various fora (see Section 6.1). Indeed, for many stocks, spawning-stock biomass is known to be an unsuitable proxy for egg production. The new method would base stock-recruitment modelling on potential egg production rather than spawning-stock biomass, and will thus be more cognisant of the deleterious effect of a compressed age structure (amongst other influential factors).
- Natural mortality M is currently fixed throughout projections. However, annual values of M are available from MSVPA and, if possible, these would be used in the new approach (after accounting for any time-series structure).
- The key justification for work on medium-term projections is to allow managers to determine the likely responses of the stock in question to specified management actions. To this end, the methodology would have the potential to allow for future imposed changes in fishing effort, gear selectivity, and catch constraints, and would enable the modelling of formal harvest control rules. WGMTERM does not currently allow for the modelling of management actions, although ICP does.

- The proposed new model will include the facility to accept a different realisation of starting values for each projection iteration, as would be produced by a bootstrapped assessment model. If such a model is not available, then starting values for each projection could be drawn from a multivariate distribution about assessment results with standard errors stipulated by the assessment model (this facility is available in both TSA and ICA).

The method would be implemented to be as general as possible, while allowing for additional model structure if data are available. It is envisaged that functional software incorporating these features, and others as need dictates, will be available by early 2003 for ICES Working Group use.

Weights-increments modelling

The second presentation (Needle, WD8) looked at some first steps taken in the pursuance of this work plan, namely the modelling of weights as increments down cohorts. WD8 applied the approach to North Sea cod, while further work during the current SGPRISM meeting extended the analyses to North Sea haddock, whiting and plaice. Results for all these stocks are summarised below.

Three different methods of generating increments were used, namely:

1) First differences: $\Delta_{a,y} = W_{a+1,y+1} - W_{a,y}$

2) Log ratios: $\Delta_{a,y} = \ln\left(\frac{W_{a+1,y+1}}{W_{a,y}}\right)$

3) Age N to age 1 ratios: $\Delta_{a,y} = \frac{W_{a,1}}{W_{a+y,y+1}}$

For each method, time-series along age-classes were formed (with the mean subtracted in each case) and a number of ARMA(p,q) models fitted with the autoregressive order p and the moving-average order q both varying between 0 and 3. The significance of the fitted model parameters was evaluated using a t-test

$$t = \frac{\text{parameter}}{\text{s.d.(parameter)}},$$

and the model was accepted if $|t| > 1.96$ for all fitted parameters. Where more than one model was accepted, the best was chosen on the basis of the lowest estimated value of the AIC test criterion (conditioned on the highest allowed value of p, in other words, 3).

Results of these analyses are given in Figures 5.1.2–5.1.5 and Table 5.1.1. ARMA model fits are distributed as follows:

ARMA model order	Number of fits	
No sig. fit	45	37.5%
0,1	32	26.6%
1,1	14	11.7%
2,2	9	7.5%
0,2	6	5.0%
1,0	4	3.3%
1,2	4	3.3%
1,3	4	3.3%
2,3	1	0.8%

A sizeable percentage of weights-increments time-series do not have a significant ARMA model fit. On the other hand, there is time-series information in many of the weight-increments datasets, and in general it would seem unwise to ignore time-series structure in these data if it is present. Where no significant ARMA model could be found, the use of simple bootstrapping is probably adequate.

5.2 Spawning-stock structure

North-east Arctic cod

Tretyak (WD10) presented a model of spawning-stock structure in Northeast Arctic cod, which he used to indicate which components of the spawning population have had the greatest influence on subsequent recruitment. The following is a brief summary of the method and conclusions from the Working Document.

Spawning-stock biomass (SSB) is a simple summary of the biomass of mature cod from different age groups. It takes into account only the age structure and mean weight of spawners at each age, and makes no cognisance of sex ratio, differences between the weights of males and females, absolute individual fecundity and the proportion of fish that skip spawning. It also suggests that all spawners are of the same quality and, as a result, that all eggs have a similar quality, viability, distribution and survival. WD10 proposes a hypothesis about inter- and intra-annual dissimilarity of spawners, according to which a simple summation of the biomass of mature cod from different age groups does not reveal the actual relationship between recruitment and spawners' abundance. An algorithm for defining the abundance of first-time and repeat spawners is presented.

The abundance of kth-time spawners at age t in year y can be estimated using

$$N^{p}_{t,k,y} = N_{t,y}\left(\delta_{t-k+1,y-k+1} - \delta_{t-k,y-k}\right),$$

where $\delta_{t,y}$ and $N_{t,y}$ are respectively the maturity-at-age and abundance-at-age for age t in year y. Coefficients of correlation between recruitment and the abundance of cod of different age spawning a different number of times indicate a weak, but stable and statistically significant positive linear relationship between recruitment and the abundance of late-maturing cod spawning for the first time at age 9 and older, as well as between recruitment and the abundance of fish at the plus-group age spawning for the 6th time or more. This permits the classification of all spawners into late-maturing (first-time spawners at age 9 and older) and early-maturing fish (all others). The first group exhibited a well-pronounced decreasing trend throughout the entire time series (Figure 5.2.1). Until the early 1960s, its abundance was close to that of the second group. Variations in these two components of the spawning stock were highly synchronous. However, at that time a change occurred in the structure of the spawning stock. The trend towards decrease in the abundance of late-maturing fish remained, while the abundance of early-maturing cod started to grow steadily.

Approximation of variations in cod recruitment by Ricker stock-recruitment models with the abundance of both spawning stock components and total spawning stock as independent variables gives the following results given in Figure 5.2.2. As expected, over the entire history of observations a statistically significant relationship exists only between recruitment and the abundance of late-maturing fish (Figure 5.2.2a). Their contribution to recruitment variance is circa 20%. The contribution of early-maturing fish to the recruitment variance is below 1%, which is rather counter-intuitive as that component has dominated the spawning stock after the 1960s and constituted more than 93% after mid-1970s (Figure 5.2.2b). This may be due to the interannual dissimilarity of early-maturing spawners which creates noise suppressing the actual dependence of recruitment, not only on the abundance of early-maturing fish, but also on the total abundance of the spawning stock (Figure 5.2.2c).

Assuming that interannual dissimilarity of the spawning stock is caused primarily by earlier maturation, we divided the time series of spawners' abundance (1949–1997) into 4 intervals. Each of these was related to a 25% interval of the logistic curve showing the age of 50% maturity (Figure 5.2.3). The 1949–1964 year-classes were assigned to the first interval, the 1965–1970 year classes to the second interval, the 1971–1975 year classes to the third interval and the 1976–1997 year classes to the fourth interval. We assumed that the age of 50% maturity approached the threshold of 6.65 years (Tretyak 2000). This led to a marked smoothing of interannual differences in quality of early-maturing spawners in the fourth interval. A decline in the abundance of older fish also reduced the dissimilarity of late-maturing cod. It can therefore be stated that interannual dissimilarity of all spawners in this interval is the lowest.

Although the abundance of late-maturing fish in the fourth interval is the lowest on the record – less than 7% of the total spawning stock – the recruitment-abundance correlation for these fish has not weakened, but even become closer (Figure 5.2.4a). For early-maturing fish this relationship acquired statistical significance when the dataset was restricted to the fourth quarter (Figure 5.2.4b). The contribution of a large amount of these fish to recruitment variance equalled that of late-maturing cod, which are only a very small fraction of the spawning stock. Addition of late-maturing to early-maturing cod does not notably change the total abundance of the spawning stock; therefore the dependence of recruitment on the total abundance became statistically significant when the dataset was restricted to the fourth quarter.

However, the total contribution of all spawners to recruitment variance did not exceed the contribution of each component of the spawning stock (Figure 5.2.4c).

The actual contribution of early- and late-maturing fish to recruitment variations is apparently somewhat greater. A determination coefficient was calculated between actual recruitment and recruitment calculated by the linear regression equation with two independent variables at the third step of recruitment approximation, and is given by

$$\sum_{j} \left(R_{3,j} - \hat{R}^{(3)}_{3,j} \right)^2 \Rightarrow \min$$

where

$$\hat{R}^{(3)}_{3,j} = a_1 \cdot \left(\alpha_1 \cdot NL_j \cdot \exp\left(-\beta_1 \cdot NL_j \right) \right) + a_2 \cdot \left(\alpha_2 \cdot NE_j \cdot \exp\left(-\beta_2 \cdot NE_j \right) \right) + a_3$$

Here NL_j is abundance of late-maturing fish in year j, NE_j is abundance of early-maturing fish in year j, and a_1, a_2, and a_3 are equation parameters calculated by the integrated gradients method. For Northeast Arctic cod this coefficient was 0.563 (Figure 5.2.5). The first independent variable in the above equation is the result of the first step of approximation, that is, the approximation of recruitment by the Ricker model for late-maturing fish only. The second variable is the result of the second step, that is, approximation by the Ricker model for early-maturing fish only.

North Sea cod and herring

Tretyak's model was applied during SGPRISM to North Sea cod and herring, in order to ascertain its general applicability and whether it would be beneficial to use it more widely.

North Sea cod abundance and recruitment estimates were taken from ICES (2002a). Maturity estimates for 1980–1995 were taken from Cook *et al.* (1999): however, these were rather noisy and were smoothed down cohorts using the logistic ogive $W_{a,y} = 1/\left(1 + \exp(\alpha - \beta a)\right)$ to prevent negative spawning abundances.

Figures 5.2.6 and 5.2.7, respectively, give the abundances of kth-time spawners for North Sea cod and herring. The relative proportions of these decline with increasing k in a straightforward manner for cod: for herring, the importance of 2nd, 3rd, 4th and 5th time spawners fluctuates more unpredictably. This is likely to be a result of the contrasting shapes of maturity ogives for the two stocks, being quite shallow for cod and very steep for herring.

Table 5.2.1. gives linear correlation coefficients between the kth-time spawning abundance at age, and the full-stock recruitment for North Sea cod. This is not the ideal diagnostic, and should in future be augmented by (for example) an analysis of Ricker model fits to each of these relationships, but it can be seen that very young and very old spawners apparently have less influence on recruitment than those of moderate age (that is, between ~5 and ~7 years old). However, very few of these correlations are statistically significant.

North Sea herring abundance, recruitment and maturity estimates were all taken from ICES (2001e). Table 5.2.2. gives linear correlation coefficients (equivalent to Table 5.2.1) for herring. Correlation coefficients are smaller for herring than for cod (indeed, none of them are statistically significant), and there is no obvious pattern to them. This may be a consequence of the very steep maturity ogive for herring.

The Study Group concluded that Tretyak's approach to the determination of the components of the spawning population which may drive recruitment to be cogent and parsimonious, and would recommend that further analysis be conducted in the future into the model and its implications. An example of these would be the determination of the influence of first-time spawners on recruitment, with further implications for management with regards to stock rebuilding strategies.

Table 5.1.1. Orders of those best-fitting ARMA model fits to weights-increments time-series for which all fitted parameters are significant. Parameter significance was determined using a t-test, while the AIC statistic was used to select the best-fitting model. - = No significant ARMA fit.

a. North Sea cod (1963–2000).

Age	First differences		Log ratios		Age N to age 1 ratios	
	AR	MA	AR	MA	AR	MA
1–2	-	-	-	-	-	-
2–3	1	0	2	2	0	1
3–4	0	3	2	3	0	3
4–5	-	-	2	2	0	2
5–6	1	1	1	1	1	2
6–7	1	1	1	3	0	1
7–8	1	1	1	1	1	1
8–9	-	-	-	-	0	3
9–10	1	1	1	1	0	3
10–11+	0	1	-	-	1	2

b. North Sea haddock (1963–2000).

Age	First differences		Log ratios		Age N to age 1 ratios	
	AR	MA	AR	MA	AR	MA
0–1	0	1	-	-	0	1
1–2	0	2	0	2	0	1
2–3	0	1	2	2	0	1
3–4	0	1	-	-	0	1
4–5	0	2	0	2	0	1
5–6	2	2	2	2	0	1
6–7	-	-	0	1	0	1
7–8	-	-	1	3	0	1
8–9	-	-	3	2	0	1
9–10+	-	-	-	-	0	1

c. North Sea whiting (1960–2000).

Ages	First differences		Log ratios		Age N to age 1 ratios	
	AR	MA	AR	MA	AR	MA
1–2	-	-	-	-	-	-
2–3	2	2	-	-	0	1
3–4	-	-	-	-	1	0
4–5	1	1	1	1	0	1
5–6	-	-	-	-	-	-
6–7	1	0	0	1	-	-
7–8+	-	-	-	-	0	3

d. North Sea plaice (1969–2000).

Ages	First differences		Log ratios		Age N to age 1 ratios	
	AR	MA	AR	MA	AR	MA
1–2	-	-	-	-	-	-
2–3	-	-	-	-	2	2
3–4	0	1	0	1	2	2
4–5	1	0	2	2	-	-
5–6	0	2	-	-	-	-
6–7	-	-	-	-	-	-
7–8	-	-	-	-	-	-
8–9	0	1	1	1	-	-
9–10	1	3	1	3	-	-
10–11	0	1	0	1	1	1
11–12	0	1	0	1	-	-
12–13	1	2	1	2	1	1
13–14	0	1	0	1	1	1
14–15+	-	-	-	-	0	1

Table 5.2.1. North Sea cod: linear correlation coefficients between kth-time spawner abundance at age and recruitment. Significant correlations (single-tailed test, 5% level) are highlighted in bold.

	Number of spawnings										
Age	1	2	3	4	5	6	7	8	9	10	11
1	-0.1232										
2	0.3160	0.0658									
3	-0.1022	-0.3008	-0.3086								
4	0.3284	0.0121	0.2012	0.4149							
5	0.3097	0.1814	-0.0020	-0.1509	-0.0317						
6	0.3066	0.5939	0.4770	0.3506	0.4445	0.4707					
7	0.4247	0.1515	0.3286	0.3410	0.3791	0.1054	0.0775				
8	-0.4963	-0.1123	-0.2921	0.5053	0.7225	0.3393	-0.1337	-0.3156			
9	-0.2654	-0.1172	0.5748	0.6154	0.5519	0.2558	-0.0095	-0.0134	-0.4344		
10	-0.3385	-0.3566	-0.4070	-0.3174	-0.4742	-0.1758	-0.2009	-0.3156	-0.6240	-0.4854	
11	-0.1640	-0.1444	-0.1665	-0.1132	0.9224	0.5503	0.5161	0.2165	-0.1325	-0.2678	-0.2476

Table 5.2.2. North Sea herring: linear correlation coefficients between kth-time spawner abundance at age and recruitment. There are no statistically significant correlations.

