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Report of the Workshop on the Decline and Recovery of cod Stocks throughout the North Atlantic, including tropho-dynamic effects (WKDRCS)

9–12 May 2006

St.John's, Canada

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Conseil International pour l'Exploration de la Mer

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Executive summary

Atlantic cod (*Gadus morhua*) stocks respond to long-term climate changes, such as the warming of the North Atlantic during the 1920s and 1930s, when cod increased rapidly in abundance off West Greenland and spread far to the north. At the same time there was increased recruitment at Iceland and increased abundance and northward expansion in the Barents Sea. By the time that the waters at West Greenland cooled in the late 1960s, the cod stock biomass had declined greatly from its peak in 1949. Both climate and the fishery contributed to the subsequent collapse of the stock, but it is not possible to make a quantitative attribution and the factors interact. In this and other cases the effective environmental factors include plankton production and other ecosystem effects. These factors often co-vary with temperature change, making it difficult to separate them from direct effects of temperature on growth, survival and recruitment.

Cod have been subjected to changes in climate and fishing intensity for centuries, but detailed information on declines and recoveries comes mainly from the past 30–40 years, which is a short time span relative to many natural phenomena. All stocks, with the exception of the Celtic Sea, have suffered prolonged periods of decline since 1970. Comparison between NW and NE Atlantic stocks reveals two major differences: (i) most NW Atlantic stocks share a pattern of increase and decline in biomass, whereas the NE Atlantic stocks do not, and (ii) although fishing mortality is generally higher on NE than on the NW Atlantic cod stocks, the declines in biomass were much greater in the NW Atlantic than in the NE. Directed fishing was halted during the early 1990s for all NW Atlantic shelf stocks from the eastern Scotian Shelf northward. All these stocks have since been characterized by low productivity, and several have shown no sign of recovery after more than a decade without directed fishing. The NW Atlantic stocks from the eastern Scotian Shelf northward inhabit areas with average temperatures below 4°C and in all of them the mean weight-at-age began a period of decline before the biomass declined. The NE Atlantic stocks all inhabit areas with average temperatures above 4°C and showed less variability in mean weight-at-age.

Both fishing and climate are implicated in the declines in cod stock biomass since 1970. In the NW Atlantic the fishing mortality increased until moratoria were imposed in the early 1990s. The decline in biomass was caused by fishing, but changes in the productivity of the stocks contributed to the collapse and there is good evidence that the decline in biomass also caused fishing mortality to increase. Fisheries management must be sensitive to possible changes in stock productivity and must either respond quickly, to prevent increased mortality and further stock decline, or regulate fishing in a precautionary way, which is robust to uncertainties about stock productivity.

Changes in weight-at-age are an important component of the variation in productivity of coldwater cod stocks. Variation in weight-at-age appears to be mainly due to changes in the environment. In the S. Gulf of St. Lawrence density-dependent growth and changes in the direction of size selective fishing mortality appear to be the most important factors and here size-at-age has remained low despite good conditions for growth and low fishing mortality. Age and size at maturity have declined in many stocks and there appears to be a genetic component to this change, in response to fishing (where it has been investigated – Arcto-Norwegian cod, S. Labrador, S. Gulf of St Lawrence). Early maturity gives a selective advantage under most high mortality regimes, but reduces population productivity if fishing mortality is reduced. The reversion to older ages and larger sizes at maturity will be slow if additive genetic variance has been depleted.

The risk of stock collapse increases when stock productivity declines. Some of the life-history characteristics (growth and maturation in particular) governing productivity can be monitored by sampling commercial and research catches and may give timely indications of changes in productivity and risk of collapse. In order to develop their routine use in assessing risk of

collapse under different fisheries management strategies, indicators of possible change in productivity (weight-at-age, condition, liver index, maturation reaction norms) should be investigated using tropho-dynamic, life history and risk assessment models.

Mean age and age diversity of spawners (and SSB) declined in many stocks in response to fishing. In many (but not all) stocks, this has resulted in a decline in recruitment rate. In Arcto-Norwegian and Icelandic cod resilience to climate change has been shown to decrease as mean age of spawners declined.

For all cod stocks, the kinds of prey and their abundance and availability vary over time. The boreal ecosystems and the Baltic Sea tend to have a narrower field of potential prey than the more southern ecosystems, and changes in the abundance or distribution of major forage species (e.g. capelin, herring) might cause food shortages for cod. This could lead to declines in condition and consequent reductions in reproductive output and even survival. Declines in prey availability have been implicated in declines in cod productivity that have lasted from one to several years, but such variability in prey has seldom been implicated as a major factor in cod stock declines. There have been suggestions that low abundance of prey may be impeding stock recovery in some areas, such as the offshore of eastern Newfoundland.

When cod stocks decline to very low abundance, the relative importance of factors governing dynamics and productivity can change. When a stock is relatively large, it may be able to sustain predation and maintain itself at relatively high abundance even when subjected to a fishery. However, if the stock has declined in abundance, for whatever reason, and predator populations have not declined, or may even have increased, then high predation mortality may impede or prevent recovery. Such impacts may occur via predation by pelagic fish on eggs and larvae of cod, as has been hypothesized for cod in the Baltic Sea, on the eastern Scotian Shelf and in the southern Gulf of St. Lawrence. It may also occur via predation on juvenile cod and perhaps even adult cod by larger predators such as seals, as has been hypothesized for the eastern Scotian Shelf, the southern and northern Gulf of St. Lawrence, and eastern Newfoundland.

In some stocks e.g. southern Gulf of St Lawrence, high natural mortality has replaced high fishing mortality, preventing recovery even when fishing pressure is low. No substantial increase in the biomass of Baltic cod can be expected without a change in environmental conditions favouring better recruitment (even at F_{PA}, which is 65% of the current fishing mortality).

A general conclusion from the experience off eastern Canada is that humans may have limited ability to “rebuild” cod stocks that have declined to very low levels. Simply turning off directed fishing may be insufficient to promote recovery. The properties of the stocks themselves and the state of the ecosystems in which the cod are embedded may be such that the stocks remain constrained to their new levels of low abundance for a considerable time.

1 Overview

1.1 Introduction

Many of the cod stocks around the North Atlantic have experienced similar trends in abundance, from high values in the 1960s that in some cases persisted into the 1970s and 1980s, to lower levels in recent years. Indeed, some Northwest Atlantic stocks declined to extremely low levels by the early 1990s and have not shown signs of recovery, despite fishing moratoria that have been in effect for more than a decade. However, the history of cod stocks during the past 3–4 decades has not been one of continuous decline. Some Northwest Atlantic stocks increased during the 1980s after reaching low levels during the 1970s, and stocks in the Northeast Atlantic have experienced both increases and decreases. Many of these stocks have also experienced changes in size-at-age and declines in age at maturity. While fishing mortality has obviously played a dominant role in the dynamics of most of these stocks, it is clear that changes in the environment have contributed to changes in recruitment, growth and natural mortality. Comparisons among stocks may help illuminate the relative roles of changes in fishing pressure, the physical environment (especially temperature) and the biotic environment, both predators and prey.

Consequently, the ICES/GLOBEC Working Group on Cod and Climate Change held a Workshop on *The Decline and Recovery of Cod Stocks Throughout the North Atlantic including tropho-dynamic effects* in May 2006, with the aim of reviewing and synthesizing knowledge regarding factors influential in the decline and recovery of cod stocks. Given the state of several cod stocks in the Northwest Atlantic, much of the discussion concerned reasons for non-recovery.

1.2 Terms of reference

According to C.Res. 2005/2/OCC12 the **Workshop on the Decline and Recovery of Cod Stocks throughout the North Atlantic including tropho-dynamic effects** [WKDRCS] (co-convened by Brian Rothschild, USA; George Lilly, Canada; Svein Sundby, Norway, and Kai Wieland, Greenland) was held in St. John's, Canada, during 9–12 May 2006 to:

a) provide an overview and comparison of the declines which have taken place in cod stocks;

b) evaluate the relative roles of fishing and climate in causing declines in abundance;

c) evaluate the causes of observed changes in rates of survival, growth and maturity, including a tropho-dynamic perspective;

d) evaluate the consequences for stock resilience of decreases in mean weight and length and age/size diversity;

e) document and comment on historic evidence of previous cod stock recoveries and the environmental and fisheries circumstances in which these occurred;

f) comment on past projections of cod stock recovery, evaluate whether they were correct and draw conclusions concerning how future projections can be improved;

g) evaluate the role of cod forage species (e.g., capelin) for variability in abundance and size-at-age of cod;

h) evaluate the role of cod predators (e.g., seals) for variability in abundance and size-at-age of cod;

i) evaluate the role of climate mediated through cod predators and prey;

j) evaluate the relationship between the decline and recovery of cod stocks and changes in the marine ecosystems.