	Number of spawnings							
Age	1	2	3	4	5	6	7	8
1								
2	0.1398							
3	-0.0395	0.0303						
4	-0.2479	-0.1294	-0.1099					
5			0.1993	0.2035				
6			0.2449	0.2465	0.2138			
7				-0.0634	-0.0475	-0.1321		
8					0.1694	-0.2870	-0.2823	
9						0.0020	-0.1823	-0.3103

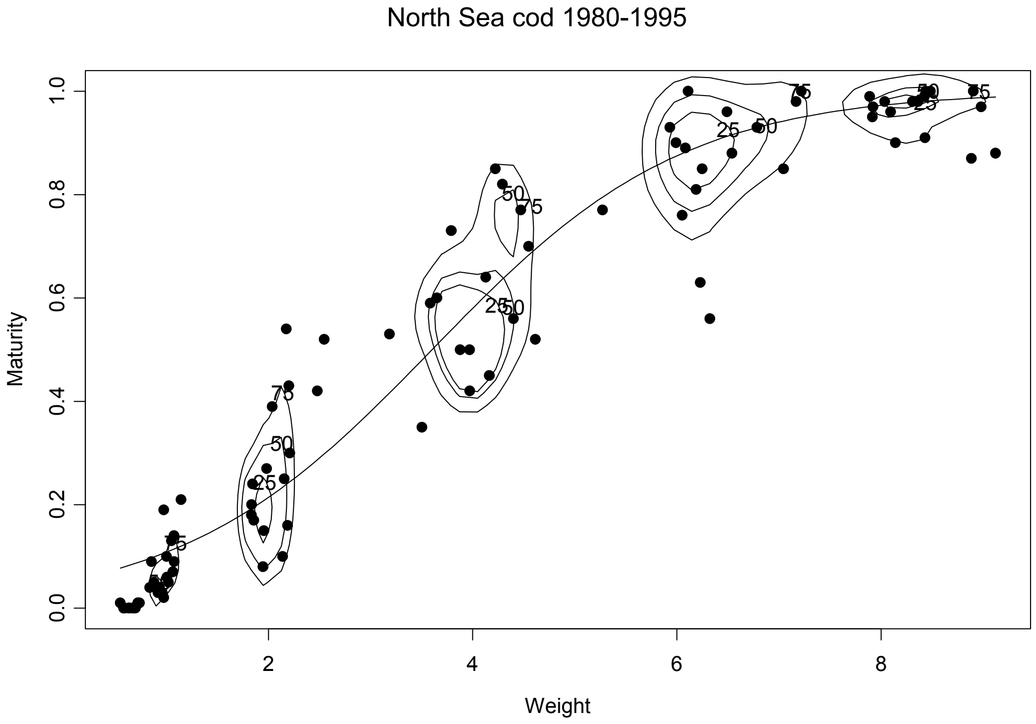
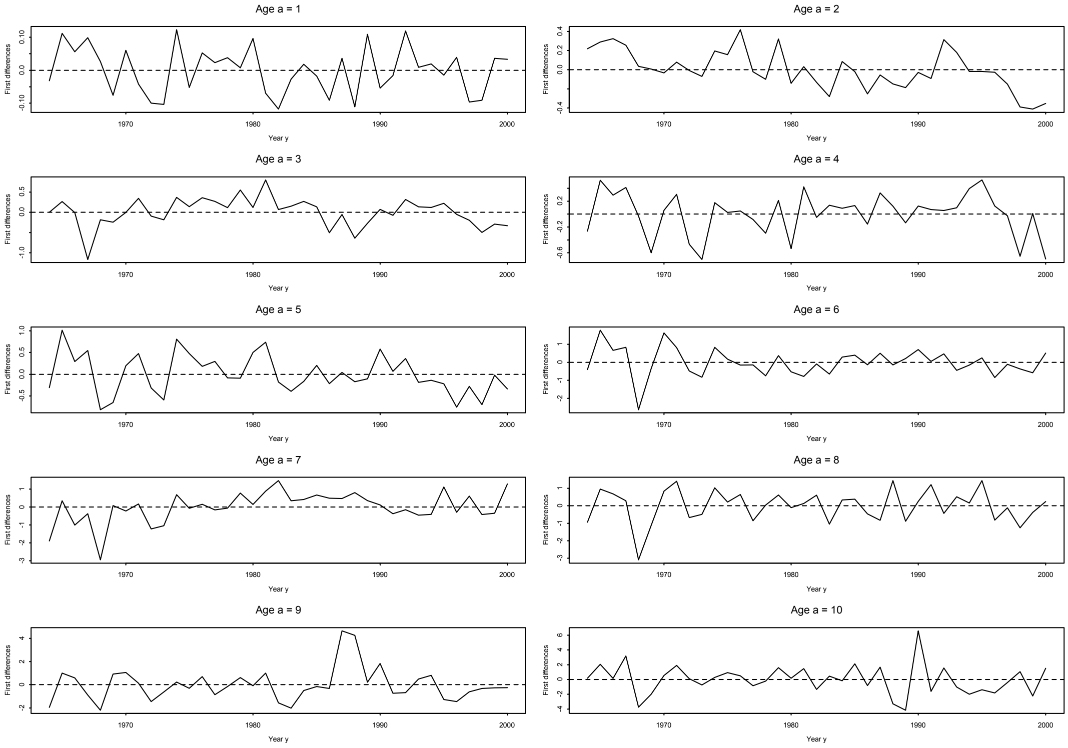


Figure 5.1.1. Scatterplot of maturity-at-age against weights-at-age for North Sea cod, ages 1–6, years 1980–1995. Maturity-at-age data are taken from Cook *et al.* (1999), and weights-at-age data from the appropriate ICES WG report (ICES 2002a). The logistic curve is a maturity ogive fitted to all data (thus ignoring age structure). The contours are empirical kernel-smoothed distributions by age: labels indicate percentile probability.

a. Using first differences to generate weights data $\left(\Delta_{a,y} = W_{a+1,y+1} - W_{a,y}\right)$:



b. Using log ratios to generate weights data $\left(\Delta_{a,y} = \ln\left(\frac{W_{a+1,y+1}}{W_{a,y}}\right)\right)$:

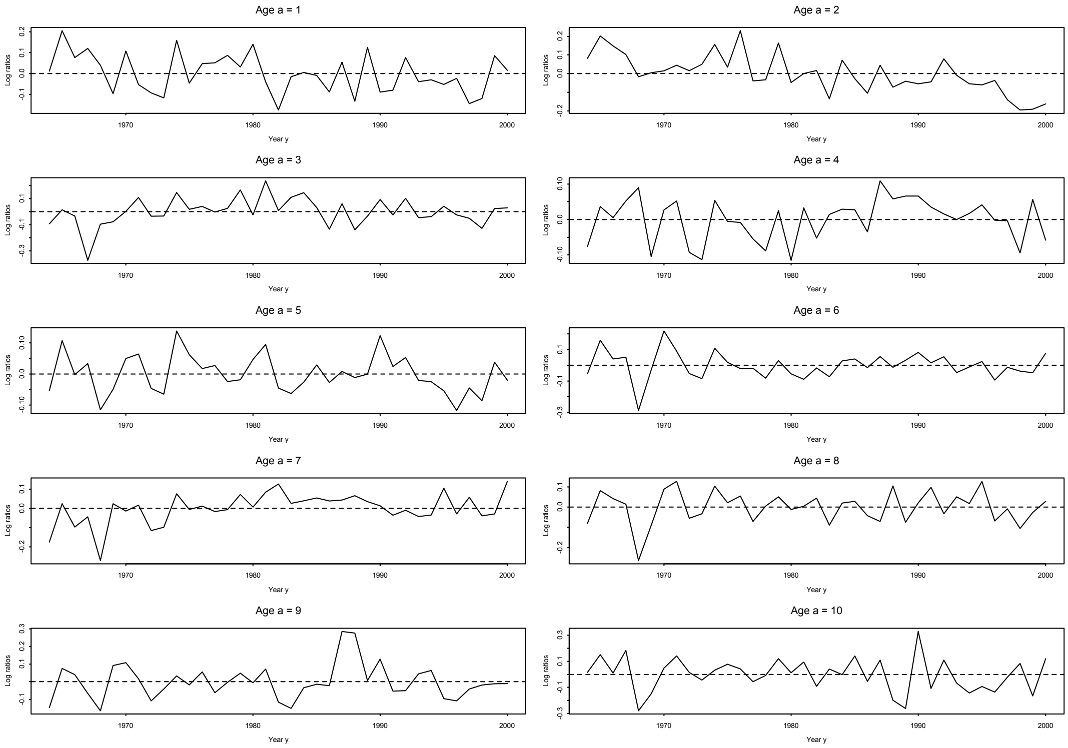


Figure 5.1.2. Time-series of weight-at-age increments by year-classes, for North Sea cod.

c. Using ratio of age N to age 1 to generate weights data $\left(\Delta_{a,y} = \frac{W_{a,1}}{W_{a+y,y+1}}\right)$:

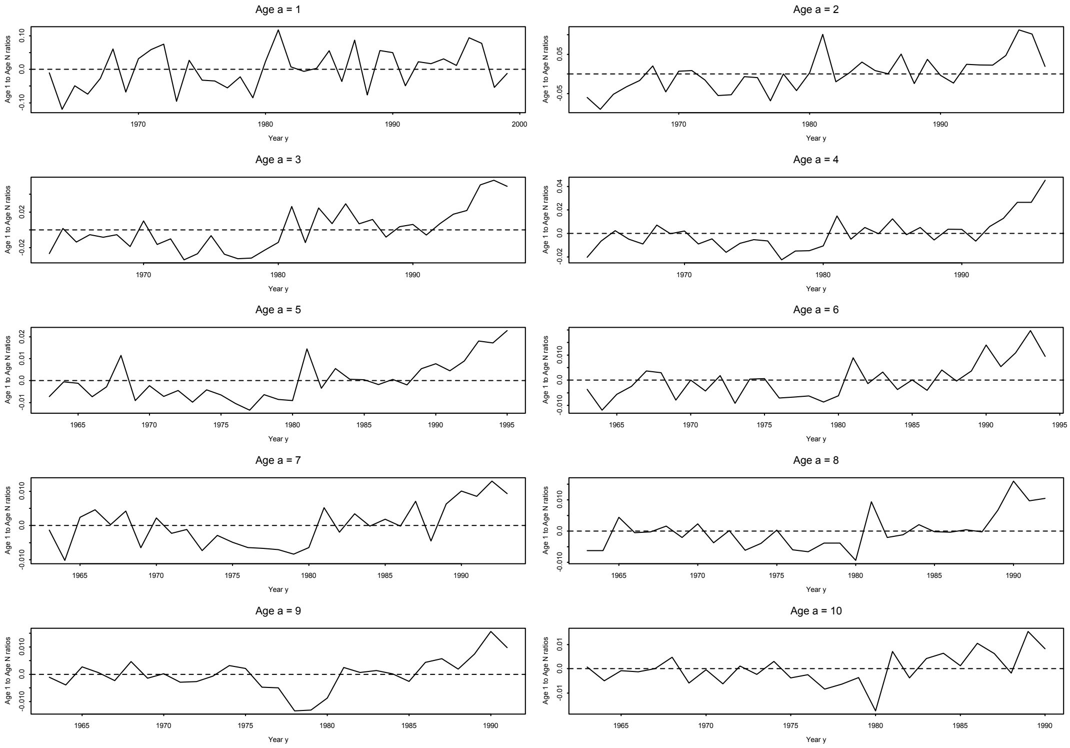
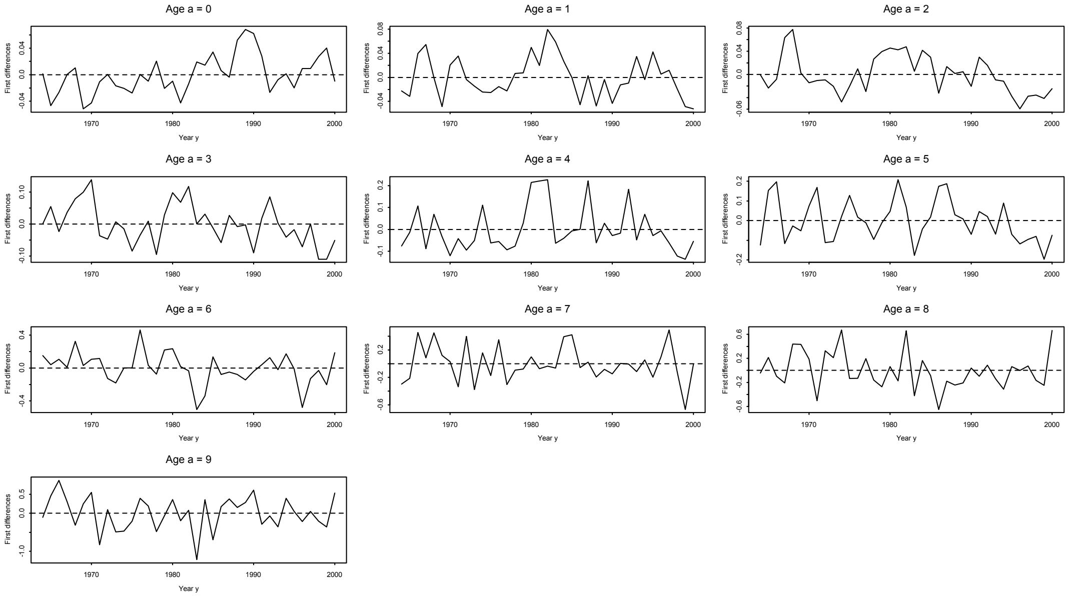


Figure 5.1.2 Continued. Time-series of weight-at-age increments by year-classes, for North Sea cod.

a. Using first differences to generate weights data $\left(\Delta_{a,y} = W_{a+1,y+1} - W_{a,y}\right)$:



b. Using log ratios to generate weights data $\left(\Delta_{a,y} = \ln\left(\frac{W_{a+1,y+1}}{W_{a,y}}\right)\right)$:

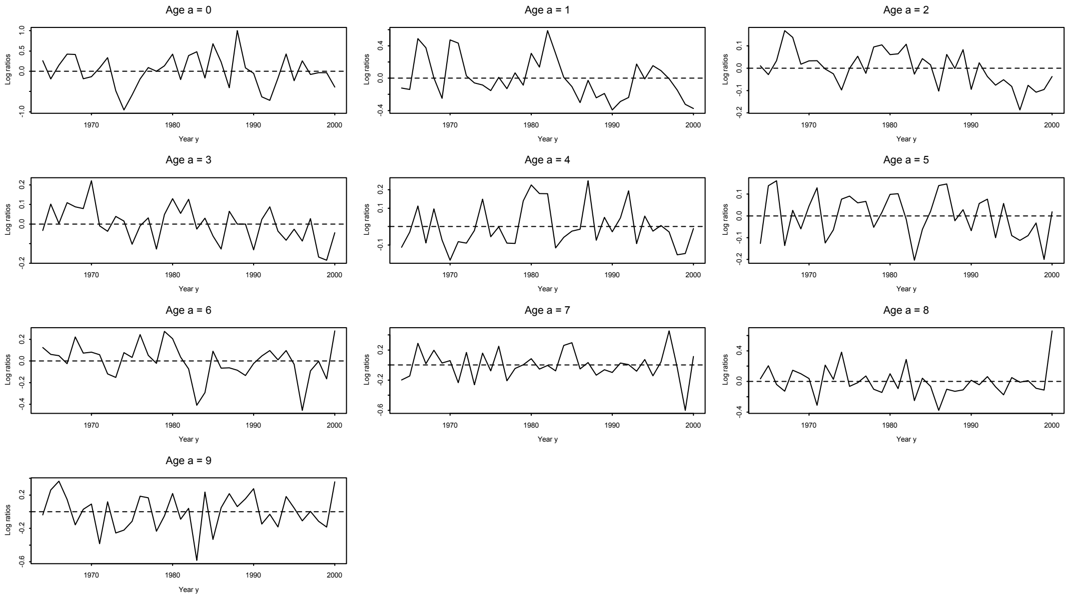


Figure 5.1.3. Time-series of weight-at-age increments by year-classes, for North Sea haddock.

c. Using ratio of age N to age 1 to generate weights data $\left(\Delta_{a,y} = \frac{W_{a,1}}{W_{a+y,y+1}}\right)$:

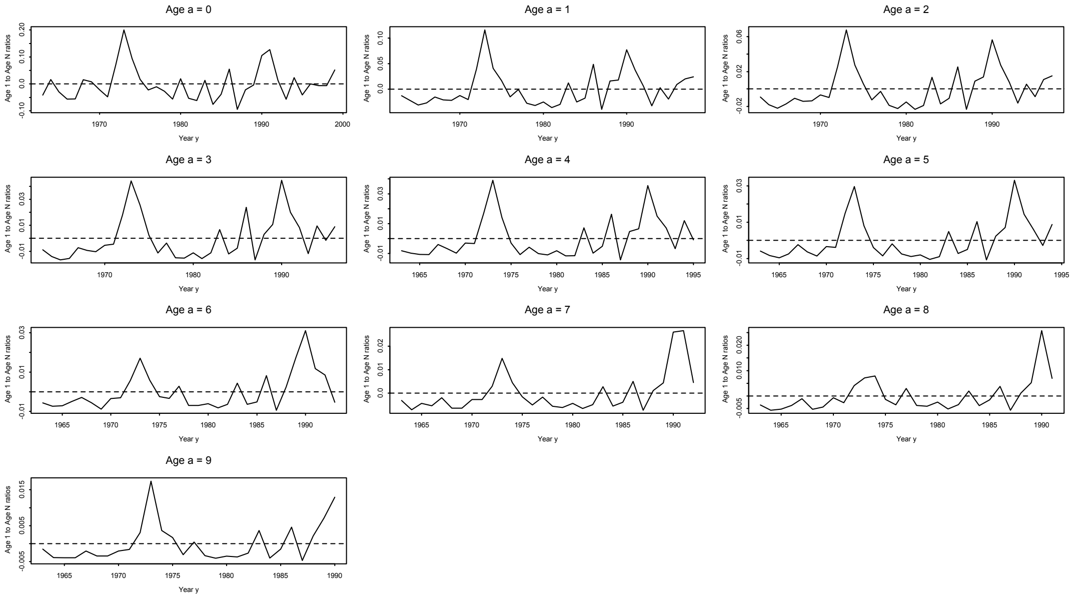
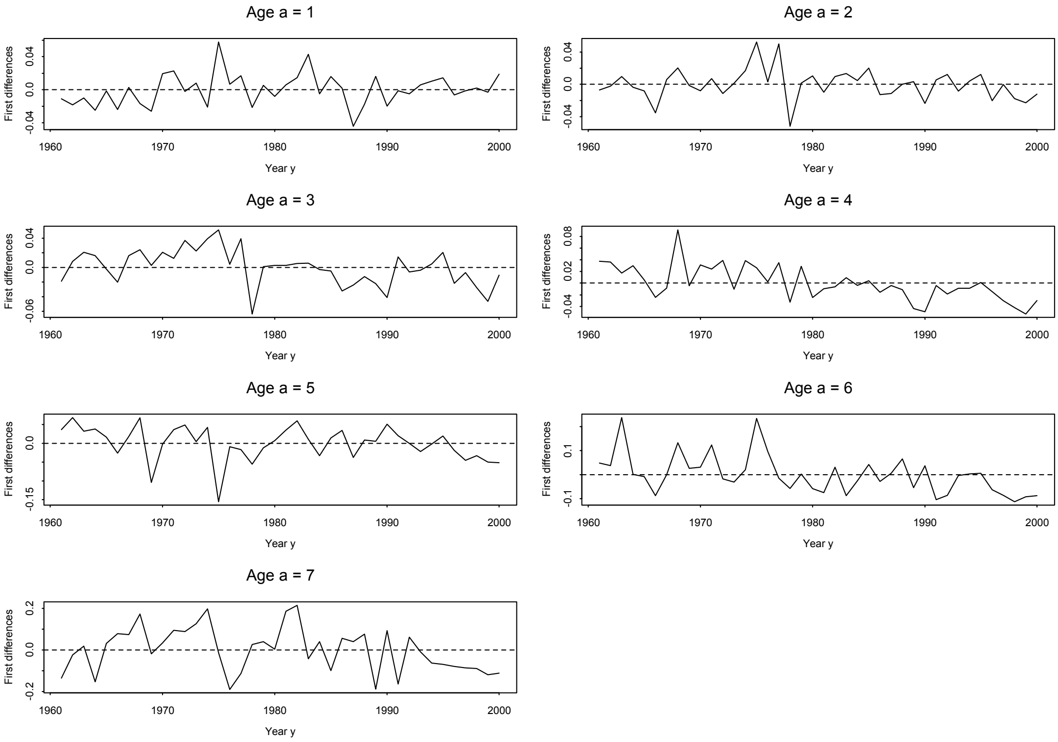


Figure 5.1.3 Continued. Time-series of weight-at-age increments by year-classes, for North Sea haddock.

a. Using first differences to generate weights data $\left(\Delta_{a,y} = W_{a+1,y+1} - W_{a,y}\right)$:



b. Using log ratios to generate weights data $\left(\Delta_{a,y} = \ln\left(\frac{W_{a+1,y+1}}{W_{a,y}}\right)\right)$:

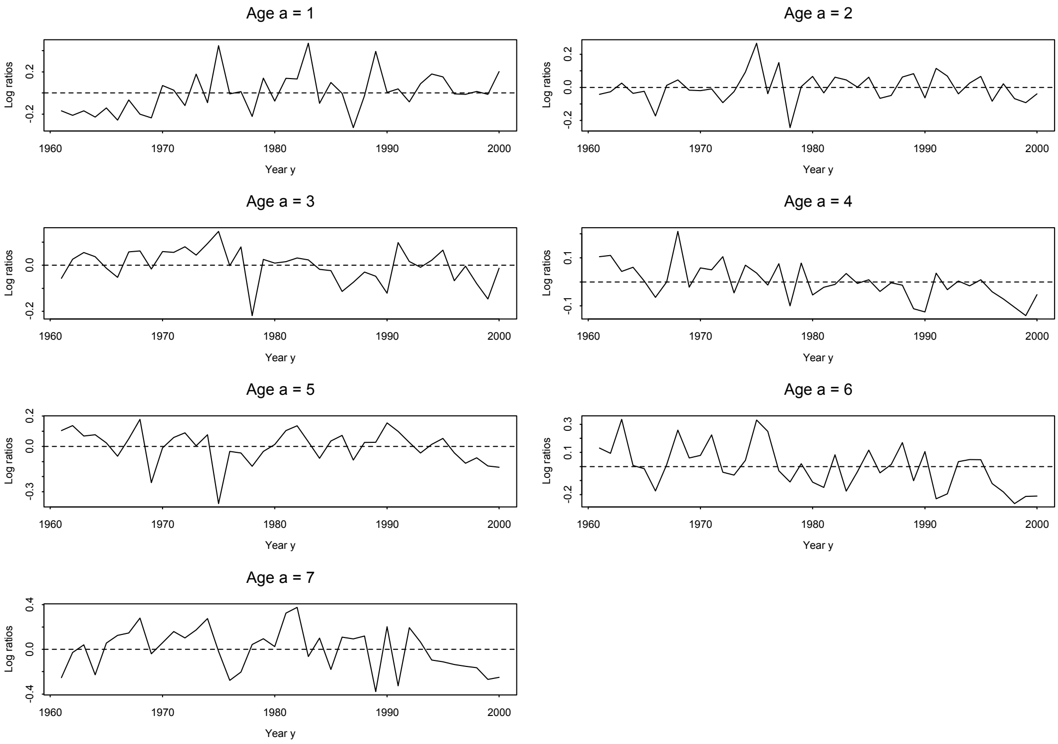


Figure 5.1.4. Time-series of weight-at-age increments by year-classes, for North Sea whiting.

c. Using ratio of age N to age 1 to generate weights data $\left(\Delta_{a,y} = \frac{W_{a,1}}{W_{a+y,y+1}}\right)$:

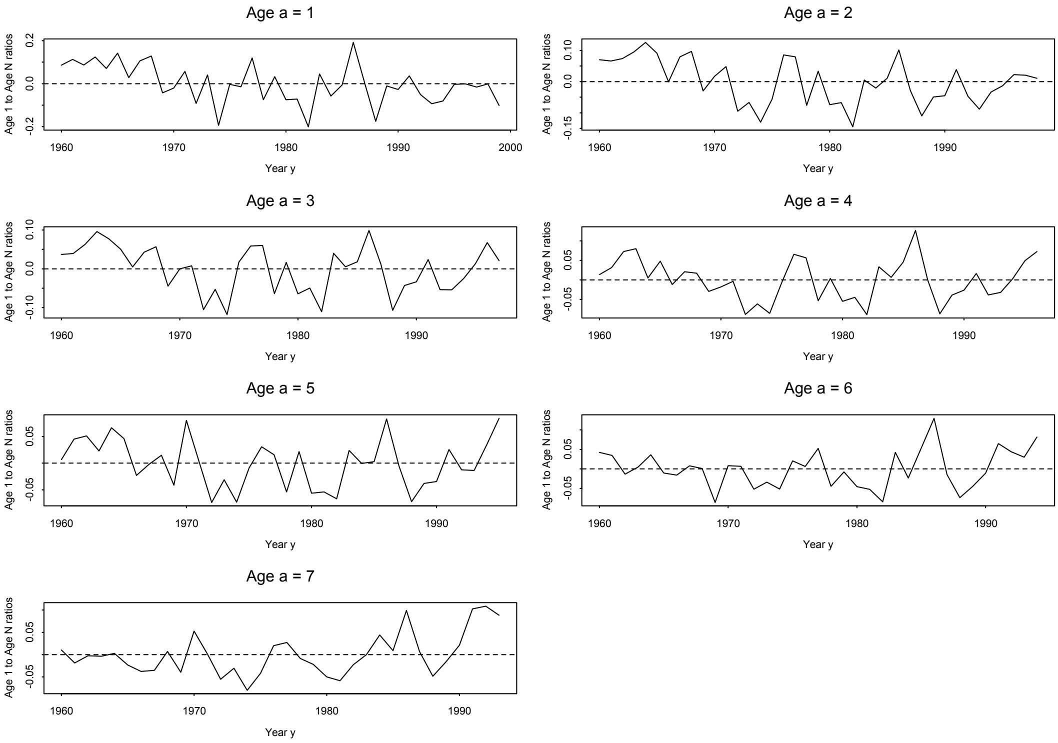
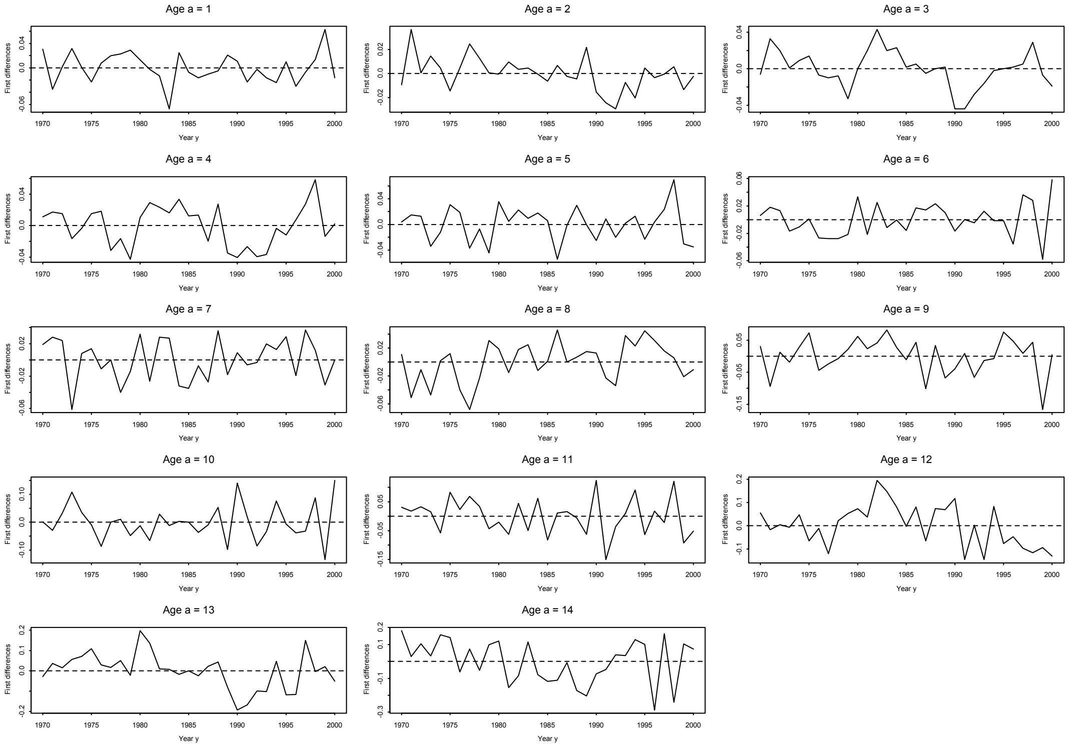


Figure 5.1.4 Continued. Time-series of weight-at-age increments by year-classes, for North Sea whiting.

a. Using first differences to generate weights data $\left(\Delta_{a,y} = W_{a+1,y+1} - W_{a,y}\right)$:



b. Using log ratios to generate weights data $\left(\Delta_{a,y} = \ln\left(\frac{W_{a+1,y+1}}{W_{a,y}}\right)\right)$:

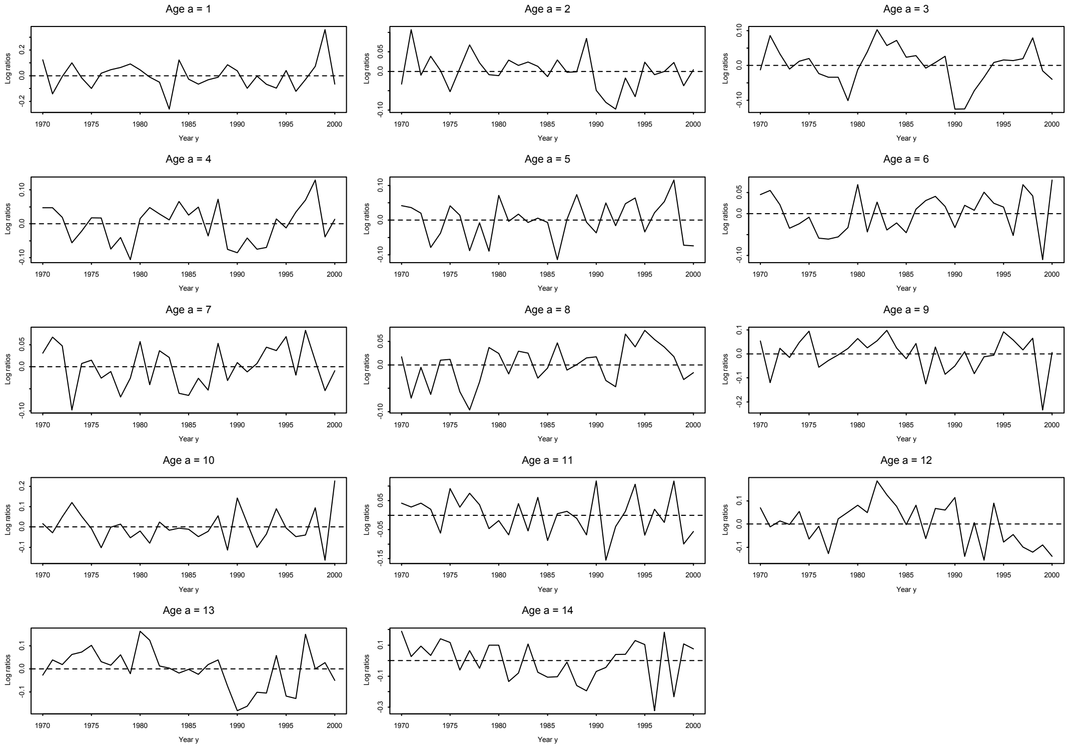


Figure 5.1.5. Time-series of weight-at-age increments by year-classes, for North Sea plaice.

c. Using ratio of age N to age 1 to generate weights data $\left(\Delta_{a,y} = \frac{W_{a,1}}{W_{a+y,y+1}}\right)$:

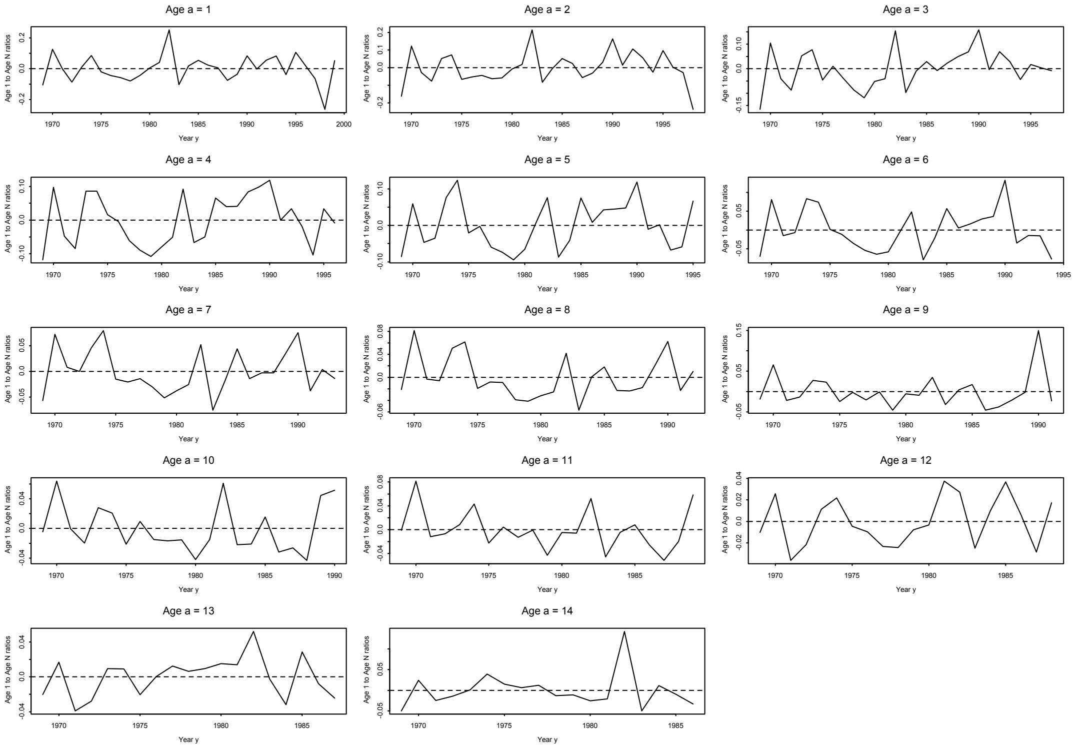


Figure 5.1.5 Continued. Time-series of weight-at-age increments by year-classes, for North Sea plaice.