WKDRCS will report by 10 June 2006 for the attention of the Oceanography Committee and ACFM, ACE, and RMC.

The co-convenors received a note from the ICES secretariat on 27 April that ‘it has been requested from the ICES Advisory programme if a draft version of the WKDRCS report would be available for the ACE (24–26 May) and ACFM (25 May–1 June) meetings’. According to this request, a draft executive summary with the main results and conclusions was prepared for presentation by Keith Brander during the ACE and ACFM meetings.

1.3 Preparation for the Workshop

In preparation for the Workshop, the ICES/GLOBEC coordinator established a website within the ICES/GLOBEC website (http://www.ices.dk/globec/) to facilitate communication among the participants before and after the workshop. Terms of reference and practical information were posted before the meeting. Data pertaining to many of the cod stocks and several papers of interest to the workshop were also posted. Leif Christian Stige and Peter Shelton provided valuable assistance and guidance in preparing the data sets.

Participants were asked to provide working papers, abstracts or electronic copies of presentations for review prior to the meeting, and these also were posted.

1.4 Workshop structure and working procedure

Participants are listed in the following Section and Annex 1. The agenda for the Workshop as adopted during the opening session of the meeting is provided in Annex 2.

The Workshop was divided into three activities: (i) presentations, (ii) break-out groups to discuss individual terms of reference and (iii) plenary review of major conclusions. It was found that the 18 presentations took much longer than expected, leaving insufficient time to discuss each term of reference in plenary as had initially been intended. Instead, each term of reference was discussed by one of four break-out groups. The break-out groups then brought the major conclusions back into plenary for review.

Each participant who made a presentation was asked to write an extended abstract that should summarize the information that he or she presented. The abstracts are provided in Annex 3 in the sequence of presentation. At the start of Annex 3 is a table that lists the first author of each abstract and indicates which terms of reference were addressed.

A contribution on Baltic cod was received from Fritz Köster (Denmark), who was unable to attend the Workshop

1.5 List of participants

There were 19 participants, including representatives from 8 countries (Austria, Canada, Greenland, the Netherlands, Norway, Spain, Sweden and USA) and the ICES/GLOBEC Coordinator.

Keith Brander	ICES/GLOBEC Coordinator
Paul Budgell	Norway
Jim Carscadden	Canada
Ghislain Chouinard	Canada
Niels Daan	Netherlands
Ken Drinkwater	Norway
Katja Enberg	Austria
Mike Hammill	Canada
George Lilly	Canada (Co-convener)

Anne Lucas	Norway	
Geir Ottersen	Norway	
Aqqalu Rosing-Asvid	Greenland	
Brian Rothschild	USA	(Co-convener)
Garry Stenson	Canada	
Svein Sundby	Norway	(Co-convener)
Henrik Svedäng	Sweden	
Doug Swain	Canada	
Antonio Vázquez	Spain	
Kai Wieland	Greenland (Co-convener)	

Participants' affiliations, telephone numbers and e-mail addresses are provided in Annex 1.

2 Results and conclusions with regard to terms of reference

2.1 ToR a) Provide an overview and comparison of the declines which have taken place in cod stocks

The analysis presented here is for the most part based on information for the period since 1970, because the quality and duration of the time-series available for comparison across stocks diminishes prior to then. The location and nomenclature for the stocks is given in Figure 1. The best single source of data and analysis for the period prior to 1970 is the Cod and Climate Change Symposium held in Reykjavik in 1993 (ICES Marine Science Symposia, Vol. 198, 693pp). The ICES/GLOBEC report on "Spawning and life history information for North Atlantic cod stocks" (ICES Cooperative Research Report, No. 274 (ICES, 2005a)) also includes much useful background information. The extended abstract by Drinkwater (Annex 3, Extended abstract 2) deals with the expansion and subsequent decline in the major cod stocks, which occurred during the period from 1920–1970 and which can be confidently ascribed, at least in part, to the multidecadal changes which occurred in climate. (This is discussed more fully under ToR e in Section 2.5).

Total landings of North Atlantic cod (*Gadus morhua*) declined from over three million tons in 1970 to less than one million tons in 2000 (Figure 2) due to changes in total stock biomass, for which the term "collapse" has frequently been used (Harris, 1998). The downward trend has been particularly marked in the NW Atlantic, where fisheries for cod on most of the Canadian shelf have been stopped or severely restricted since the early 1990s, with the aim of allowing the stocks to recover. There are as yet few signs of recovery in most Canadian stocks. The declines which have occurred in the NE Atlantic stocks, while serious, have not been as extreme as those in the NW Atlantic (Figure 3 and Table 1 column 7) and cod fisheries have continued, with restrictions on total catch and some seasonal and area closures.

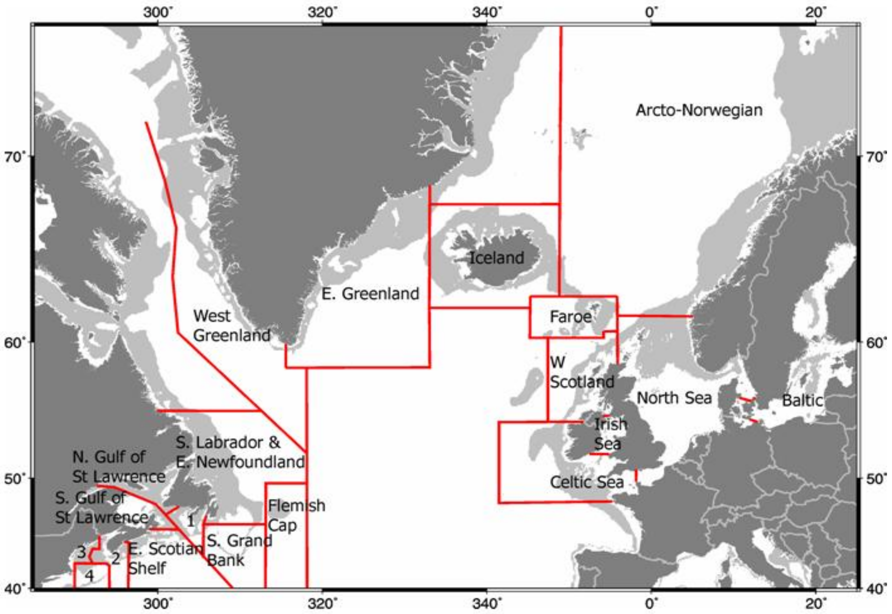

Figure 1. Names of stocks that correspond to the area codes given in Table 1. 1-S.Newfoundland, 2-W. Scotian Shelf, 3-Gulf of Maine, 4-Georges Bank. The divide between NE and NW Atlantic falls between East and West Greenland. NEAFC region 1 includes the E Greenland, Iceland, Faroe and Arcto-Norwegian stocks. The other NE Atlantic stocks (excluding the Baltic) are in NEAFC region 2.

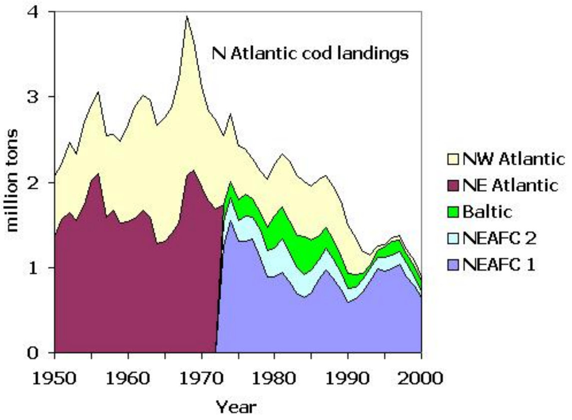

Figure 2. Total landings of cod.

Moving window time series analysis can be used to provide rule-based definitions of “periods of decline and recovery”, characterised by their duration and amplitude. The rule used here to define “prolonged” is a period in which there is a decline in at least 5 years within any 7-year window. The amplitude (or % decline) can be estimated as the value at the end of the period of decline divided by the value at the beginning. The outcome of applying these definitions can be seen in columns 6 and 7 of Table 1.