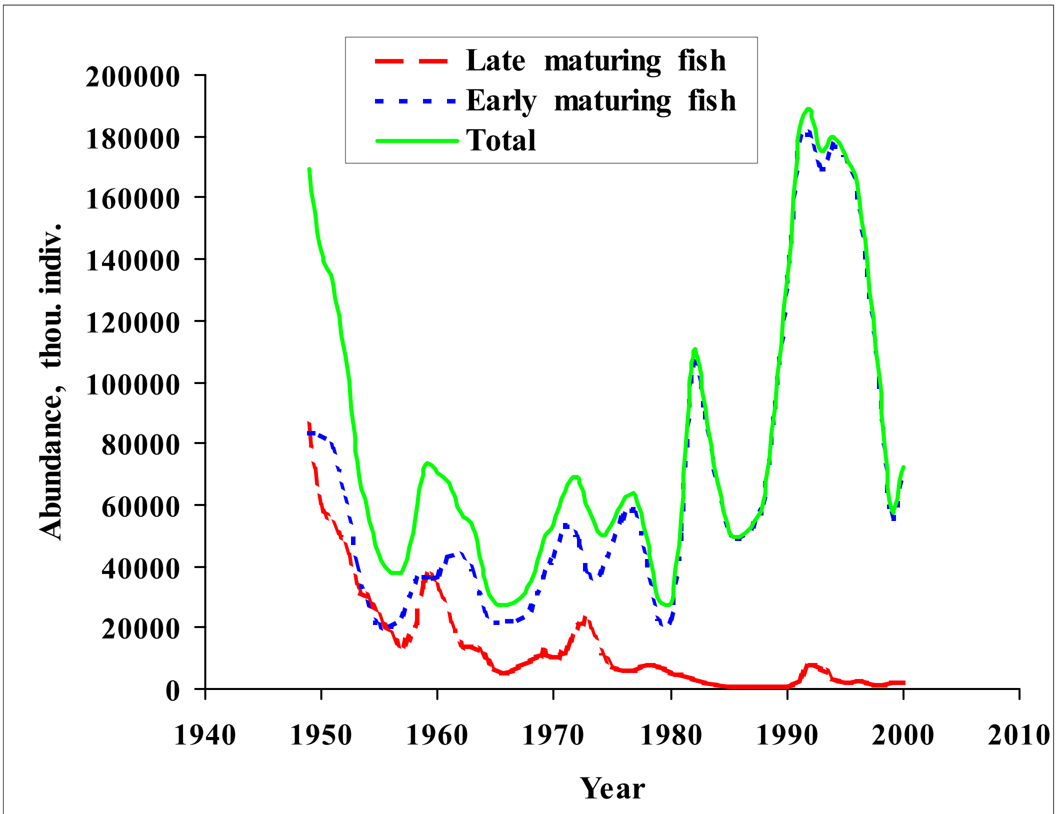


Figure 5.2.1. Abundance of late- and early- maturing cod and total abundance of mature cod in different years.

Figure 5.2.1. Northeast Arctic cod.

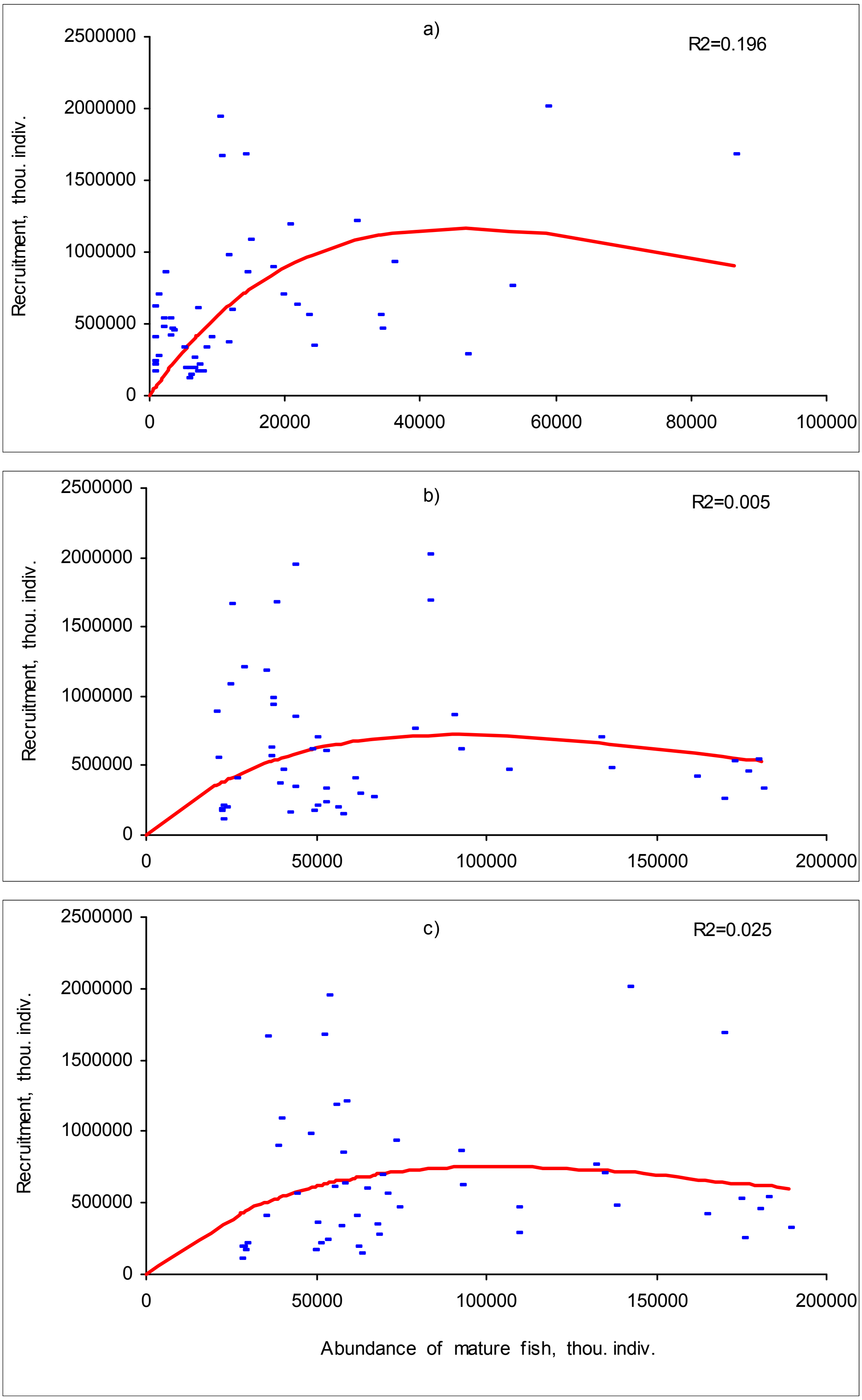


Figure 5.2.2. Ricker stock-recruitment model fits for Northeast Arctic cod (1949–1997), using the abundance of a) late maturing and b) early maturing fish, as well as c) total abundance.

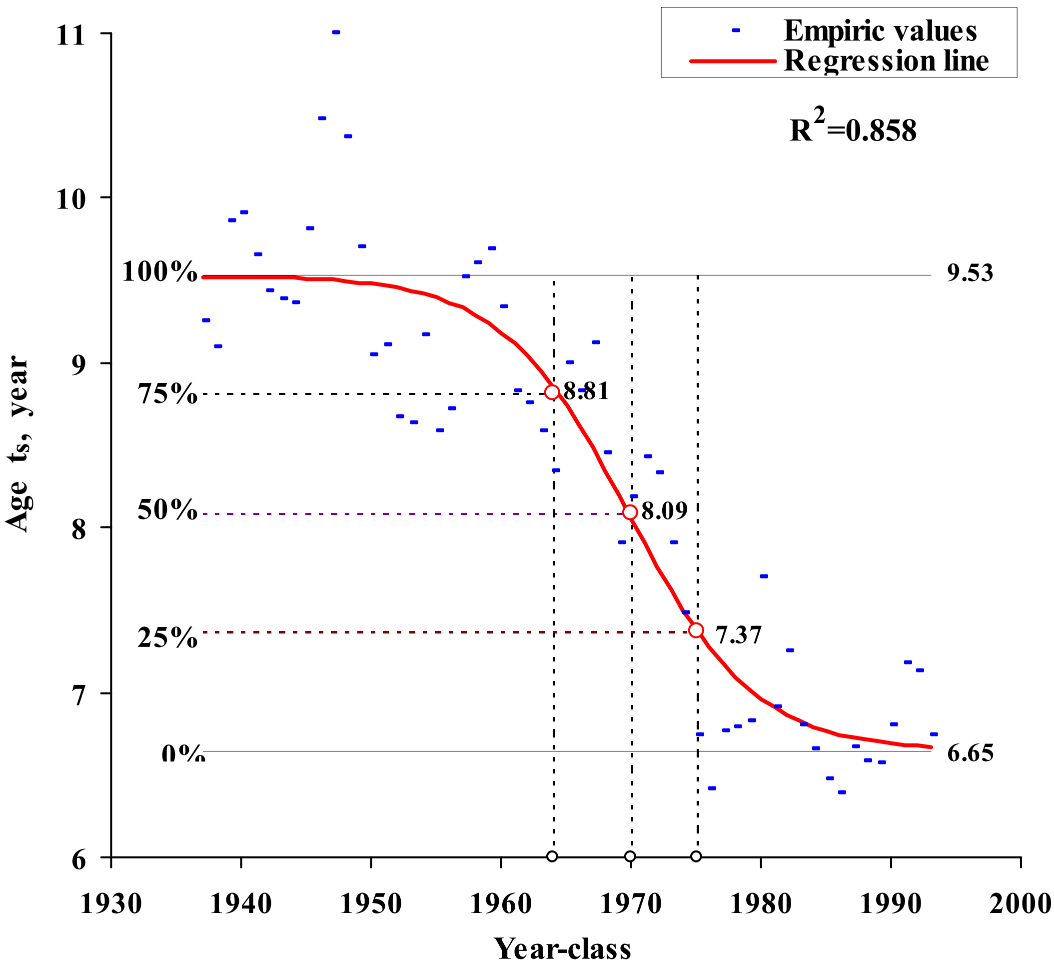


Figure 5.2.3. Age of 50% maturity (t_s) in different year classes of cod

Figure 5.2.3. Northeast Arctic cod.

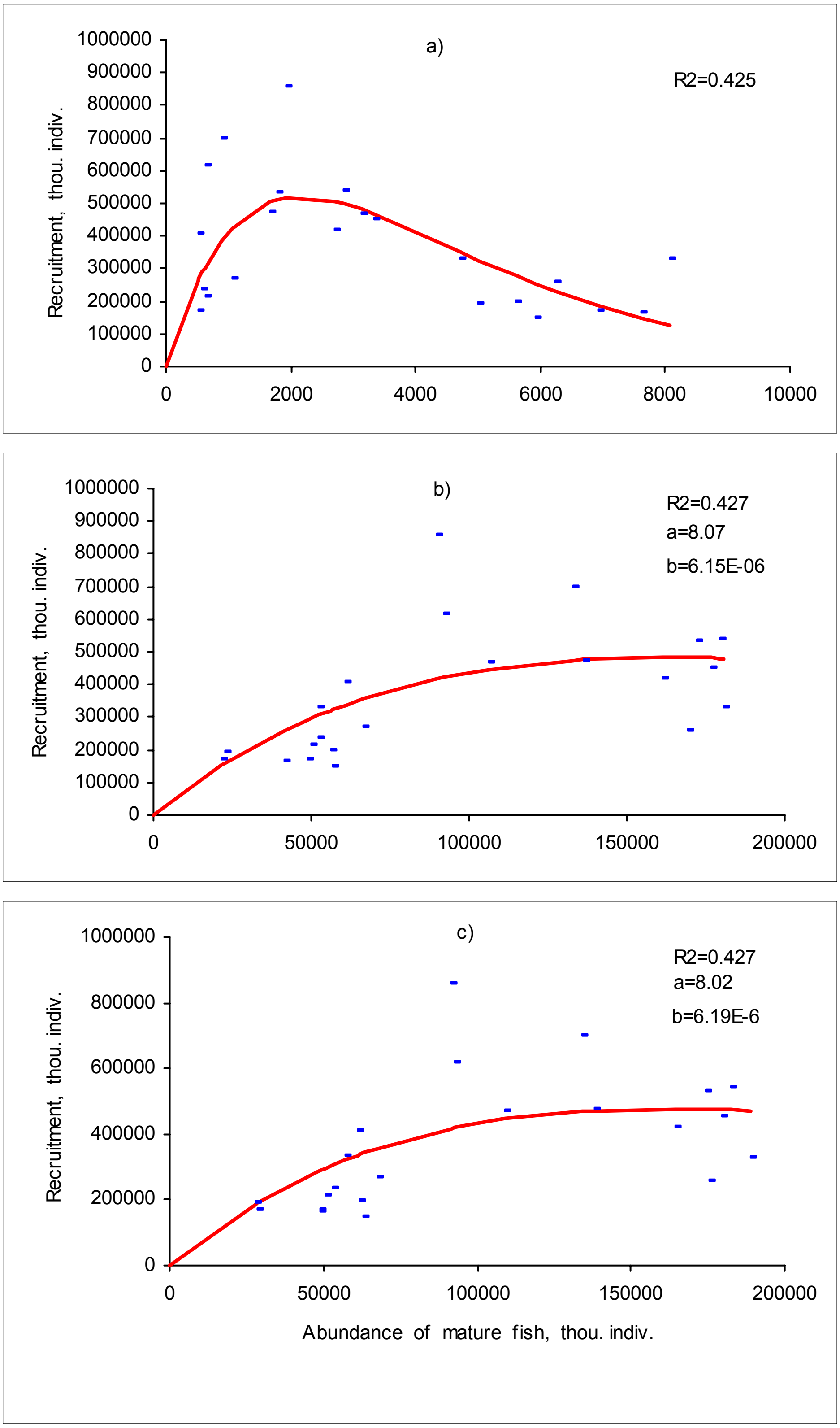


Figure 5.2.4. Ricker stock-recruitment model fits for Northeast Arctic cod (1976–1997), using the abundance of a) late maturing and b) early maturing fish, as well as c) total abundance.

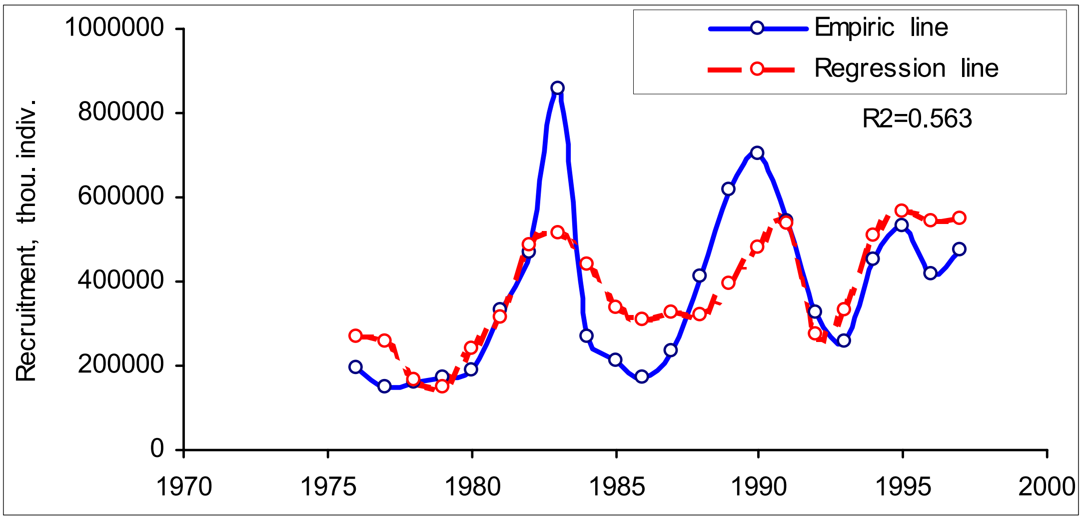
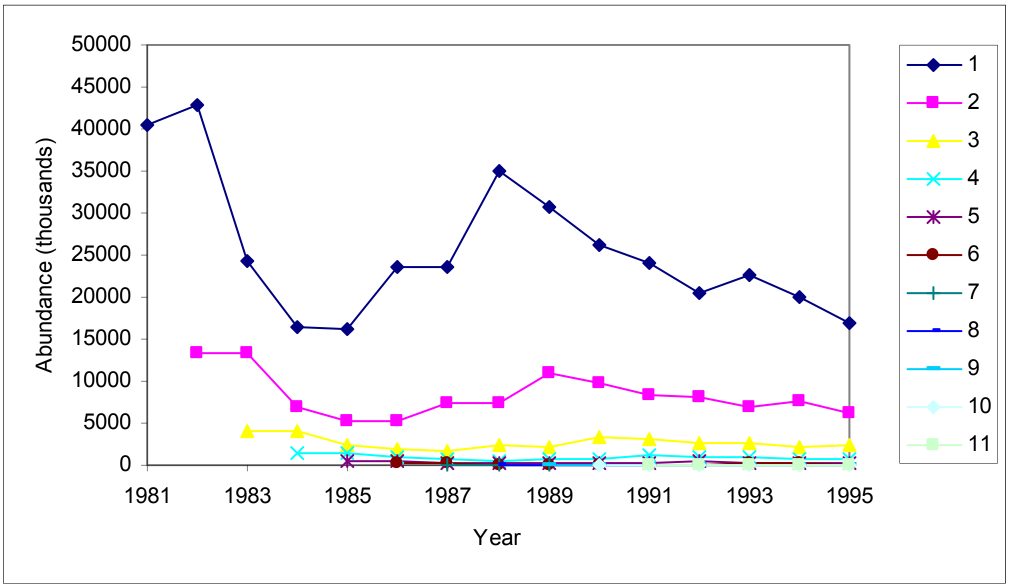


Figure 5.2.5. Sequential approximation of recruitment to Northeast Arctic cod by linear regression equations with two independent variables.



Figures 5.2.6. Abundance of North Sea cod spawning for the kth time. The legend gives values of k.

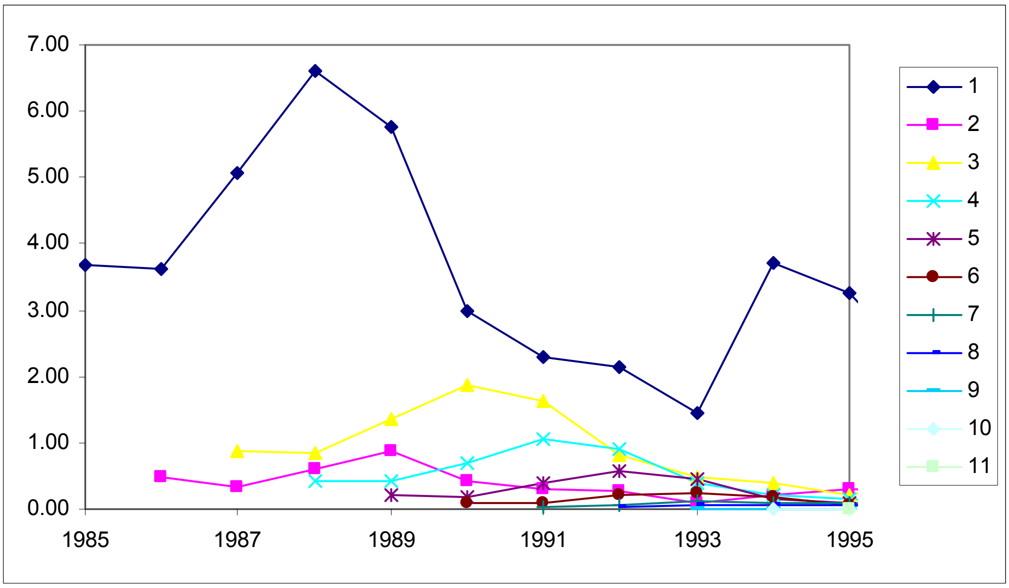


Figure 5.2.7. Abundance of North Sea herring spawning for the kth time. The legend gives values of k.

6 RECOMMENDATIONS

6.1 Recommendations for future work

This third meeting of SGPRISM is to be its last. The proposed work plan for development of medium-term projection software and methodology (see Section 5.1) calls for such software to be finalised by early 2003, for subsequent ICES certification and use by stock assessment Working Groups during that year. Before this programming exercise can be completed, there needs to be a thorough collation and evaluation of the appropriate data available for each stock in the ICES area, along with analyses of which process models would be suitable for incorporation in stock projections. It is probable that this work could only realistically be undertaken by a dedicated Study Group - the alternative would be for stock assessment Working Groups to collate data and formulate process models, but to demand this of them would be unreasonable given their current workloads. To this end, SGPRISM makes the following recommendation.

A **Study Group on Growth, Maturity and Condition Indices in Stock Projections** [SGGROMAT] (Co-chairs: C. L. Needle, UK and C. T. Marshall, Norway) be established to meet at ICES Headquarters, Copenhagen, Denmark from 5–10 December 2002 to:

a) collate data on weights, maturity, condition, fecundity, and age-length and length-weight keys for stocks in the North Sea, Irish Sea, Northeast Arctic and Baltic Sea;
b) develop the implementation of growth, maturity and condition models for use in projections for those stocks for which data are available; and
c) agree an intersessional programme to apply the findings of the Study Group to areas not covered by ToR a).

SGGROMAT will report for the attention of the Resource Management, Living Resources, Oceanography and Baltic Committees. The report will be brought to the attention of the Working Group on Methods on Fish Stock Assessments [WGMG] and ACFM.

Intersessional work implementing growth and condition models for North Sea and Northeast Arctic cod is planned for the summer of 2002 (as a collaborative effort between scientists from Aberdeen and Bergen), and it is intended that SGGROMAT will follow this lead and apply it to other stocks where possible. The key justification for SGGROMAT is that, without it, assessment Working Groups will not be able to use the new medium-term projection methodology. If this is so, they will need to revert to such approaches as WGMTERM, and Darby (BD4, BD5) has shown that assuming fixed weights-at-age in particular can seriously degrade stock projections. The output from SGGROMAT would take the form of Working Papers to each assessment Working Group, proposing candidate projection models for application to stocks within their remit.

Participants at SGGROMAT should include process modellers, assessment scientists, and data collators. The purpose of locating the meeting at ICES Headquarters in Copenhagen, Denmark is to permit ready access to all available assessment Working Group reports and datasets, along with such relevant sources as the IBTS database. SGGROMAT should precede the January 2003 meeting of WGMG, which will review it and recommend (or otherwise) its findings to assessment Working Groups meeting in 2003.

SGPRISM would recommend further that the Working Group on Recruitment Processes [WGRP] pursues process studies in such a way that outcomes and results can be used to drive projection models.

6.2 Links to other groups and activities

In this section is a partial listing of on-going international collaborative groups investigating aspects of the reproductive variability of marine fish stocks, biological processes contributing to recruitment and numerical approaches to quantifying uncertainty in medium-term stock forecasts.

6.2.1 NAFO Working Group on Reproductive Potential

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, Canada). A third Working Group meeting has been proposed for autumn 2002. It is anticipated that the information compiled by the working group will benefit fisheries management by developing methods for incorporating relevant information on stock structure into conventional assessment.

6.2.2 ICES Working Group on Recruitment Processes

The ICES Working Group on Recruitment Processes [WGRP] (Co-chairs: P. Pepin, Canada, and R. Nash, Isle of Man) worked by correspondence in 2001 but will meet in 2002 to address the following tasks.

a) Review multidisciplinary projects dealing with recruitment research, with attention to providing a synthesis of the projects and highlight unresolved issues, which deserve further consideration.
b) Consider the results of the SGPRISM's examination of the STEREO project, along with concurrent and subsequent investigations.
c) Evaluate an analysis of simulations exploring the effects of stock structural factors on the parameters of stock-recruitment relationships with a view to preparing a case for a Study Group on evaluating the impact of these factors on stock projections, and in the light of results from the Workshop on the Transport of Cod Larvae held immediately prior to the meeting.
d) Consider a synthesis of the 2000 Theme Session on *Spatial and Temporal Patterns in Recruitment Processes* to be prepared by the Session's Convenors as well as a synthesis of recruitment issues presented at the SAP symposium held in December 2000.
e) Identify areas in the study of recruitment processes where sufficient progress has been achieved with the objective of developing a workshop dealing with specific case studies.
f) 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.

The report from the second meeting of SGPRISM (ICES 2001a) contains an examination of the STEREO project which will allow the Working Group on Recruitment Processes to address its second ToR b). In addition, this report of the third meeting of SGPRISM includes a number of concurrent and subsequent investigations, which should lead to a refinement of the present approach to incorporating stock structure and environmental information into stock assessment and projection procedures.

SGPRISM suggests that drivers for weight-at-age and maturity-at-age should be investigated on a stock by stock basis.

6.2.3 ICES International Bottom Trawl Survey Working Group

The ICES International Bottom Trawl Survey Working Group [IBTSWG] (Chair: A.W. Newton, UK) meets in 2002 with a ToR j) *to consider the additional collection of data on the condition of cod (liver weights) caught during the first quarter IBTS in the North Sea and recommend a protocol on how to collect such data*. The collection of such data, which could be used to evaluate the reproductive potential of cod stocks, was a recommendation from the second meeting of SGPRISM (ICES 2001a).

Field and laboratory studies of fish growth indicate that condition varies rapidly within and across years in response to changes in the balance between energy intake (e.g., feeding) and expenditure (e.g., spawning). This has important implications for the reproductive potential of demersal stocks such as the Barents Sea and Icelandic cod where the fecundity/length relationships are significantly affected by inter-annual variation in the condition of spawners. For many stocks it is difficult to assess the magnitude of variability in condition because condition time series are non-existent or of limited temporal/spatial scope. In such cases, the sampling protocols of research surveys should be adapted such that individual-level information on total body and/or liver weights is collected on an annual basis for selected species. When adapting the sampling protocols special consideration should be given to the following:

a) how the condition index should be formulated for the species of interest (e.g., weight-based versus lipid-based); and
b) how sub-sampling strategies as well as the temporal and spatial coverage of the survey affect the accuracy of the condition index.

6.2.4 ICES Working Group on Methods on Fish Stock Assessments

The work of SGPRISM has relevance to the ICES Working Group on Methods on Fish Stock Assessments; specifically in respect of models for weight-at-age, maturity-at-age and condition factors for both historical stock assessment and medium-term projections.

6.2.5 ICES Study Group on the Further Development of the Precautionary Approach to Fishery Management

The ICES Study Group on the Further Development of the Precautionary Approach to Fishery Management [SGPA] (Co-chairs: Colin Bannister, UK, and Manuela Azevedo, Portugal) meets in 2002 with a ToR:

b) to continue the development of the framework for formulating advice for:
   i) stocks under full analytical assessment
      - where the reference points are based on F_{loss} and B_{loss}
      - where the reference points are based on historical evidence of reduced recruitment at low SSB levels

The segmented regression approach presented at this meeting by O'Brien and Maxwell (WD3, WD4) potentially provides an objective technique whereby biomass reference points might be developed. SGPRISM proposes that the approach be investigated further with a view to addressing the ToR b) of the SGPA.

6.2.6 ICES Planning Group on North Sea Cod and Plaice Egg Surveys

The ICES Planning Group on North Sea Cod and Plaice Egg Surveys [PGEGGS] (Chair: John Casey, UK) meets in 2002 with a ToR b) *to co-ordinate the timing, area allocation and sampling protocol for plankton surveys; including sampling of adults to determine fecundity, atresia, maturity and sex ratio*. SGPRISM suggests that this planning group be made aware of the current SGPRISM report, particularly in respect of the Section 2 which discusses reproductive potential for North Sea cod.

7 WORKING DOCUMENTS AND BACKGROUND MATERIAL PRESENTED TO THE STUDY GROUP

At the Study Group twelve working documents (WD1-WD12) and six background documents (BD1-BD6) were presented and discussed. These are listed below, together with the reference codes used in the text of this report.

Working document: WD1

Bogstad, B. Predation by herring on capelin larvae – incorporation in capelin management.

Working document: WD2

Witthames, P.R. Reproduction and stock evaluation for recovery (RASER).

Working document: WD3

O'Brien, C.M., and Maxwell, D.L. Stock-recruitment modelling based upon a segmented regression approach – the case of North Sea cod.

Working document: WD4

O'Brien, C.M., and Maxwell, D.L. Stock-recruitment modelling based upon a segmented regression approach – the case of Bay of Biscay anchovy.

Working document: WD5

Bogstad, B. Incorporating process information in recruitment predictions for Northeast Arctic cod.

Working document: WD6

Nash, R.D.M., and Dickey-Collas, M. At what point in the life history is year class strength determined? An examination of North Sea herring (*Clupea harengus*).

Working document: WD7

Armstrong, M., Dickey-Collas, M., and Gerritsen, H. Estimation of reproductive characteristics of Irish Sea cod.

Working document: WD8

Needle, C. Exploratory analyses: weights-at-age modelling

Working document: WD9

Marshall, C.T., Yaragina, N.A., Thorsen, A., and Kjesbu, O.S. Incorporating reproductive potential into stock-recruitment models for Northeast Arctic cod.

Working document: WD10

Tretyak, V.L. Spawning stock structure of Northeast Arctic cod.

Working document: WD11

Clark, R., and Fox, C. Modelling the effects of climatic change on North Sea cod stocks.

Working document: WD12

Reeves, S.A. Possible approaches to using process information in medium-term projections for Eastern Baltic cod.

Background document: BD1

Report of the 2nd Working Group Meeting, NAFO Scientific Council Working Group on Reproductive Potential, St. Petersburg, Russia, 23–26 October 2001.

Background document: BD2

NAFO Working Group on Reproductive Potential – current and proposed terms of reference.

Background document: BD3

NAFO Working Group on Reproductive Potential – data on reproductive potential for Atlantic cod in ICES sub-areas I and II.

Background document: BD4

Darby, C. Estimation bias in the North Sea short-term forecasts. Working paper presented to the ICES Working Group on Methods on Fish Stock Assessments, ICES Headquarters, Copenhagen, Denmark, 3–7 December 2001.

Background document: BD5

Darby, C. Over-estimation bias in the North Sea cod short-term forecasts. Working paper presented to the ICES Working Group on Methods on Fish Stock Assessments, ICES Headquarters, Copenhagen, Denmark, 3–7 December 2001.

Background document: BD6

Needle, C.L. ARMA and VARMA models in medium-term projections. Working paper presented to the ICES Working Group on Methods on Fish Stock Assessments, ICES Headquarters, Copenhagen, Denmark, 3–7 December 2001.

8 REFERENCES

Alcaraz, M. 1997. Copepods under turbulence: grazing, behaviour and metabolic rates. *Sci. Mar.* **61:** 177–195.

Anon. 1997. Preliminary Report of the International 0-group survey in the Barents Sea and adjacent waters in 1996. ICES CM 1997/G:31.

Anon. 2001a. Report from the 2001 joint Russian-Norwegian meeting to assess the Barents Sea capelin stock. Vadsø, Norway, 5–7 October, 2001. Working Document to the 2001 ACFM meeting.

Anon. 2001b. dst2. Development of structurally detailed statistically testable models of marine populations. QLK5-CT1999–01609. Progress report for 1 January 2000 to 31 December 2000. Marine Research Institute Technical Report nr. 78, Marine Research Institute, Reykjavik, Iceland.

Bagge, O., Thurow, F., Steffensen, E. and Bay, J. 1994. The Baltic cod. *Dana* **10**: 1–29.

Bailey, K.M. and Houde, E.D. 1987. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. mar. Biol.*, **25**: 1–83

Blanchard, J.L. 2000. Maternal contribution to the reproductive potential of a recovering fish stock: variability in the fecundity and condition of haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf. M.Sc. Thesis, Dalhousie University, Halifax, N.S. 110 pp.

Bogstad, B. and Mehl, S. 1997. Interactions Between Cod (*Gadus morhua*) and Its Prey Species in the Barents Sea. Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97–01: 591–615. University of Alaska Fairbanks.

Bogstad, B., Lilly, G. R., Mehl, S., Pálsson, Ó. K., and Stefánsson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland and eastern Newfoundland*). ICES mar. Sci. Symp*. **198**: 576–599.

Brander, K. 1996. Effects of climate change on cod (*Gadus morhua*) stocks. In: *Global warming: Implications for freshwater and marine fish*. Wood, C.M. and McDonald, D.G. (eds.) Cambridge University Press, p. 255–278.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *J. Mar. Sci.* **52:** 1–10.

Bromley, P.J. 2000. Growth, sexual maturation and spawning in central North Sea plaice (*Pleuronectes platessa* L.), and the generation of maturity ogives from commercial catch data. *J. Sea Res.* **44:** 27–43.

Bromley, P.J., Ravier, C. and Witthames, P.R. 2000. The influence of feeding regime on sexual maturation, fecundity and atresia in first-time spawning turbot. *J. Fish Biol*. **56**: 264–278.

Brown, J.A., Pepin, P., Methven, D.A. and Somerton, D.C. 1989. The feeding, growth and behaviour of juvenile cod, *Gadus morhua* L., in cold environments. *J. Fish Biol.* **35:** 373–380.