A working definition of a collapsed stock is one which has declined to 5% or less of the biomass that it had at the beginning of the period of decline. A further important characteristic of a collapsed stock is whether (or over what time scale) the decline is reversed. One can propose at least three possibilities: In the first of these, the stock immediately begins to recover when the adverse factors causing the collapse (excessive fishing; adverse environment) cease. In the second, the stock remains collapsed because the adverse factors continue. In the third, the adverse factors cease, but the stock remains collapsed because of a system change, which is not reversible in the short or medium term (e.g. ecosystem change, predator pit, depensatory relationship between stock and recruitment, change of the genetic structure of the stock).

Trends in total biomass since 1970 are shown in Figure 3 and the periods of prolonged decline in biomass are marked by a sequence of open boxes along the x-axis. Comparison between NW and NE Atlantic stocks reveals two major differences: (i) the NW Atlantic stocks show shared patterns of increase and decline in biomass, whereas the NE Atlantic stocks do not (ii) the decline in the NW Atlantic stocks was much greater than in the NE Atlantic. A further major difference (Table 1 column 4) is that all the NW Atlantic stocks considered, with the exception of Georges Bank, live in areas where the average annual bottom temperature is below 4^{o}C, whereas all the NE Atlantic stocks are in warmer average temperatures. Since the relationship between temperature (T) and growth rate (g) and recruitment (R) is roughly parabolic (Brander, 2000), dg/dT and dR/dT decline as temperature increases. The effects of temperature variability are therefore expected to be greater at low (e.g. <4^{o}C) than at high e.g. (>4^{o}C) temperatures.

The six cod stocks in Canadian waters all experienced a prolonged period of decline which began in the mid 1980s and ended in the mid 1990s. The decline in biomass in these six stocks was in every case preceded by a decline in the mean weight-at-age (marked by arrows on Figure 3). The relationship between changes in mean weight-at-age, temperature and biomass is discussed in the extended abstract and paper by Brander.

Table 1. Stock names, area codes and data sources. Areas occupied by each stock are taken from Myers *et al.* (2001). Mean bottom temperatures are from Brander (1995) and Myers *et al.* (2001). Year ranges are the first and last years of "periods of prolonged decline" identified using seven year moving-window time-series analysis.

Cod Stock	NAFO or ICES code	Area (km^2)	Temp. ^{o}C	Age range biomass	Period of declining biomass	% decline	Data sources and ICES assessment WG codes
S Labrador	2J3KL	253492	0	3-13	1985-95	5%	(Bishop *et al.* 1993); (Lilly *et al.* 2003); (Lilly and Murphy, 2004)
S. Grand Bank	3NO	121246	1.75	3-13	1984-95	3%	(Healey *et al.* 2003)
S. Newfoundland	3Ps	70510	2.5	3-13	1985-93	26%	(Brattey *et al.* 2003)
N Gulf	3Pn4RS	89041	1	3-13	1983-94	6%	(Fréchet *et al.* 2003)
S. Gulf	4TVn	118343	1.75	3-15	1986-93	20%	(Chouinard *et al.* 2003)
E. Scotian Shelf	4VsW	102428	3.75	1-15	1985-93	10%	(Mohn *et al.* 1998)
Georges Bank	5Z	102596	8	1-10	1988-95	27%	(Hunt and Hatt, 2002); (O'Brien *et al.* 2002)
Greenland offshore	NAFO1 ICES XIV		1.6	3-10	1966-75	5%	NWWG (ICES, 1996)
Arcto-Norwegian	I,II	592610	4	3+	1993-2000	44%	AFWG (ICES, 2005b)
Iceland	Va	237031	5.8	3+	1987-94	49%	NWWG (ICES, 2005c)
Faroe	Vb1	36236	7.4	2+	1984-91	19%	NWWG (ICES, 2005c)
E. Baltic	IIId, 25-29	216833	5	2-7	1983-92	20%	WGBFAS (ICES, 2005c)
North Sea	IIIa,IV,VIId	539823	8.6	1-10	1980-93	33%	WGNSSK, (ICES, 2006a)
Irish Sea	VIIa	48263	10	1-6	1987-96	38%	WGNSDS (ICES 2006b)
Celtic Sea	VIIe-f	155358	11	1-6	none	none	WGSSDS (ICES 2006c)

With the exception of the Celtic Sea, NE Atlantic cod stocks also declined after 1970, but the declines do not share a common pattern and are much smaller than those among the Canadian stocks. In the NE Atlantic there have also been a number of periods of rapid increase in total biomass. For example, the stock at Faroe declined to 19% over the period from 1984–91, but increased quickly to the 1984 level by 1996. On both sides of the N Atlantic, changes in mean weight-at-age are smaller in the warmer water stocks (Georges Bank, North Sea, Irish Sea and Celtic Sea) and there are no prolonged periods of decline in weight-at-age in any of these areas, or in the Baltic.

The offshore cod stock at Greenland is included in Table 1, but lacks a complete, consistent time series since 1992 because the biomass is too small to assess. A more detailed account of the periods of expansion and decline in the Greenland stock is provided in Annex 3, Presentation 7 by Wieland *et al.* and also in ICES Cooperative Research Report, No. 274. For West Greenland, two prolonged periods of decline in total biomass can be distinguished, i.e. 1950 to 1975 and 1987 to 1995, for which the proportion of biomass found in the final year of the period amounted to 2.7 and less than 1 % of the initial value, respectively. During each of the two periods, fishing mortality (or exploitation rate (catch/survey biomass)) increased considerably and the mean latitude of the catch (or survey biomass) decreased. No general relationship between mean latitude of the distribution and sea temperature was found, but the two variables were significantly correlated for the years 1987 to 1992. The latter suggests that decreasing temperature has accelerated a homing migration of maturing fish towards East Greenland (and further to Iceland) of those year-classes, which are assumed to have originated mainly from Iceland (see e.g. Storr-Paulsen *et al.*, 2004). Results from multiple linear regression analysis indicate that fishing mortality together with emigration (but neither temperature on its own nor recruitment failure) has been the ultimate cause for the decline in stock biomass in both periods (Table 1).

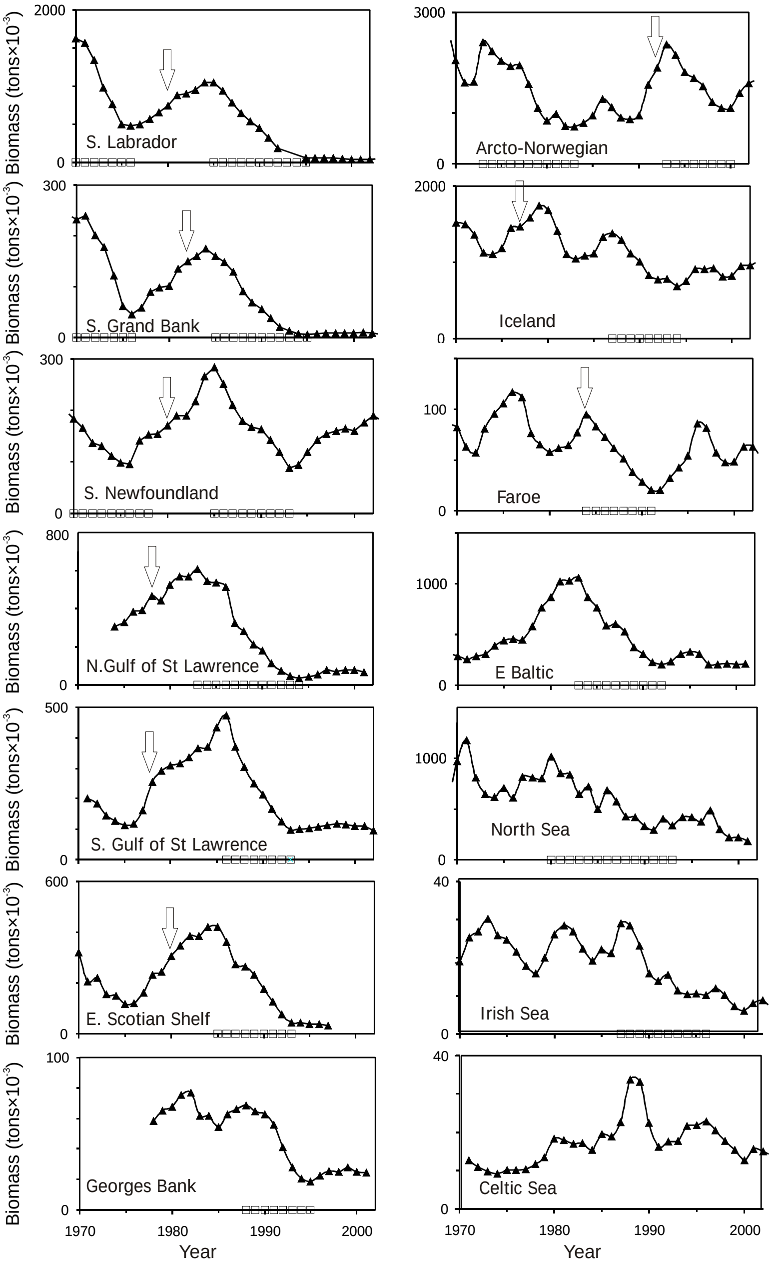

Figure 3. Trends in total biomass for North Atlantic cod stocks. The open squares along the axis represent prolonged periods of decline. The arrows indicate the beginning of periods of decline in weight-at-age (see Annex 3, Extended abstract 1). Data sources are shown in Table 1