Cook, R.M., Kunzlik, P.A., Hislop, J.R.G., Poulding, D. 1999. Models of growth and maturity for North Sea cod. *J. Northw. Atl. Fish. Sci*., **25**: 91–99.

Daan. N. 1981. Comparison of estimates of egg production of the southern Bight cod stock from plankton surveys and market statistics. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer*. **178**: 242–243.

deYoung, B. and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Can. J. Fish. Aquat. Sci.* **50:** 2729–2741.

Dower, J.F., Miller, T.J. and Leggett, W.C. 1997. The role of microscale turbulence in the feeding ecology of larval fish. *Adv. Mar. Biol.* **31:** 170–220.

Dutil, J.-D., Castonguay, M., Gilbert, D. and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **56:** 1818–1831.

Fiksen, Ø., Utne, A.C.W., Aksnes, D.L., Eiane, K., Helvik, J.V. and Sundby, S. 1998. Modelling the influence of light, turbulence and ontogeny on ingestion rates in larval cod and herring. *Fish. Oceanogr.* **7:** 355–363.

Fox, C.J., Planque, B. and Darby, C.D. 2000. Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L.) around the United Kingdom and the influence of sea temperature. *J. Sea Res.* **44:** 159–168.

Frøysa, K. G., Bogstad, B., and Skagen, D. W. 2002. Fleksibest – an age-length structured fish stock assessment tool with application to Northeast Arctic cod (*Gadus morhua* L.). *Fisheries Research* **55**: 87–101.

Gamito, S. 1998. Growth models and their use in ecological modelling: an application to a fish population. *Ecol. Model.* **113:** 83–94.

Graham, M. 1924. The annual cycle in the life of the mature cod in the North Sea. *Fishery Invest., London (2)* **6**:1–77.

Gjøsæter, H., and Bogstad, B. 1998. Effects of the presence of herring on the stock-recruitment relationship of Barents Sea capelin (*Mallotus villosus*). *Fisheries Research* **38**: 57–71.

Gjøsæter, H., Bogstad, B., and Tjelmeland, S. 2002. Assessment methodology for Barents Sea capelin (*Mallotus villosus* Müller). *ICES mar. Sci. Symp*. (Under revision).

Grønkjær, P. and Wieland, K. 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. *Mar. Ecol. Prog. Ser.*, **154**: 91–105.

Gulland, J.A. 1977. *Fisheries Population Dynamics.* London: John Wiley and Sons.

Hamre, J. 1985. Assessment and management of Barents Sea capelin. Pp. 5–24 In: Gjøsæter, H. (ed). Proc. Soviet-Norwegian symposium on the Barents Sea capelin, Bergen 14–17 August 1984. Institute of Marine Research, Bergen, Norway.

Hamre, J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. *Biodiversity and Conservation* **3**: 473–492.

Heessen, H.J.L. 1993. The distribution of cod (*Gadus morhua*) in the North Sea. *NAFO Sci. Coun. Studies* **18:** 59–65.

Henderson, B. A., Trivedi, T. and Collins, N. 2000. Annual cycle of energy allocation to growth and reproduction of yellow perch. *J. Fish Biol.* **57**: 122–133.

Hermann, A.J., Hinckley, S., Megrey, B.A. and Napp, J.M. 2001. Applied and theoretical considerations for constructing spatially explicit individual-based models of marine larval fish that include multiple trophic levels. *J. Mar. Sci.* **58**: 1030–1041.

Hermann, A.J., Rugen, W.C., Stabeno, P.J. and Bond, N.A. 1996. Physical transport of young pollock larvae (*Theragra chalcogramma*) near Shelikof Strait as inferred from a hydrodynamic model. *Fish. Oceanography* **5**: 58–70.

Hinrichsen, H.H., Möllmann, C., Voss, R., Köster, F.W. and Kornilovs, G. 2001a. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) survival and growth. *Can. J. Fish. Aquat. Sci*. (submitted).

Hinrichsen, H.-H., M.A. St.John, E. Aro, P. Grønkjær, and Voss, R. 2001b. Testing the larval drift hypothesis in the Baltic Sea: Retention vs. dispersion due to the influence of the wind driven circulation. *ICES J. Mar. Sci*., **58**: 973–984.

Holt, E.W.L. 1893. North Sea investigations. *J. Mar. Biol. Ass. U.K.* **3**:78–122.

Huse G., and Toresen, R. 2000. Juvenile herring prey on Barents Sea capelin larvae. *Sarsia* **85**:385–391.

ICES 2000a. Report of the Study Group on Incorporation of Process Information into Stock Recruitment Models, Lowestoft, UK, 23–26 November 1999. ICES CM 2000/C:01.

ICES 2000b. Report of the ICES Advisory Committee on Fishery Management, 2000. *ICES Coop. Res. Rep.* **242**.

ICES 2001a. Report of the Study Group on Incorporation of Process Information into Stock Recruitment Models, Lowestoft, UK, 23–26 January 2001. ICES CM 2001/C:02.

ICES 2001b. Report of the Arctic Fisheries Working Group, Bergen, Norway 24 April – 3 May 2001. ICES C.M. 2001/ACFM:19, 380pp.

ICES 2001c. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group Reykjavik 18–27 April 2001. ICES C. M. 2001/ACFM:17, 239pp.

ICES 2001d. Report of the Arctic Fisheries Working Group, Copenhagen, 22–31 August 2001. ICES CM 2001/ACFM:02

ICES 2001e. Report of the Herring Assessment Working group for the Area South of 62ºN, March 2001. ICES CM 2001/ACFM:12.

ICES 2002a. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak, 19–28 June 2001, Hamburg, Germany. ICES CM 2002/ACFM:01.

ICES 2002b. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy, ICES Headquarters, Copenhagen, Denmark, 4–13 September 2001. ICES CM 2002/ACFM:06.

ICES 2002c. Report of the Working Group on Methods on Fish Stock Assessments, ICES Headquarters, Copenhagen, Denmark, 3–7 December 2001. ICES CM 2002/D:08.

Kjesbu, O.S., Klungsøyr, J., Kryvi, H., Witthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic 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., Greer Walker, M. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research* **40**:303–321.

Köster, F.W. and Möllmann, C. 1997. Predation by sprat and herring on early life stages of cod and sprat in the central Baltic. Proceedings Symposium on Forage Fishes in Marine Ecosystems, Alaska Sea Grant College Program No. 97–01: 41–70.

Köster, F.W. and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES J. mar. Sci*. **57**: 310–323.

Köster, F.W., Wieland, K., Rohlf, N., Kraus, G., Hinrichsen, H.-H. and Möllmann, C. 2001a. Egg developmental success of Baltic cod: the impact of oxygen deficiency. *Fish. Oceanogr*. (submitted).

Köster, F.W., Hinrichsen, H.-H., Schnack, D., St. John, M. A., MacKenzie, B.R., Tomkiewicz, J. and Plikshs, M. 2001b. Developing Baltic cod recruitment models II: Incorporation of environmental variability and species interaction. *Can. J. Fish. Aquat. Sci*. **58**: 1535–1557.

Köster, F.W., C Möllmann, S. Neuenfeldt, M. Vinther, G. Kraus, and Voss, R. 2001c. Fish stock development and environment variability in the Central Baltic Sea. ICES C.M. 2001/U:06

Köster, F.W., Hinrichsen, H.-H., Schnack, D., St. John, M.A., MacKenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2001d. Recruitment of Baltic cod and sprat stocks: Identification of critical life stages and incorporation of environmental variability and spatial heterogeneity into stock-recruitment relationships. *Scientia Marina*, (submitted).

Kraus, G., Müller, A., Trella, K. and Köster, F.W. 2000. Fecundity of Baltic cod: Temporal and spatial variability. *J. Fish Biol.*, **56**: 1327–1341.

Kraus, G., Tomkiewicz, J. and Köster, F.W. 2001. Egg production of Baltic cod: The impact of variations in sex ratio, maturity and fecundity. *Can. J. Fish. Aquat. Sci.* (submitted).

Lambert, Y. and Dutil, J.-D. 1997. Condition and energy reserves of Atlantic cod *(Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. *Can. J. Fish. Aquat. Sci*. **54**:2388–2400.

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

Leising, A.W. and Franks, P.J.S. 1999. Larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) growth on Georges Bank: a model with temperature, prey size, and turbulence forcing. *Can. J. Fish. Aquat. Sci.* **56:** 25–36.

Ma, Y., Kjesbu, O.S., and Jørgensen, T. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci*. **55**: 900–908.

MacKenzie, B.R., M. St. John, and Wieland, K. 1996. Eastern Baltic cod. Perspectives from existing data on processes affecting growth and survival of eggs and larvae. *Mar. Ecol. Prog. Ser*., **134**: 265–281.

MacKenzie, B.R. and Köster, F.W. 2001. CORE/STORE Project: A case study with cooperation between countries inside and outside the EU. ICES C.M. 2001/U:00

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

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, 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.

Marshall, C.T., Yaragina, N.A., Ådlandsvik, B. and Dolgov, A.V. 2000. Reconstructing the stock/recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. *Can. J. Fish. Aquat. Sci*. **57**: 2433–2442.

Marshall, C. T., Yaragina, N. A., and Thorsen, A. 2001. Evaluating the effectiveness of biological reference points in conserving reproductive potential. ICES C. M. 2001/V:17.

Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. *Can. J. Fish. Aquat. Sci*. **55**: 1372–1377.

Marteinsdottir, G and Steinarsson, A. 1998. Maternal influence on size and viability of Iceland cod, *Gadus morhua*, eggs and larvae. *Journal of Fish Biology*. **52**: 1241–1258.

Marteinsdottir, G., A. Guðmundsdóttir, V. Þorsteinsson and G. Stefánsson. 2000. Spatial variation in abundance, size composition and viable egg production of spawning cod (*Gadus morhua* L.) in Icelandic waters. *ICES J. Mar. Sci*. **57**:824–830.

Megrey, B.A. and Hinckley, S. 2001. Effect of turbulence on feeding of larval fishes: a sensitivity analysis using an individual-based model. *J. Mar. Sci.* **58:** 1015–1029.

Mehl, S. and Sunnanå, K. 1991. Changes in growth of Northeast Arctic cod in relation to food consumption in 1984–1988. *ICES mar. Sci. Symp*. **193**:109–112.

Möllmann, C., Kornilovs, G. and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *J. Plank. Res*. **22**: 2015–2038.

Möllmann, C., Kornilovs, G., Sidrevics, L. and Köster, F.W. 2001. Variability in population biology of calanoid copepods in the Central Baltic Sea. ICES CM 2001/U:08.

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.

Murawski, S.A., Rago, P.J. and Trippel, E.A. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science*, **58**:1002–1014.

Myers, R.A. 1998. When do environment-recruitment correlations work? *Rev. Fish Biol. Fish.* **8:** 285–305.

Myers, R.A., Mertz, G. and Barrowman, N.J. 1995. Spatial scales of variability in cod recruitment in the North Atlantic. *Can. J. Fish. Aquat. Sci.* **52:** 1849–1862.

Myers, R.A., Mertz, G. and Bridson, J. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Can. J. Fish. Aquat. Sci.* **54:** 1400–1407.

Needle, C. L., O'Brien, C. M. and Darby, C. D. 2001. Ogive characterisations in medium-term stock projections. ICES CM 2001/V:19.

Needle, C. L., O'Brien, C. M., Darby, C. D. and Smith, M. T. 2000. The use of recruitment time-series structure and environmental information in medium-term stock projections. ICES CM 2000/V:05.

Needle, C. L., O'Brien, C. M., Darby, C. D. and Smith, M. T. (in press). Incorporating time-series structure and environmental information in medium-term stock projections, *Scientia Marin*a.

Neuenfeldt, S. and Köster, F.W. 2000. Trophodynamic control on recruitment success in Baltic cod: The influence of cannibalism. *ICES J. Mar Sci.*, **57**: 300–309.

O'Brien, C.M., Fox, C.J., Planque, B. and Casey, J. 2000. Climate variability and North Sea cod. *Nature* **404:** 142.

Oosthuizen, E., and Daan, N. 1974. Egg fecundity and maturity of North Sea cod, *Gadus morhua*. *Neth. J. Sea Res*. **8**: 378–397.

Ottersen, G. and Loeng, H. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. *J. Mar. Sci.* **57:** 339–348.

Ottersen, G., Loeng, H. and Raknes, A. 1994. Influence of temperature variability on recruitment of cod in the Barents Sea. *ICES mar. Sci. Symp*. **198**: 471–481.

Ottersen, G., Michalsen, K. and Nakken, O. 1998. Ambient temperature and distribution of Northeast Arctic cod. *J. Mar. Sci.* **55:** 67–85.

Ottersen, G., and Stenseth, N. C. 2001. Atlantic climate governs oceanographic and ecological variability in the Barents Sea. *Limnol. Oceanogr*. **46**: 1774–1780.

Ottersen, G.S. and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. *Fish. Oceanogr.* **4:** 278–292.

Painting, S.J., Hutchings, L., Huggett, J.A., Korrûbel, J.L., Richardson, A.J., and Verheye, H.M. 1998. Environmental and biological monitoring for forecasting anchovy recruitment in the southern Benguela upwelling region. *Fish. Oceanogr*. **7**: 364–374.

Patterson, K.R., Cook, R.M., Darby, C.D., Gavaris, S., Mesnil, B., Punt, A.E., Restrepo, V.R., Skagen, D.W., Stefánsson, G. and Smith, M. 2000. Validating three methods for making probability statements in fisheries forecasts. ICES CM 2000/V:06.

Paulik, G.J. 1973. Studies of the possible form of the stock-recruitment curve. *Rapp. P-V Réun. Cons. Int. Explor. Mer.* **164**: 302–315.

Planque, B. and Fox, C.J. 1998 Interannual variability in temperature and the recruitment of Irish Sea cod. *Mar. Ecol. Prog. Ser.* **172:** 101–105.

Planque, B. and Frédou, T. 1999 Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **56:** 2069–2077.

Plikshs, M., Kalejs, M., and Graumann, G. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES CM 1993/J:22

Purchase, C.F. and Brown, J.A. 2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. *J. Fish Biol.* **58:** 36–52.

Quinlan, J.A. and Crowder, L.B. 1999. Searching for sensitivity in the life history of Atlantic menhaden: inferences from a matrix model. *Fish. Oceanogr.* **8:** 124–133.

Reeves, S. and Cook, R. 1994. Demersal Assessment Programs, September 1994. Working Document to the 1994 meeting of the ICES North Sea Demersal Working Group.

Reid, P.C., Borges, M.F. and Svendsen, E. 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery *Fish. Res.* **50**: 163–171.

Rideout, R.M., Burton, M.P.M., and Rose, G.A. 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. *J. Fish Biol.* **57**: 1429–1440.

Rijnsdorp, A.D., Daan, N., Beek, F.A. van, Heessen, H.J.L. 1991. Reproductive variability in North Sea plaice, sole, and cod. *J. Cons*. **47**: 352–375.

Schnack, D and Köster, F.W. 2001. Environmental and fisheries influences on fish stock recruitment in the Baltic Sea (STORE). Summary of results 1999–2000. ICES CM 2001/Mini Symp. U: 15

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**: 1882–1890.

Secor, D.H. 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment of Chesapeake Bay striped bass. *ICES J. Mar. Sci*. **57**: 403–411.

Shannon, C.E. 1948. A mathematical theory of communication. *Bell. Syst. Tech. J.* **27**: 379–423.

Shepherd, J. G. 1997. Prediction of year-class strength by calibration regression analysis of multiple recruit index series. *ICES J. mar. Sci*. **54**: 741–752.

Sparholt, H., Aro, E. and Modin, J. 1991. The spatial distribution of cod (*Gadus morhua* L.) in the Baltic Sea. *Dana* **9:** 45–56.

St. John, M.A., Mosegaard, H., Hinrichsen, H.-H., Grønkjær, P., Köster F.W., Hüssy, K. and Nielsen, R. 2000. Baltic Cod: Resolving processes determining spatial and temporal windows of survival. ICES CM 2000/N:2.

Swain, D.P. and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St, Lawrence. *Canadian Journal of Fisheries and Aquatic Science* **50:** 725–733.

Taylor, C.C. 1956. Cod growth and temperature. *Rapp. P-v. Réun. Cons. Int. Explor. Mer.* 366–370.

Toresen, R. and Østvedt, O.J. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus,* Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries,* **1**:231–256.

Tretyak, V. L. 1999. On possibility of the use of the Ricker's model 'Stock-recruitment' for estimation of recruitment of Northeastern Arctic cod population. ICES C.M. 1999/Y:12.