In summary, all N Atlantic cod stocks have suffered prolonged periods of decline since 1970, with the exception of the Celtic Sea. 5 NW Atlantic stocks began a period of decline in the mid 1980s and the biomass at the end of the decline was 10% or less of the original level. These stocks all inhabit areas with average temperatures below 4°C and in all of them the mean weight-at-age began a period of decline before the biomass declined. The NE Atlantic stocks, which are in average temperatures above 4°C, declined less than those in the NW Atlantic.

2.2 ToR b) Evaluate the relative roles of fishing and climate[1] in causing declines in abundance

2.2.1 Attribution

Variation in fish stocks is driven principally by fishing and environmental factors, but it is difficult to evaluate their relative roles. The problem of attributing cause or responsibility (also called the identifiability problem) is common to many fields and has its own literature (e.g. Stone and Allen, 2005). An example is the case of the legal liability of the tobacco industry for smoking-induced damage to health. Of more relevance to fisheries is perhaps the question recently raised concerning the possibility of suing for damage to the climate (Allen, 2003). A formal attribution analysis requires one or more models which can simulate scenarios with and without the various factors under investigation and thus evaluate the contribution of each factor e.g. (Sarmiento *et al*., 2005). Such an analysis is more difficult if the factors are not independent of each other and one of the principal new findings which is reported here and in other recent literature is that the effects of fishing and environment interact.

The information here is not a formal attribution analysis, but we provide some of the evidence which may be relevant to set up such an analysis. There is no doubt that both fishing and environment can and have caused declines in fish abundance in the past. At long time scales environmental effects are obvious; one need only recall the history of the North Atlantic since the last glacial maximum (~18000 years ago) to appreciate that cod populations in most areas are relatively recent. At shorter time scales the history of the cod population at Greenland in the 20th century shows how rapidly a population can expand during favourable environmental conditions (Wieland *et al*., Annex 3, Extended abstract 7).

2.2.2 Effects of fishing and environment in causing stock decline

A great deal of interesting new research is in progress on the history of fishing and its effects in causing stock declines (e.g. Poulsen *et al*., 2006; Jackson *et al.*, 2001). A factor such as fishing, which causes mortality to exceed natural mortality, results in reduced stock biomass. There is a compensatory increase in productivity, which results from the higher growth rate of the remaining (smaller) fish and from higher recruitment per unit biomass. The compensatory increase (which does not require density dependent growth) provides the surplus production on which a sustainable fishery can be based. In a sustainable fishery the biomass levels out after the initial decline from the pristine state. However if the biomass is reduced beyond the level which can be sustained by increasing recruitment per unit biomass, then the stock will continue to decline. The greatest fishing mortality which a stock can sustain, without collapse is determined by the recruitment per unit biomass and not by biomass *per se*. Recruitment per unit biomass depends on the condition, specific fecundity and egg quality of individual fish and on the survival of the progeny until they recruit to the adult stock. Since all of these are affected by environmental conditions, so is recruitment per unit biomass. This means that a stock which had previously been able to sustain a certain level of fishing mortality may no longer be able to do so if the environment becomes less favourable. Several of the presentations at the workshop showed evidence that environmental and ecosystem changes had probably affected recruitment per unit biomass (e.g. Chouinard, Annex 3, Extended abstract 5; Ottersen, Annex 3, Extended abstract 8).

The two factors, fishing and environment, differ in fundamental ways. Fishing is, in principle, a controllable factor (although the past record of fisheries management suggests that in

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[1] The ToR asks about effects of “climate” but we have chosen to interpret this widely to include environmental factors at most time and space scales. i.e. most “non-fishing” factors. In some cases biological environmental factors may have a strong influence via ecosystem and trophic linkages.

practice the control is very weak; Figure 4). The environment is not controllable or at least the agencies through which it might be controlled are less direct and longer term. Environmental factors can be regarded as having both positive and negative impacts on fish stocks, whereas the impact of fishing is principally negative. Thus one can confidently attribute expansion of range or biomass to favourable environmental circumstances but rarely to favourable fishing practices. There may be ways in which fishing can have positive impacts, via cultivator effects, or selection (including removal of predators or competitors) which favours particular desirable species or properties of populations. It is unlikely that any of the recently observed declines in biomass can be attributed only to one factor.

2.2.3 Trends in fishing mortality and biomass – NW Atlantic cod stocks

Trends in fishing mortality over the period since 1970 are shown in Figure 4 and in a standardised form for five of the stocks in Figure 3 of the extended abstract by Rothschild (Annex 3, Extended abstract 3). The years in which a period of prolonged decline in biomass began (from Table 1) are marked with an arrow for each stock. The Canadian shelf stocks share a common pattern of decline in biomass, which began in 1984–85 in the northern areas, but there is no obvious, common, large-scale change in fishing mortality preceding the decline. In fact the only clear common pattern of change in fishing mortality is that it increased in all areas in the years after the biomass had begun to decline. This suggests that the decrease in biomass may have played a role in precipitating the increase in fishing mortality, rather than (or as well as) the other way round. There are several reasons why fishing mortality can increase when biomass declines: (i) if weight-at-age declines, as it did in all these stocks, then an equivalent weight of catch consists of larger numbers of smaller fish (ii) a fixed TAC regime permits (and may promote) increased fishing mortality when biomass declines, particularly if catchability increases as the stock declines (see Rose and Kulka, 1999 and Figure 5) (iii) if fish are smaller or in poor condition due to declining weight-at-age then “high-grading” (increase in the proportion of discarded fish) may occur. There can therefore be positive feedback if a decline in biomass, which may be due in part to fishing mortality, causes further increase in fishing mortality. In the case of the Canadian stocks there is good evidence that the stocks became less productive from 1980, due to adverse environmental change, which resulted in reduced weight-at-age and later to reduced reproductive output (Drinkwater, 2002; Dutil and Brander, 2003; Shelton *et al*., 2006) see also extended abstracts by Rothschild (Annex 3, Extended abstract 3) and by Brander (Annex 3, Extended abstract 1). The environmental changes are not limited to changes in the physical environment and in some cases ecosystem and trophic effects may have been prominent. Figure 4 in the extended abstract by Rothschild (Annex 3, Extended abstract 3) show the imputed stock-recruitment relationship for 9 NE Atlantic stocks and provides evidence that there may be depensatory effects at low stock sizes.

If, as suggested (and further discussed below), there is interaction between effects of fishing and of environment on stock biomass then their influence cannot be separated. It is quite possible that neither the fishing pressure nor the adverse environmental regime from the mid 1980s would on its own have caused the NW Atlantic stocks to collapse. One of the lessons from this is that fisheries management regimes must either be sensitive to possible changes in stock productivity (by monitoring growth, realised reproductive output, natural mortality and environmental trends) or regulate fishing in a precautionary way, which is robust to uncertainties about stock productivity.

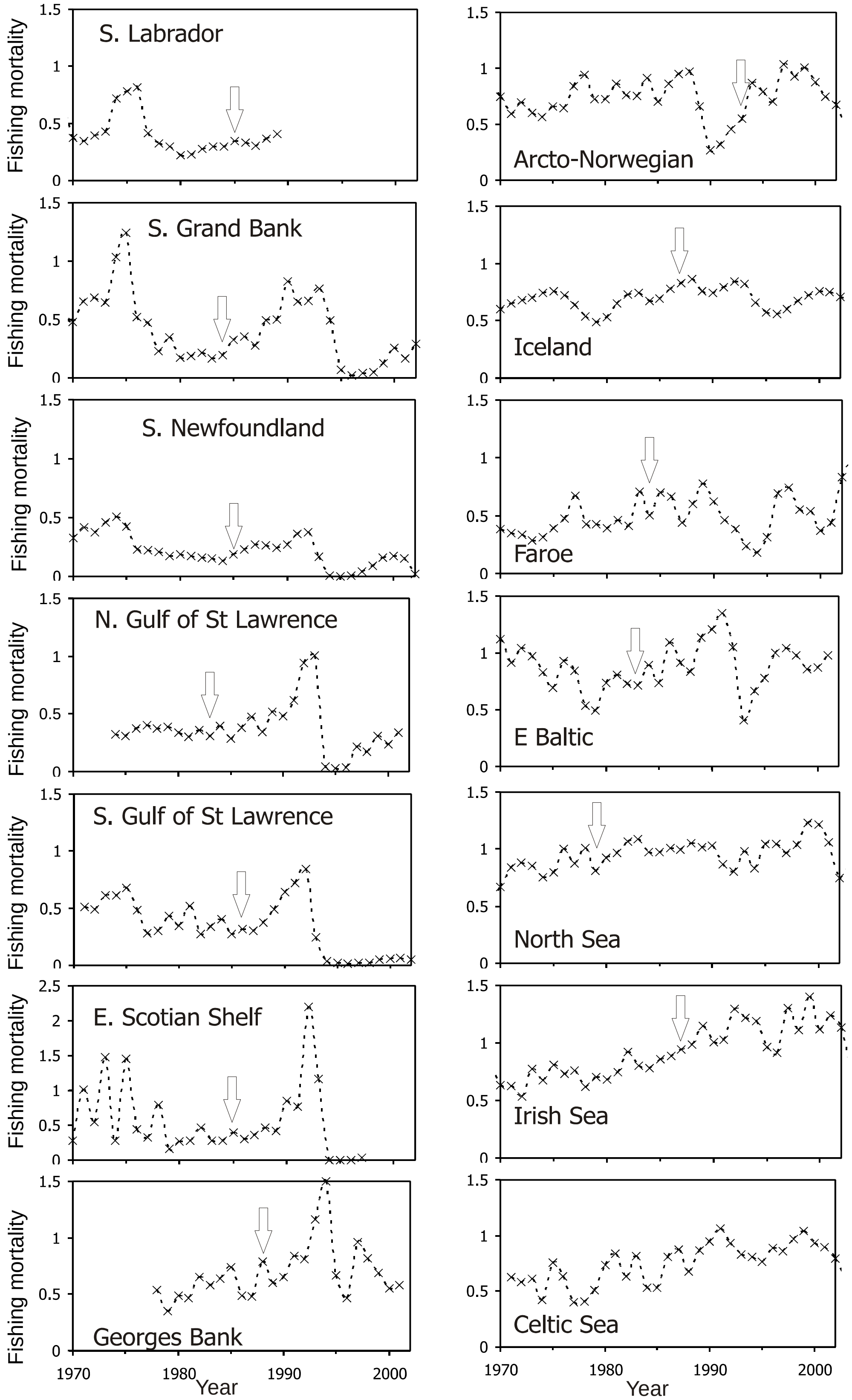

Figure 4. Trends in fishing mortality for North Atlantic cod stocks. The arrows indicate the beginning of periods of prolonged decline in biomass, as explained in Section 2.1. Data sources and the age ranges for the averages are shown in Table 1. Note that the scale for the E Scotian Shelf goes up to 2.5.

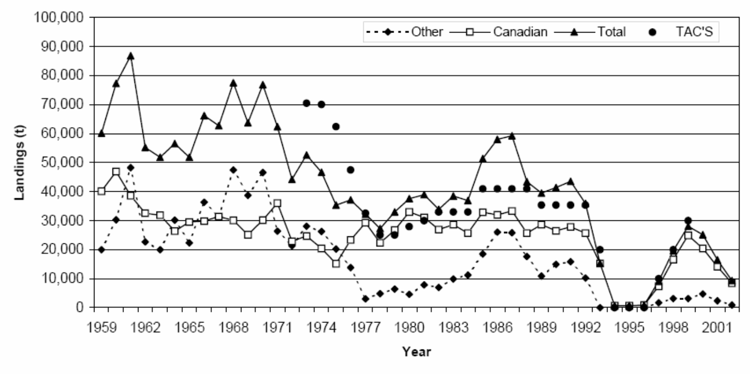

Figure 5. Reported landings of cod in S. Newfoundland and Total Allowable Catches. A prolonged decline in biomass began in 1985 (Table 1). TACs remained unchanged until 1988 and then decreased by a small amount for a further four years. (Brattey *et al.*, 2002)

2.2.4 Trends in fishing mortality and biomass - NE Atlantic cod stocks

The NE Atlantic stocks in Figure 4 all show rising trends in fishing mortality at annual rates ranging from 0.5% (Iceland) to 1.9% (Irish Sea) since 1970, with the exception of the Baltic, but there is no common pattern of shorter scale variability within this. The biomass trends also lack an obvious common pattern, with periods of prolonged decline beginning at different times (Figure 4). A number of interesting questions, which are relevant to the attribution issue, arise from the comparing the cod stocks in the NE Atlantic with those in the NW Atlantic. For example, why are the declines in biomass less extreme and of shorter duration in the NE Atlantic, given that fishing mortality is generally higher? Why is there no large-scale common pattern of increase and decline in the NE Atlantic similar to that which occurred in the NW Atlantic from 1976 to 1996?

There are probably two principal reasons for these differences: (i) with the exception of Georges Bank, the NW Atlantic stocks all live at lower temperatures, and growth and recruitment are therefore more strongly affected by changes in temperature and (ii) the NW Atlantic cod stocks occupy an area, whose oceanographic characteristics are influenced by the cold Labrador Current. The warmer water stocks in the NW Atlantic (Georges Bank, Flemish Cap) fit least to the general pattern of change in biomass. Many factors other than temperature are of course required to account for observed changes in growth and recruitment for particular areas and time periods (Swain *et al.*, 2003). Another factor which may be acting on all NW Atlantic stocks, but not on NE Atlantic cod is change in natural mortality (see Sections 2.7 and 2.8), but there is very little information on possible changes in adult natural mortality for NE Atlantic stocks.

The NE Atlantic stocks have higher growth rates, mature at younger ages, and have higher surplus production than the colder NW Atlantic stocks (Dutil and Brander, 2003). The temperature ranges at which they occur are generally less extreme and therefore have less effect on growth and recruitment. However once again the exceptions are instructive, since the NE Atlantic stock showing the most prolonged and profound decline in biomass since 1970 is the E Baltic, which lies at the extreme of other environmental factors, including salinity and oxygen (Koster *et al.*, 2005; Köster (Annex 3, Extended abstract 11)).

It is certainly not the case that environmental factors are unimportant in accounting for changes in cod biomass in NE Atlantic stocks. In fact they are implicated in almost every instance (Brander, 2005; Brander and Mohn, 2004; Stige L.C *et al.*, 2006; Beaugrand *et al.*, 2003; Ottersen *et al.*, 2006; Drinkwater *et al.*, 2003; Koster *et al.*, 2005; Steingrund and Gaard, 2005), but the contributions of fishing and environment and their interactions are not known.

One of the most interesting, paradoxical examples, for which no environmental influence has been claimed to date, is the Celtic Sea. This is the cod stock living at the highest average temperature, with the highest growth rate, condition and surplus production. It is also the only NE Atlantic stock showing a rising trend in biomass from 1970–2002 (by 1.6% annually) in spite of fishing mortality rates which have increased annually by 1.8% over this period. The explanation of these trends poses a challenge for any model which purports to predict the effects of future climate change on cod stocks.

2.2.5 Interaction between fishing and climate

For the Canadian shelf a case was made above that the cod stocks became less resilient to fishing mortality because of changes to their productivity (growth and reproductive output) caused by adverse environmental changes. This is an example of interaction between climate and fishing, but by no means the only one. Several recent papers (Brander 2004; Brander and Mohn 2005; Ottersen *et al*. 2006; Stige in press) have explored the evidence that changes in stock biomass and demographic structure (principally age composition), which are mainly due to fishing, cause stocks to become more sensitive to environmental variability. See also the extended abstract by Rothschild.