Tretyak, V.L. 2000. Modelling of age-dependent instantaneous coefficients of natural mortality for Northeast Arctic cod. ICES C.M. 2000/V: 09, 23pp.

Trippel, E.A. 1999. Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *J. Northw. Atl. Fish. Sci*. **25**: 61–81.

Uzars, D. and Plikshs, M. 2000. Cod (*Gadus morhua callarias* L.) cannibalism in the Central Baltic: Interannual variability and influence of recruitment, abundance and distribution. *ICES J. Mar. Sci*. **57**: 324–329.

Vallin L. and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*. Implications for stock structure effects on recruitment. *Fish. Res*. **49**: 21–37.

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

Wieland, K. and Jarre-Teichmann, A. 1997. Prediction of vertical distribution and ambient development temperature of Baltic cod (*Gadus morhua* L.) eggs. *Fish. Oceanogr*. **6**(3):172–187.

Witthames, P.R., and Greer Walker, M. 1995. Determinacy of fecundity and oocyte atresia in sole (*Solea solea*) from the Channel, North Sea and the Irish Sea. *Aquat. Living Res*. **8**: 91–109.

Yaragina, N.A., and Marshall, C.T. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). *ICES J. Mar. Sci*. **57**: 42–55.

APPENDIX A: AVAILABLE DATA ON REPRODUCTIVE POTENTIAL OF NORTHEAST ARCTIC COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL

Common name:	ATLANTIC COD	**Species:**	*Gadus morhua*
Area:	ICES SUB-AREAS I AND II	**Stock:**	NORTHEAST ARCTIC
Created by:	C.T. MARSHALL/N.A. YARAGINA 2001–08	**Updated by:**	

Data status

Year	Stock size	Stock composition	Age	Sex ratio	Maturity	Fecundity	Weight	Condition	Additional data
2001	√	√	√	(√)	√		√	√	
2000	√	√	√	(√)	√	√	√	√	
1999	√	√	√	(√)	√	√	√	√	
1998	√	√	√	(√)	√		√	√	
1997	√	√	√	(√)	√		√	√	
1996	√	√	√	(√)	√		√	√	
1995	√	√	√	(√)	√		√	√	
1994	√	√	√	(√)	√		√	√	
1993	√	√	√	(√)	√		√	√	√
1992	√	√	√	(√)	√		√	√	√
1991	√	√	√	(√)	√	√	√	√	√
1990	√	√	√	(√)	√		√	√	√
1989	√	√	√	(√)	√	√	√	√	√
1988	√	√	√	(√)	√	√	√	√	√
1987	√	√	√	(√)	√	√	√	√	√
1986	√	√	√	(√)	√	√	√	√	√
1985	√	√	√	(√)	√		√	√	√
1984	√	√	√	(√)	√		√	√	√
1983	√	√	√	(√)	√		√	√	√
1982	√	√	√	(√)	√		√	√	√
1981	√	√	√	(√)	√		√	√	√
1980	√	√	√	(√)	√		√	√	√
1979	√	√	√	(√)	√		√	√	√
1978	√	√	√	(√)	√		√	√	√
1977	√	√	√	(√)	√		√	√	√
1976	√	√	√	(√)	√		√	√	√
1975	√	√	√	(√)	√		√	√	√
1974	√	√	√	(√)	√		√	√	√
1973	√	√	√	(√)	√		√	√	√

Table layout and preparation coordinated by NAFO WG members Jay Burnett, Joanne Morgan and Jonna Tomkiewicz.

Data status

Year	Stock size	Stock composition	Age	Sex ratio	Maturity	Fecundity	Weight	Condition	Additional data
1972	√	√	√	(√)	√		√	√	√
1971	√	√	√	(√)	√		√	√	√
1970	√	√	√	(√)	√		√	√	√
1969	√	√	√	(√)	√		√	√	√
1968	√	√	√	(√)	√		√	√	√
1967	√	√	√	(√)	√		√	√	√
1966	√	√	√	(√)	√		√	√	√
1965	√	√	√	(√)	√		√	√	√
1964	√	√	√	(√)	√		√	√	√
1963	√	√	√	(√)	√		√	√	√
1962	√	√	√	(√)	√		√	√	√
1961	√	√	√	(√)	√		√	√	√
1960	√	√	√	(√)	√		√	√	√
1959	√	√	√	(√)	√		√	√	√
1958	√	√	√	(√)	√		√	√	
1957	√	√	√	(√)	√		√	√	
1956	√	√	√	(√)	√		√	√	
1955	√	√	√	(√)	√		√	√	
1954	√	√	√	(√)	√		√	√	
1953	√	√	√	(√)	√		√	√	
1952	√	√	√	(√)	√		√	√	
1951	√	√	√	(√)	√		√	√	
1950	√	√	√	(√)	√		√	√	
1949	√	√	√	(√)	√		√	√	
1948	√	√	√	(√)	√		√	√	
1947	√	√	√	(√)	√		√	√	
1946	√	√	√	(√)	√		√	√	

APPENDIX B: BASIS, QUALITY AND FORMAT OF DATA ON REPRODUCTIVE POTENTIAL OF NORTHEAST ARCTIC COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL

Common name: ATLANTIC COD

Area: ICES SUB-AREAS I AND II

Stock: NORTHEAST ARCTIC

REPRODUCTIVE STRATEGY: DETERMINATE BATCH SPAWNER **Ref. no.:** 1

TIMING OF SPAWNING: FEB-MAY **Ref. no.:** 2

OPTIMAL TIME FOR MATURITY SAMPLING: JAN-MAR **Ref. no.:** 3

RECOMMENDED METHOD FOR FECUNDITY ANALYSIS:

GRAVIMETRIC, STEREOMETRIC OR AUTO-DIAMETRIC **Ref. no.:** 4,5

Data basis, format and quality

Variables	Year range	Data basis (A/L/W)	**Data origin**	**Sampling frequency**	**Notes on data, methods and contents**	**Ref. No.**
Stock size	1946–2001	A	CC, S	Q,A	VPA	6
Stock composition	1978–2001	L,A,W	CC, S	Q	Winter survey	6
	1985–2001	L,A,W			Lofoten survey	6
	1946–2000	L,A,W			Russian survey	6,7
	1932–1979	L,A			Norwegian sampling of commercial fishery	8
Age determination	1946–2001	A	CC, S	Q	Otoliths	33, 50
Sex ratio	1985–1996	L	S	A	Winter + Lofoten surveys combined	9
	1950's-1990's	A	CC,S	10 YEAR MEANS		10
Maturity:						
A. Ogives (E)	1946–2001	A	S	A		6, 10
B. Skip of spawning	1985–1996	L	S	A		9
	1991–1992	L,A	S	A		51
C. Spawning probability						
D. Other	1923–1976	A, L	CC	M	Spawning check in otolith	11
	1989–1997	A, L	S		sex differences in ogive	12
	1950's-1990's	A	CC,S		sex differences in ogive	10
	1940's-1950's				Sorokin maturity scale	56, 57
Fecundity:						

Table layout and preparation coordinated by NAFO WG members Jay Burnett, Joanne Morgan and Jonna Tomkiewicz.

Data basis, format and quality						
Variables	Year range	Data basis (A/L/W)	**Data origin**	**Sampling frequency**	**Notes on data, methods and contents**	**Ref. No.**
A. Estimation	1986–1991	L, W	EW		Gravimetric	4
	1999	L, W	EW		auto-diametric	5
	1971–1972	L,W,A			gravimetric	42
	1990, 1991, 1993–1996, 1999	L,W,A			gravimetric	52
B. First time vs. repeat spawners	1989–1992	L,W	X		Spawners held in captivity over consecutive seasons	13,14
C. Atresia	lab expt	L,W	EC		Laboratory-reared cod	15
D. Other	lab expt		EC		Effects of starvation on relative fecundity	20
Weight:						
A. Commercial fisheries data	1946–2001	A	CC, S	A	Russian+Norwegian	6,8
	1949–1993	A	CC, S	A	Russian	53
B. Survey data	1984–2001	A	S	A	Russian+Norwegian	6
C. Other	1913–1953	L	CL	A	Historical data on size from Lofoten	47
Condition:						
A. Fulton						
B. HSI	1927–1996	L	CC	M	By 10-cm length class	16
	1828–1842	-	CL	A	industrial index of liver	48
C. Energy	1946–1996	L	CC,S	A	Total lipid energy in livers of mature females	17
D. Other	1929–1982	W	CL	A	median spawning intensity based on roe samples	2
Egg viability:						
A. Egg quality	lab expt		EC		Cortical reaction following fertilization	18
	lab expt		EC		egg diameter and dry weight	19
	lab expt		EC		egg diameter in relation to maternal size	1
	lab expt		EC		egg diameter in relation to maternal condition	15
	lab expt		EC		egg dry weight in relation to spawning experience	13
	lab expt		EW		buoyancy studies	30
B. Fertilisation success	lab expt		EC		Incomplete hardening of chorion associated with poor fertilization	18
	lab expt		EC		links between broodstock, egg quality and fertilization	21
	lab expt		EW		links between length and condition of females and fertilization	27

Data basis, format and quality						
Variables	Year range	Data basis (A/L/W)	**Data origin**	**Sampling frequency**	**Notes on data, methods and contents**	**Ref. No.**
C. Egg mortality	lab expt 1983–1984		EC S	 A	Links between egg mortality and spawning experience field estimate of egg mortality	14 22
D. Other	review review review lab expt		 EC		Broodstock management and egg rearing egg quality maternal effects fatty acid composition	23 24 25 26
Larval viability:						
A. Hatching success						
B. Larvae quality	mesocosm mesocosm		EC EC		Relationship between larval growth and survival and links to broodstock relationship between larval growth and survival	28 29
C. Mortality	1983–1985 1983–1985		S S		Mortality and first-feeding mortality estimates from ichthyoplankton surveys	31 32
D. Other						
Spawning time	consult original reference				ref. 34 describes seasonal activity of thyroid gland	2,3,34
Contamination	1993		S	A	Concentration of heavy metals, PAH, and organochlorine discussed in relation to egg abnormalities	35
Environmental key factors	consult original reference				Temperature, wind stress	36, 37,54
Other factors or parameters	consult original reference				Cannibalism, overwintering of recently settled juveniles historical data on Barents Sea	38 39 55

APPENDIX C: STUDIES OF REPRODUCTIVE POTENTIAL OF NORTHEAST ARCTIC COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL.

ATLANTIC COD

Area: ICES SUB-AREAS I AND II

Stock: NORTHEAST ARCTIC

Estimation of reproductive potential

Subject	**Brief description**	**Year range**	Ref. No.
Potential or realised egg production	Estimates of total egg production (also referred to as population fecundity)	1985–1996	9, 40, 41, 42, 43, 44
Viable egg and larvae production	Estimates of relative abundance of eggs and larvae from Russian ichthyoplankton surveys conducted from April-July	1959–1993	45
Critical life stages	Early pelagic juveniles and 0-group surveys		32, 46
Environmental influences	Influence of wind and temperature on S/R relationship		37
Stock recruitment relations	Biomass-based S/R relationship bioenergetic index of reproductive potential	1946–1989 1946–1996	37 17
Other studies	Reconstructing the S/R relationship using the total lipid energy contained in the livers of mature females	1946–1996	17, 49

APPENDIX D: DATA SOURCES FOR NORTHEAST ARCTIC COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL

C
N ATLANTIC COD

Area: ICES SUB-AREAS I AND II

Stock: NORTHEAST ARCTIC

Stock size	6	6. ICES 2001. Report of the Arctic Fisheries Working Group. ICES CM 2001/ACFM:19.
Stock composition	6,7,8	7. Ponomarenko, V.P., Ponomarenko, I.Ya., and Yaragina, N.A. 1980. Growth and maturation of the Lofoten-Barents Sea cod. ICES CM 1980/G:25. 8. Jørgensen, T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influences. ICES J. mar. Sci. 49: 263–277.
Age determination	33 50	33. Rollefsen, G. 1933. The otoliths of the cod. Fiskeridirektoratets skrifter, serie havundersøkelser 4: 1–14. 50. Mankevich E.M., 1966. Methods of taking and reading the age samples of cod. Materially rybocoz. issledov. Severnogo basseina, Murmansk, v.7, p.53–56. (In Russian).
Sex ratio	9	9. Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Can. J. Fish.
Maturity:		
A. Ogives (E)	10	10. Ponomarenko, I.Ya., and Yaragina, N.A. 1994. Maturity rate of the Lofoten-Barents Sea cod in 40's and 90's. ICES CM 1994/G:30.
B. Skip of spawning	9, 51	51. Oganesyan S.A., 1993. Periodicity of the Barents Sea cod reproduction. ICES C.M. 1993/G:64
C. Spawning probability		
D. Other		11. Jørgensen, T. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). J. Cons. int. Explor. Mer 46: 235–248. 12. Ajiad, A., Jakobsen, T., and Nakken, O. 1999. Sexual difference in maturation of Northeast Arctic cod. J. Northw. Atl. Fish. Sci. 25: 1–15. 56. Sorokin V.P., 1957. Ovogenesis and sexual cycle in cod (*Gadus morhua morhua* L.) Trudy PINRO, 10: 125 – 144 (in Russian). (English translation No.72F49, Ministry of Agriculture, Fisheries and Food, United Kingdom 1961). 57. Sorokin V.P., 1960. Sexual cycle and spermatogenesis in cod. Trudy PINRO, 12: 71- 87 (in Russian).

Fecundity:		
A. Estimation	4,5,42,52	4. 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 Res. 40: 303–321. 5. Thorsen, A., and Kjesbu, O.S. in press. A rapid method for estimation of follicle size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. J. Sea Res. 52. Kiseleva V.M., 2000. Individual and Population fecundity of the Barents Sea cod in the 90's. Materials of the session of PINRO on the results of research in 1998–1999. Murmansk: PINRO Press, Part 1, p.10–22. (in Russian).
B. First time vs. repeat spawners	13,14	13. Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 53:610–620. 14. Solemdal, P., Kjesbu, O.S., and Fonn, M. 1995. Egg mortality in recruit- and repeat-spawning cod - an experimental study. ICES CM 1995/G:35.
C. Atresia	15	15. Kjesbu, O.S., Klungsøyr, J., Kryvi, H., Witthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48: 2333–2343.
D. Other	20	20. Karlsen, Ø., Holm, J.C., and Kjesbu, O.S. 1995. Effects of periodic starvation on reproductive investment in first-time spawning Atlantic cod (*Gadus morhua* L.). Aquaculture 133: 159–170.
Weight:		
A. Commercial fisheries data	53	53. Ozhigin V.K., Tretyak V.L., Yaragina N.A., Ivshin V.A., 1994. Dependence of the Barents Sea cod growth upon conditions of their feeding on capelin and water temperature. ICES C.M. 1994/G:32
B. Survey data		
C. Other	47	47. Rollefesen, G. 1954. Observations on the cod and cod fisheries of Lofoten. Rapp. P.-v. Réun. Cons. perm. int. Explor. mer 136: 40–47.
Condition:		
A. Fulton		
B. HSI	16, 48	16. Yaragina, N.A., and Marshall, C.T. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES J. Mar. Sci. 57:42–55. 48. Øiestad, V. 1994. Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. ICES mar. Sci. Symp. 198: 17–30.
C. Energy	17	17. Marshall, C.T., Yaragina, N.A., Ådlandsvik, B., and Dolgov, A.V. 2000. Reconstructing the stock-recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. Can. J. Fish. Aquat. Sci. 57:2433–2442.
D. Other		