For example Ottersen (Annex 3, Extended abstract 8) shows that the recruitment of Arcto-Norwegian cod has become sensitive to temperature variability as the mean age in the spawning stock has declined. The sensitivity of European shelf cod stocks south of 62°N to variability in the NAO appears to be high when spawning biomass is low (Brander, 2005). More recently Stige *et al.* (in press) have confirmed the geographic pattern of the influence of the NAO on North Atlantic cod stocks, but ascribed the increased sensitivity to a time trend (the causes of which are unknown).

With regard to attribution and the relative roles of fishing and climate, one can conclude that there are interactions; stocks may become more sensitive to the effects of fishing when climate conditions are adverse and more sensitive to climate when fishing causes changes in population processes (growth, condition, maturity, fecundity, realised reproductive output and natural mortality) and in demographic properties (age structure, geographic sub-structure). Many of these processes and properties are quite easy and cheap to monitor in a timely way, in order to give advance warning of changes in sensitivity and thus help to evaluate the risks to future trends in biomass with greater confidence.

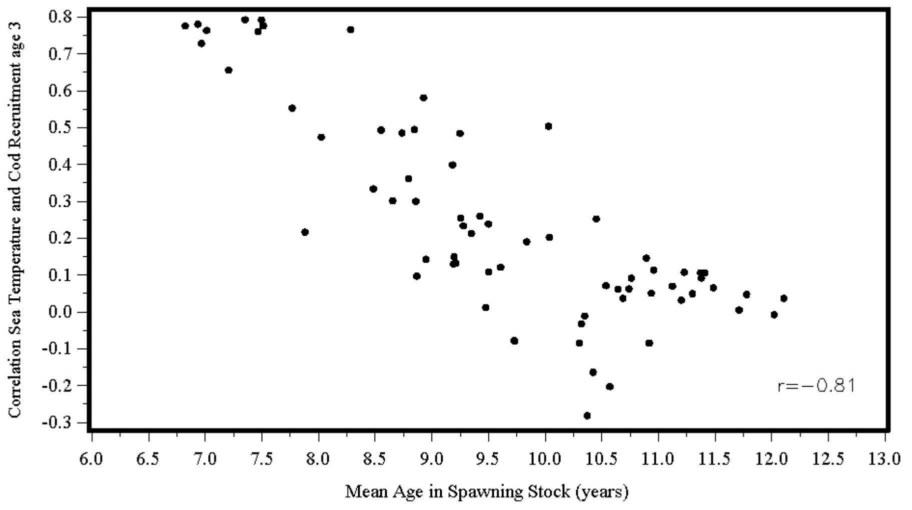

Figure 6. The correlation between sea temperature on the Kola Section and recruitment to the Arcto-Norwegian cod stock is higher when the mean age in the spawning stock is low (see Ottersen (2005) and Ottersen (Annex 3, Extended abstract 8) for more details).

In summary, both fishing and climate are implicated in the declines in cod stock biomass since 1970. In the NW Atlantic the fishing mortality increased until moratoria were imposed in the early 1990s. The decline in biomass was caused by fishing, but changes in the productivity of the stocks contributed to the collapse. There is good evidence that the decline in biomass causes fishing mortality to increase. Fisheries management must be sensitive to possible changes in stock productivity and must either respond quickly, to prevent increased mortality and further stock decline, or regulate fishing in a precautionary way, which is robust to uncertainties about stock productivity. Fishing mortality on NE Atlantic stocks is generally higher than in the NW Atlantic and increased at annual rates from 0.5% (Iceland) to 1.9% (Irish Sea) from 1970 to 2002. However although the NE Atlantic cod stocks have declined, none has collapsed to the extent shown in the NW Atlantic. Growth rates have remained high. There are interactions between fishing and environmental factors in both directions.

2.3 ToR c) Evaluate the causes of observed changes in rates of survival, growth and maturity, including a tropho-dynamic perspective

2.3.1 Growth and survival

Brander (in press; see Annex 3, Extended abstract 1) compared trends in total biomass and weight-at-age for 15 NW and NE Atlantic cod stocks. Here, trends in weight of individual cod are represented by stock weight-at-age averaged over five age groups, beginning in each case with the age at which the fish attain 1 kg in weight. For ten out of the 15 stocks investigated prolonged periods of decline in biomass (see Section 2.1 for definition) were preceded or coincided with declines in mean weight-at-age. The lag between the decline in biomass and the decline in weight-at-age was 5 years for 4 of the 6 stocks in Canadian waters, 2 years for the S. Grand Bank stock and 8 years for the S. Gulf of St Lawrence. With the exception of the Celtic Sea, NE Atlantic cod stocks also declined after 1970, but the declines do not share a common pattern and are much smaller than those among the Canadian stocks. On both sides of the N Atlantic, changes in mean weight-at-age are smaller in the warmer water stocks (Georges Bank, North Sea, Irish Sea and Celtic Sea) and there are no prolonged periods of decline in weight-at-age in any of these areas, or in the Baltic.

Changes in mean weight-at-age are generally attributed to changes in growth rate due to three main types of cause: (i) “environmental” factors, the principal one being ambient temperature;

(ii) food availability (including density dependent effects); and (iii) selective effects of fishing (Krohn *et al*., 1997; Swain *et al*., 2003 [2]), but it can be difficult to disentangle these, because their effects can be direct or indirect and they interact with each other. For example, temperature has a direct (positive or negative) effect on growth rate and also an indirect effect by altering the production of food organisms (ICES, 2002b). Another reason why it is difficult to assign causes with confidence is the poor quality of field information on the contributing factors. Interannual changes in temperature may be represented by mean bottom temperature at a fixed station or by a value for the area occupied by cod during an annual fishing survey (i.e. ambient temperature is unknown); population biomass is used to represent density dependent effects (i.e. intensity of competition for food is unknown) and selective effects of fishing are inferred from sizes backcalculated from otolith increments (i.e. actual selection by fishing activity is unknown). For the S. Gulf of St Lawrence stock changes in size-selective mortality were the major cause of change in size-at-age (Sinclair *et al*., 2002a, 2002b). Other detailed studies of the growth changes in individual Canadian cod stocks support the existence of a temperature effect, but also effects of prey availability (Krohn *et al*., 1997), density dependence and a common pattern of residuals, which may be due to size-selective mortality (Swain *et al*., 2003). Section 2.7.1 has more on this topic and the report of the ICES/GLOBEC Workshop on the Dynamics of Growth in Cod (ICES, 2002b) also has a more extensive treatment of many of the issues.

The hypothesis that growth is density-dependent is not refuted by the overwhelmingly positive relationships between total biomass and weight-at-age (Figure 7), but it suggests that density dependent effects are neither widespread nor influential. Density-dependent growth may occur in situations where there is competition for a limited supply of food or some other essential item, but direct evidence of such competition is difficult to obtain. By definition, density-dependence is more likely where density is high (relative to food availability and requirement). The Eastern Baltic is the only stock with a significant negative relationship between weight-at-age and stock abundance (Figure 7), however, this has been ascribed to the closely coupled predator-prey relationships between cod and its principal prey species, sprat and herring, rather than to density-dependence (Gislason, 1999). In contrast, size-at-age declined sharply as abundance rapidly increased in the late 1970s and early 1980s in the southern Gulf of St. Lawrence stock, and recent findings support that this has been caused mainly by a density-dependent decrease in growth rate in addition to a change in the direction of size selective mortality (Sinclair *et al*., 2002a,b; Swain *et al*., 2003; Chouinard and Swain, unpubl.; Swain, unpubl.; see Annex 3 for extended abstracts).

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[2] The phenotypic effects of size-selective fishing may change the mean weight-at-age without affecting the growth rate. Size –selective fishing may also have genotypic effects (see Section 2.3.2)

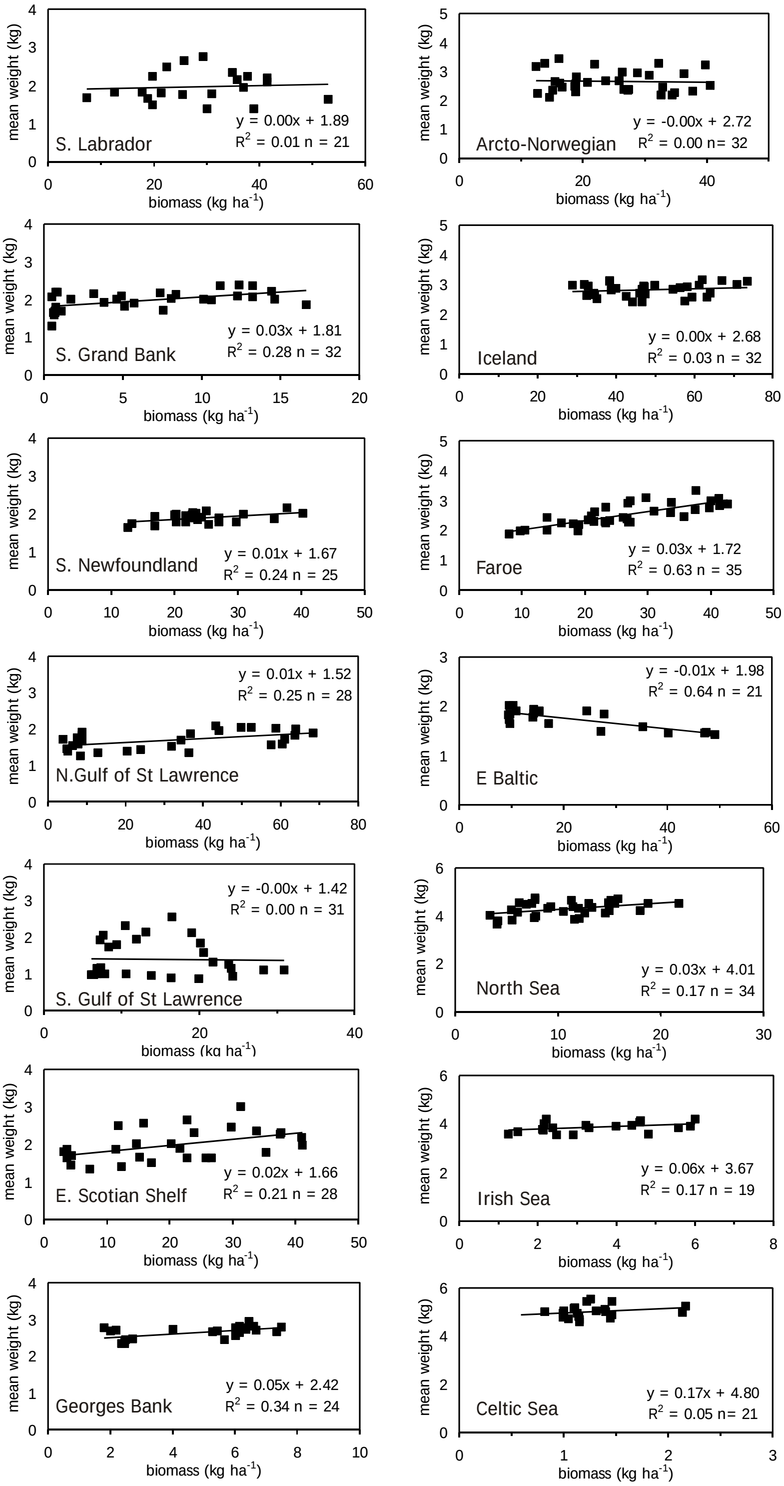

Figure 7. Mean weight-at-age (kg) and biomass per unit area (kg ha-1), with regression equation, value of R2 and number of observations (n). From Brander (in press).

2.3.2 Maturity

Decline of mean age at maturity, mean age and age diversity of the spawning stock as a response to fishing is a common phenomenon. For cod, Marteinsdottir *et al.* (2005) reported a decrease of older fish and age diversity of mature fish for 12 out of 16 stocks for which sufficient data have been available (Table 2). The change in age structure of the spawning stock was in particular pronounced for Arcto-Norwegian cod, with a sharp decline in mean age and in the proportion of repeat spawners (Ottersen *et al.*, 2006; see Annex 3, Extended abstract 8).

Changes in maturity schedule may arise through three different mechanisms: 1) direct demographic response, which means that as the total mortality increases, the stock becomes dominated by younger individuals and as result the average age at maturity decreases; 2) phenotypic plasticity, when growth rate and maturation are affected by environmental conditions (temperature, light, oxygen etc.) and food availability (including density dependent effects). The scope for phenotypic plasticity is well illustrated by recent experiments which reared Norwegian coastal cod to maturity in 2 years instead of the normal 4–8 years (Karlsen *et al.*, 2006).; 3) genetic response, when harvesting selectively removes a particular size range and causes a change in the genetic structure of the stock. Fishing can select for earlier or for later maturation (Law, 2000). Such changes may occur within just a few generations (Conover and Munch, 2002). It is difficult to judge which of the above mechanisms is behind the observed decline in age and size at maturity in several cod stocks just by observing the maturity ogives or trends in age and size at maturity. However, fisheries-induced genetic changes can be inferred estimating the probabilistic maturation reaction norms (PMRN) (Heino *et al.*, 2002).

Changes in the PMRN occurred during the 1960s and 1970s in the southern Gulf of St. Lawrence stock, and preliminary analyses relating the change in length at age between parents and their offspring to the selection differential experienced by parents suggest a significant genetic response to size selective mortality (Swain, Annex 3, Extended abstract 14). Furthermore, these changes were found to be in the direction expected for evolutionary responses to fishing. Changes in the probabilistic reaction norms for age and size at maturation have also been demonstrated for several other stocks on both sides of the Atlantic, and it has been concluded that these are genetic responses to harvesting (Enberg, Annex 3, Extended abstract 13).

Table 2. Rate of change in catch, stock biomass, spawning stock biomass, recruitment, proportion of age 6 or 10+ and age diversity (H) among cod stocks in the North Atlantic (NAC: Northeast Arctic / Arcto-Norwegian cod; [1] Grand Bank, 9+: Increase in proportion of 10+ in recent years due to the strong year classes from 1989–1990 and lower recruitment compare to the earlier years). From Marteinsdottir *et al.* (2005).

		% changes in landings and demographic properties					
Stock	Years of landings/ demographic properties	Landings	Biomass	SSB	R	Prop old (10+ or 6+)	Age Diversity (H)
Arcto-Norwegian	1946-2003 1946-2003	-41	-59	-57	-53	-96	-23
E. Baltic	1966-2003 1966-2003	-50	-48	-45	-44	77	13
W. Baltic	1970-2003 1970-2003	-32	-56	-51	-71	-0.2	-14
Kattegat	1971-2003 1971-2003	-77	-87	-86	-88	-58	-18
North Sea	1963-2003 1963-2003	-50	-63	-74	-61	-67	-17
W. Scotland	1966-2003 1978-2003	-85	-79	-77	-81	125	3
Irish Sea	1968-2003 1968-2003	-59	-67	-74	-71	-89	-63
Celtic Sea	1971-2003 1971-2003	85	36	19	99	-64	-19
Faroes	1961-2003 1961-2003	29	23	4	-2	1	0
Iceland	1955-2003 1955-2003	-54	-64	-79	-25	-94	-14
W. Greenland	1924-2003 1982-2003	-79	-99	-98	na	na	na
S. Labrador	1959-1993 1962-1993	-70	Na	-62	-95	-97	na
Flemish Cap	1959-1998 1972-2001	-84	-95	-87	-98	na	na
Grand Bank	1953-1994 1959-2002	-82	-95	-90	-99	136[1]	0.9
S. Gulf of St.Lawrence	1964-1995 1974-2003	-91	-33	30	-61	na	na
N. Gulf of St.Lawrence	1965-1995 1971-2002	-76	-78	-78	-86	-81	-43
E. Scotian Shelf	1958-1993 1970-2002	-52	Na	-75	-81	-72	na
Gulf of Maine	1960-2001 1982-2001	-67	-34	-21	-47	-48	na
George Bank	1960-2001 1978-2001	-49	-73	-72	-79	-74	-4.1

2.4 ToR d) Evaluate the consequences for stock resilience of decreases in mean weight and length and age/size diversity

Food intake is partitioned beween metabolic maintenance costs, somatic growth and reproduction. Maintenance costs take priority. A decline in population mean weight-at-age or condition may be an indication that food is limited, with adverse consequences for reproductive output and for resilience. The highest mortality which a stock can sustain without collapsing due to recruit overfishing is determined by the recruitment per unit of spawning biomass. An analysis of the observed trends in weight-at-age (see Brander, Annex

3, Extended abstract 1) and their possible consequences for reproductive output trends would require a method such as Dynamic Energy Budgetting (Nisbet *et al.*, 2000), but this has not been carried out to date.