Egg viability:		
A. Egg quality	18, 19, 30	18. Kjørsvik, E., and Lønning, S. 1983. Effects of egg quality on normal fertilization and early development of cod, *Gadus morhua L.* J. Fish Biol. 23: 1–12. 19. Knutsen, G.M. and Tilseth, S. 1985. Growth, development, and feeding success of Atlantic cod larvae *Gadus morhua* related to egg size. Trans. Am. Fish. Soc. 114: 507–511. 30. Davenport, J., Lønning, S., and Kjørsvik, E. 1981. Osmotic and structural changes during early development of eggs and larvae of the cod, Gadus morhua L. J. Fish Biol. 19: 317–331.
B. Fertilisation success	21, 27	21. Kjørsvik, E., Stene, A., and Lønning, S. 1984. Morphological, physiological and genetical studies of egg quality in cod (*Gadus morhua* L.) In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (ed.), The propagation of cod Gadus morhua L. Flødevigen rapportser. 1: 67–86. 27. Solemdal, P. and others. 1993. Size of spawning Arcto-Norwegian cod (*Gadus morhua* L.) and the effects on their eggs and early larvae. ICES CM 1993/G:41.
C. Egg mortality	22	22. Fossum, P. 1988. A tentative method to estimate mortality in the egg and early fish larval stages with special reference to cod (*Gadus morhua* L.) FiskDir. Skr. Ser. HavUnders. 18: 329–349.
D. Other	23, 24, 25	23. Kjørsvik, E., and Holmefjord, I. 1995. Atlantic halibut (Hippoglossus hippoglossus) and cod (*Gadus morhua*). In: N.R. Bromage and R.J. Roberts (ed.), Broodstock management and egg and larval quality. Blackwell Science, Cambridge. p 169–196. 24. Kjørsvik, E., Mango-Jensen, A. and Holmefjord, I. 1990. Egg quality in fishes. Adv. Mar. Biol. 26: 71–113. 25. Solemdal, P. Maternal effects - a link between the past and the future. J. Sea Res. 37: 213–227. 26. Ulvund, K.A., and Grahl-Nielsen, O. 1988. Fatty acid composition in eggs of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 45: 898–901.
Larval viability:		
A. Hatching success		
B. Larvae quality	28, 29	28. Blom, G., Svåsand, T., Jørstad, K.E., Otterå, H., Paulsen, O.I., and Holm, J.C. 1994. Comparative survival and growth of two strains of Atlantic cod (*Gadus morhua*) through the early life stages in a marine pond. Can. J. Fish. Aquat. Sci. 51: 1012–1023. 29. van der Meeren, T., Jørstad, K.E., Solemdal, P., and Kjesbu, O.S. 1994. Growth and survival of cod larvae (*Gadus morhua* L.): comparative enclosure studies of Northeast Arctic cod and coastal cod from western Norway. ICES mar. Sci. Symp. 198: 633–645.
C. Mortality	31, 32	31. Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). Rapp. P.-v- Réun. Cons. int. Explor. Mer 1991: 209–219. 32. Sundby, S., Bjørke, H., Soldal, A. V., and Olsen, S. 1989. Mortality rates during the early life stages and year-class strength of northeast Arctic cod (*Gadus morhua* L.) Rapp. P.-v. Réun. Cons. int. Explor. Mer 191: 351–358.
D. Other		

Spawning time	2, 34	2. Pedersen, T. 1984. Variation in peak spawning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (editors), The propagation of cod Gadus morhua L. Flødevigen rapportser. 1: 301–316. 34. Woodhead, A.D. 1959. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. J. mar. biol. Ass. U.K. 38: 407–415.
Contamination	35	35. Mukhina, N.V., Plotitsyna, N.F., and Golubeva, T.A. 1996. Disturbances in embryogenesis of cod from the Lofoten-Barents Sea stock. ICES C.M./Q:6.
Environmental key factors	36, 37, 38, 39, 54	36. Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia 85: 277–298. 37. Ottersen, G. and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fish. Oceanogr. 4: 278–292. 38. Bogstad, B. and Mehl, S. 1997. Interactions between Atlantic cod (Gadus morhua) and its prey species in the Barents Sea. In Proceedings of the international symposium on the role of forage fishes in marine ecosystems. Alaska Sea Grant College Program Report No. 97–01, pp 591–615. 39. Ponomarenko, I.Ya. 1984. Survival of bottom-dwelling young cod in the Barents Sea and its determining factors. In: O.R. Godø and S. Tilseth (editors), Reproduction and recruitment of Arctic cod. Proceedings of the Soviet-Norwegian symposium, Leningrad 26–30 September 1983. pp. 213–229. 54. Tretyak V.L., Ozhigin V.K., Yaragina N.A., Ivshin V.A., 1995. Role of oceanographic conditions in Arcto-Norwegian cod recruitment dynamics. ICES C.M. 1995/ Mini:15. Mini-symposium on Arctic Oceanographic Processes.
Estimation of reproductive potential:		
A. Potential or realised egg production		40. Sundby, S. and Solemdal, P. 1984. The egg production of Arcot-Norwegian cod (*Gadus morhua* L.) in the Lofoten area estimated by egg surveys. In: O.R. Godø and S. Tilseth (editors), Reproduction and recruitment of Arctic cod. Proceedings of the Soviet-Norwegian symposium, Leningrad 26–30 September 1983. pp. 116–137. 41. Sundby, S. and Bratland, P. 1987. Spatial distribution and production of eggs from Northeast-arctic cod at the coast of northern Norway 1983–1985. Fisken Hav. 1987: 1–58 (in Norwegian). 42. Aldonov, V.K., Borisov, V.M., and Serebryakov, V.P. 1982. Fecundity of Arcto-Norwegian cod spawning populations. ICES CM/G:19. 43. Serebryakov, V.P. 1990. Population fecundity and reproductive capacity of some food fishes in relation to year-class strength fluctuations. J. Cons. int. Explor. Mer 47: 267–272. 44. Serebryakov, V.P. 1991. Predicting year-class strength under uncertainties related to survival in the early life history of some North Atlantic commercial fish. NAFO Sci. Counc. Studies 16: 49–55.
B. Viable egg and larvae production		45. Mukhina, N.V. 1999. The use of Russian ichthyoplankton survey data in the forecasting of recruitment to Arcto-Norwegian cod stock. ICES CM 1999/Y:15.

C. Critical life stages	32, 46	46. Helle, K., Bogstad, B., Marshall, C.T., Michalsen, K., Ottersen, G., and Pennington, M. 2000. An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.) Fish. Res. 48: 55–67.
D. Environmental influences		
E. Stock recruitment relations		
Other references	1, 3, 49, 55	1. Kjesbu, O.S. 1989. The spawning activity of cod, Gadus morhua L. J. Fish Biol. 34: 195–206. 3. Bergstad, O.A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fish. Res. 5: 119–161. 49. Nilssen, E.M., Pedersen, T., Hopkins, C.C.E., Thyholt, K., and Pope, J.G. 1994. Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography, and predator-prey energetics. ICES mar. Sci. Symp. 198: 449–470. 55. Maslov N.A., 1944. The bottom-fishes of the Barents Sea and their fisheries. Transactions of PINRO, vol. 8, p. 3–186 (In Russian).

APPENDIX E: AVAILABLE DATA ON REPRODUCTIVE POTENTIAL OF NORTH SEA COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL

Common name:	COD	**Species:**	*Gadus morhua*
Area:	ICES AREA IV	**Stock:**	NORTH SEA
Created by:	PETER WRIGHT 2001–31–05	**Updated by:**	

Year	Stock size	Stock composition	Age	Sex ratio	Maturity	Fecundity	Weight	Condition	Additional data
2001									
2000	√	√		√					
1999	√	√		√	√	√	√	√	√
1998	√	√		√	√				
1997	√	√		√	√				
1996	√	√		√	√				
1995	√	√		√	√				
1994	√	√		√	√				
1993	√	√		√	√				
1992	√	√		√	√				
1991	√	√		√	√				
1990	√	√		√	√		√		
1989	√	√		√	√		√		
1988	√	√	√	√	√		√		
1987	√		√	√	√				
1986	√	√		√	√				
1985	√	√		√	√				
1984	√	√		√	√				
1983	√	√		√	√				
1982	√	√		√	√				
1981	√	√		√	√				
1980	√	√		√	√				
1979	√	√							
1978	√	√							
1977	√	√							
1976	√	√							
1975	√	√							
1974	√	√							
1973	√	√							
1972	√	√			√	√			
1971	√	√	√			√			

Table layout and preparation coordinated by NAFO WG members Jay Burnett, Joanne Morgan and Jonna Tomkiewicz.

Year	Stock size	Stock composition	Age	Sex ratio	Maturity	Fecundity	Weight	Condition	Additional data
1970	√	√				√	√		
1969	√	√	√		√	√	√		
1968	√		√		√				
1967	√	√	√						
1966	√	√	√						
1965	√		√						
1964	√	√							
1963	√	√							
1962									
1961									
1960									
1934					√				
1893					√				
1891						√			
1920–63	√	√							

Table layout and preparation coordinated by NAFO WG members Jay Burnett, Joanne Morgan and Jonna Tomkiewicz.

APPENDIX F: BASIS, QUALITY AND FORMAT OF DATA ON REPRODUCTIVE POTENTIAL OF NORTH SEA COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL

STOCK: NORTHEAST ARCTIC

AREA: ICES AREA IV

REPRODUCTIVE STRATEGY: DETERMINATE BATCH SPAWNER **Ref. no.:** 16

TIMING OF SPAWNING: JANUARY -APRIL **Ref. no.:** 6,16

OPTIMAL TIME FOR MATURITY SAMPLING: DECEMBER-JANUARY **Ref. no.:** 6

RECOMMENDED METHOD FOR FECUNDITY ANALYSIS:

PRE-BREEDING SEASON AND ESTIMATE SEASONAL ATRESIA **Ref. no.:** 6,16

Data basis, format and quality

Parameters	Year range	Data basis (A/L/W)	**Data origin**	**Sampling frequency**	**Notes on data, methods and contents**	**Ref. No.**
Stock size	1920–1963 1963–2000	A A	CL CL, CC in some areas after 1990	M M	VPA but high uncertainty in estimates Catch at age analysis (VPA)	20 1
Stock composition	1963 – 2000 1970s, 1988–90, 1999	L, A L,A, W	CL CL,CC	M	Catch at age analysis (VPA) No routine weight measurements	1 11, 12, 13
Age determination	1963 – 2000	otoliths	C,L	M	age based assessments	1
Sex ratio	1963–2000	L, A	S	A	Surveys	13
Maturity:						
A. Ogives	1883, 1924, 1968–72 1980–1995 1995–2001	A,L, W	S	A	dedicated study dedicated study dedicated study analysis from ICES IBTS analysis of survey data in progress P. Wright, FRS	2 3 4 5 13
B. Skip of spawning						
C. Spawning probability	1953–90		S	A	from egg surveys review	6 7
D. Other						
Fecundity:						
A. Estimation	<1891 1969 1970 -72 1999	A,L A,L A,L,W A,L,W	 S S	 A A	 n=92 n=26	8 9 4 10
B. First time vs. repeat spawners						
C. Atresia						
D. Other						

Data basis, format and quality

Parameters	Year range	Data basis (A/L/W)	Data origin	Sampling frequency	Notes on data, methods and contents	Ref. No.
Weight:						
A. Commercial fisheries data	1970s 1988–90		CC		no regular sampling	11 11 12
B. Survey data			S			
C. Other						
Condition:						
A. Fulton						
B. HSI	1969–70 1999		CC, S	M	few data 1st quarter	11 10
C. Energy						
D. Other						
Egg viability:						
A. Egg quality	1970–72	A,L,W	S	A	n=30 weights	4
B. Fertilisation success						
C. Egg mortality					size selective mortality	14
D. Other						
Larval viability:						
A. Hatching success						
B. Larvae quality						
C. Mortality						
D. Other					study of temperature related larval development	15
Spawning time	1953–90		S	A	plankton surveys	5, 16
Contamination						
Environmental key factors			S		regional trophic studies temperature effects on recruitment	17, 18 19
Other factors or parameters						

APPENDIX G: STUDIES OF REPRODUCTIVE POTENTIAL OF NORTH SEA COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL.

STOCK:	NORTHEAST ARCTIC
AREA:	ICES IVA

Estimation of reproductive potential

Subject	**Short description**	**Year range**	Ref. No.
Potential or realised egg production			
Viable egg and larvae production			
Critical life stages	REVIEW OF GADOID STOCK CHANGES	1962–1993	21
Environmental influences			
Stock recruitment relations	REVIEW OF GADOID STOCK CHANGES	1962–1993	21
Other studies			

APPENDIX H: DATA SOURCES FOR NORTH SEA COD. ADAPTED FROM TABLES PREPARED BY THE NAFO WORKING GROUP ON REPRODUCTIVE POTENTIAL.

STOCK: NORTHEAST ARCTIC

AREA: ICES IVA

Data sources		
Parameters	**Ref. No.**	**Data sources** (literature reference or contact person)
Stock size	1 20	ICES (2001) Report of the ICES Advisory Committee on Fishery Management, 2000. ICES Co-operative Research Report No 242, 361–366. Pope, J. G., and Macer, C. T. (1996) An evaluation of the stock structure of North Sea cod, haddock and whiting since1920, together with a consideration of the impact of fisheries and predation effects on their biomass and recruitment, 53, 1157–1169.
Stock composition	1	ICES (2001) Report of the ICES Advisory Committee on Fishery Management, 2000. ICES Cooperative Research Report No 242, 361–366.
Age determination	1	ICES (2001) Report of the ICES Advisory Committee on Fishery Management, 2000. ICES Cooperative Research Report No 242, 361–366.
Sex ratio		
Maturity:		
A. Ogives	2 3 4 5	Holt, E.W.L (1893) North Sea Investigations. Journal of the Marine Biological association, UK, 78–122 Graham, M. (1924) The annual cycle of the mature cod in the North Sea Fishery Investigations, London (2) 6,1–77. Oosthuizen and Daan (1974) Egg fecundity and maturity of North Sea cod, *Gadus morhua*. Netherlands Journal of Sea Research 8(4), 378–397 Cook, R.M., Kunzlik, P.A., Hislop, J.R.G. and Poulding, D. (1999) Models of growth and maturity for North Sea cod, Journal of the Northwest Atlantic Fisheries Science 25, 91–99.
B. Skip of spawning		
C. Spawning probability	6 7	Brander, K.M. (1994) The location and timing of cod spawning around the British Isles ICES (1994). Spawning and life history information for North Atlantic cod stocks, ed. K. Brander. ICES Cooperative Research Report 205
D. Other		
Fecundity:		
A. Estimation	**8** **9** **4** **10**	Fulton, T.W. (1891). The comparative fecundity of sea fishes. Report of the Fishery Board of Scotland, 9, 243–268. Schopka, S.A. (1971), Fortpflanzungrate bei Herings- und Kabeljaupopulationen. Ber dt. Wiss. Kommn. f Meeresforsch N.F. 22, 31–79 Oosthuizen and Daan (1974) Egg fecundity and maturity of North Sea cod, *Gadus morhua*. Netherlands Journal of Sea Research 8(4), 378–397 Wright, P. unpublished data
B. First time vs. repeat spawners		
C. Atresia		

Data sources		
Parameters	**Ref. No.**	**Data sources** (literature reference or contact person)
D. Other		
Weight:		
A. Commercial fisheries data	11 12	FRS Marine Laboratory, Aberdeen, Scotland CEFAS Fishery laboratory, Lowestoft, England other EU institutes
B. Survey data	13	ICES International bottom trawl surveys, H. Sparholt, ICES Headquarters
C. Other		
Condition:		
A. Fulton	11, 12, 1	available from individual length and weight data sources
B. HIS		liver weights 1969,70 and 1999- FRS Marine Laboratory, Aberdeen, Scotland
C. Energy		
D. Other		
Egg viability:		
A. Egg quality	4	Oosthuizen and Daan (1974) Egg fecundity and maturity of North Sea cod, *Gadus morhua*. Netherlands Journal of Sea Research 8(4), 378–397
B. Fertilisation success		
C. Egg mortality	14	Rijnsdorp, A. D., and Jaworski (1990) A. Size-selective mortality in plaice and cod eggs: a new method in the study of egg mortality. *Journal du Conseil International pour l'Exploration de la mer* **47**, 256–263.
D. Other		
Larval viability:		
A. Hatching success		
B. Larvae quality		
C. Mortality		
D. Other	15	Thompson, B.M., and Riley, J.D. (1981). Egg and larval development studies in the North Sea cod (*Gadus morhua* L.) Rapp. P-v. Reun. Cons. Int. Explor. Mer 178, 553–559.
Spawning time	5 **16**	Brander, K.M. (1994) The location and timing of cod spawning around the British Isles Hislop, J.R.G. (1984) A comparison of the reproductive tactics and strategies of cod, haddock whiting and Norway pout in the North Sea.
Contamination		
Environmental key factors	17 18 19	Munk. P. (1997). Prey size spectra and prey availability of larval and small juvenile cod. J. Fish. Biol. 51(Suppl.A): 340–351. Munk. P., Larsson, P.O., Danielssen, D., and Moksness, E. (1995). Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. Mar. Ecol. Prog. Ser. 125: 21–30. Planque, B. & Frédou, T (1999). Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science 56*, 2069–2077.
Estimation of reproductive potential:		
A. Potential or realised egg production		
B. Viable egg and larvae production		

Data sources		
Parameters	**Ref. No.**	**Data sources** (literature reference or contact person)
C. Critical life stages	21	ICES (2001) Workshop on Gadoid stocks in the North sea during the 1960s and 1970s. The Fourth ICES/GLOBEC Backward Facing Workshop ICES Cooperative Research Report 244, pp55.
D. Environmental influences		
E. Stock recruitment relations		
Other references		