The consequences for stock resilience of decreases in mean weight-at-age have been explored quite extensively for the S. Labrador and S. Gulf of St Lawrence stocks (Krohn and Kerr, 1997; Chouinard and Swain, Annex 3, Extended abstract 5; Swain, Annex 3, Extended abstract 14). In both areas size-selective fishing on younger ages may have been a major factor in causing mean weight-at-age to decrease (food environment and temperature also played a part). The reduction in mean weight-at-age was already evident before 5 years of age and persisted in the cohorts as they grew older. There are a number of implications from these studies.

1) Change in growth rate may have a big effect on the trajectory for recovery, as shown in Figure 8.
2) Changes in growth due to selective fishing are, in principle, controlable and deleterious changes, such as occurred in several Canadian stocks in the 1980s, should be avoided. This becomes even more important if, as seems to be the case, selective fishing causes genetic change.
3) If changes arise at young ages and persist as the cohorts mature, then they should be accounted for in stock predictions.

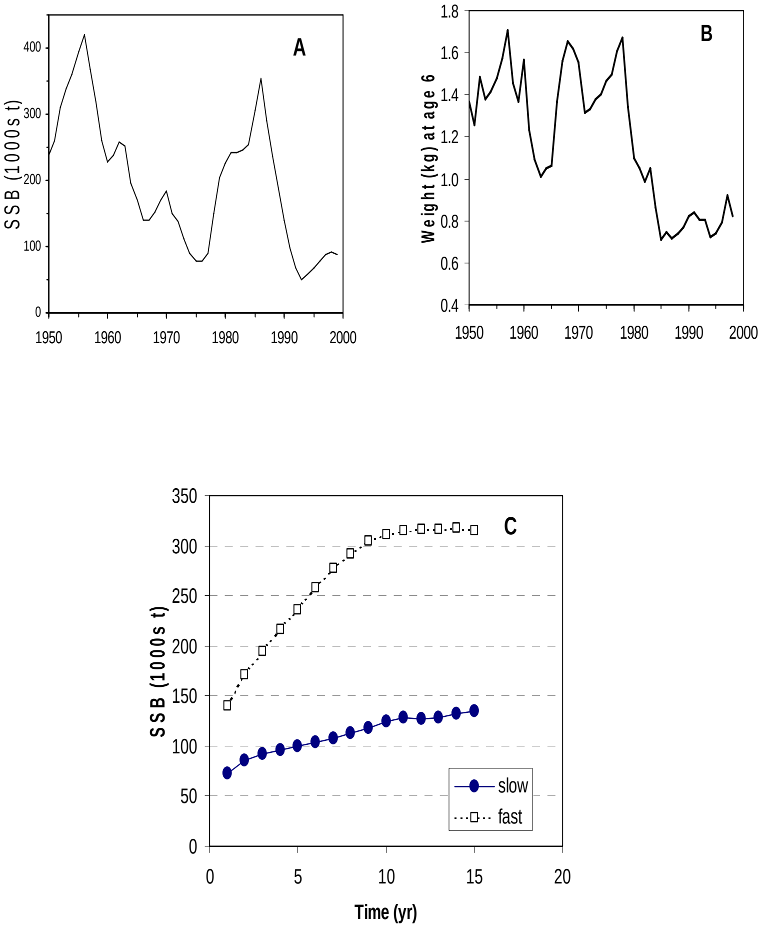

Figure 8. (from ICES, 2002b) Effect of variation in growth on biomass of southern Gulf of St. Lawrence cod. A. Spawning stock biomass (SSB). B. Weight at age 6. C. Simulated recovery from stock collapse assuming either the fast growth rates of the mid 1970s or the slow growth of the early 1990s. Note that the simulated recoveries do not include changes in natural mortality, recruitment and genetic structure which may have occurred (see Chouinard and Swain, Annex 3, Extended abstract 5).

A diverse age structure or high proportion of old fish (see Table 2) may enhance reproductive potential and/or reduce the sensitivity of recruitment to environmental variability. This has been demonstrated for a number of stocks including Icelandic cod and Arcto-Norwegian cod (Marteinsdottir *et al*., 2005; Ottersen *et al*., 2006) and has also been proposed for other cod stocks, e.g. Eastern Baltic cod and Georges Bank cod (Wieland *et al*., 2000). In contrast, age structure does not seem to affect recruitment rate for southern Gulf of St. Lawrence cod (Swain and Chouinard, 2000) or for S.Labrador cod (Drinkwater, pers. comm.).

Fishing generally selects particular sizes or maturity states of fish. The factors causing this selection are catchability, availability, market requirements, gear selection, fishing on spawning or feeding aggregations etc. The heritability of the traits which are selected (growth and maturation) is sufficient to cause changes in gene frequencies and eventually loss of genotypes and alleles. Because such genetic changes are not rapidly reversible this may slow the time trajectory for recovery of a stock. Fishing can select for fast or slow growth rates and for early or late maturation. For some stocks (Arcto-Norwegian, S. Gulf of St Lawrence) the age and size selection has changed over time.

In many cases growth and maturation rates have been observed to increase quickly, presumably because there had not been adverse genetic changes in the population. Flemish Cap cod (Vázquez and Cerviño, 2005 (see Annex 3, Extended abstract 12) showed a rapid return to larger size-at-age when fishing pressure was released, and cod in Greenland waters, showed larger size-at-age when stock biomass started to increase again in the late 1990s than it had been at the end of the preceded period of decline (Rätz and Lloret, 2005).

Even though some cod stocks have been closed for directed fishing, recovery of stock biomass has been slow. In addition to changes in the ecosystem (see Section 2.10), e.g. resulting from a restructuring of the food web due to cascading effects (Frank *et al*., 2005), genetic changes associated with the population collapse may explain the unexpected delay in the response to released fishing pressure (Marteinsdottir *et al*., 2005; Chouinard *et al*., 2003). Reductions in genetic variability *per se* impair the ability to respond to a changing environmental. Also, size-selective fishing mortality (see Section 2.3) may shift the life history characteristics of a population away from optimal trait value under natural selection. The return to the 'natural' trait optimum may then take a considerable number of generations even under a scenario of little contemporary fishing (Enberg, Annex 3, Extended abstract 13).

2.5 ToR e) Document and comment on historic evidence of previous cod stock recoveries and the environmental and fisheries circumstances in which these occurred

The long-term trend in biomass of all Atlantic cod stocks has been downward since 1970 with the exception of the Celtic Sea (Brander, Annex 3, Extended abstract 1). The biomass of three stocks collapsed to 5% or less of the level at the beginning of the prolonged period of decline (S. Labrador, S.Grand Bank and W. Greenland offshore) and a further two stocks collapsed to between 6 and 10% (N.Gulf of St Lawrence and E. Scotian Shelf). None of these has recovered significantly, so in the recent history of Atlantic cod we have no examples of recovery from collapse or from a small biomass.

To find examples of sustained increases in stock biomass of cod we need to examine the early period of the 20th century (Drinkwater, 2006; Drinkwater, Annex 3, Extended abstract 2). The warming period of 1920s–1960s affected air and sea temperatures for most of the northern North Atlantic, with the latter extending from the surface down to 200 m and more. This covers most of the cod habitat except along the southeast coast of Canada and the northeastern United States. Temperature anomalies were greatest in the more northern areas.

The best documented biological change that occurred during the warm event was the increased abundance of Atlantic cod off West Greenland (Wieland *et al*., Annex 3, Extended abstract 7).

From the late 1910s to the early 1930s they not only increased in numbers but also spread gradually northward from near the southern tip of Greenland to Upernavik, a distance of over 1200 km (Jensen, 1939). The increased abundance led to the development of a cod fishery, which quickly replaced sealing as the main industry in West Greenland.

The cod off West Greenland probably originated from Iceland. At least 5% of Icelandic pelagic juvenile cod larvae were caught in the Denmark Strait beween Iceland and Greenland in 21 out of a 26 year time-series. However, they only survive in years when conditions in Greenland waters are favourable (ICES, 2002a). Zooplankton samples (1950–1985) show abundance, dominated by *Calanus finmarchicus*, was much greater during the warmer 1950s and very early 1960s compared to remaining relatively cool years (Pedersen and Rice, 2002). These authors found that approximately 25% of the interannual variability in cod larval abundance could be accounted for by the abundance indices of zooplankton.

Prior to the 1920s warming, cod spawned almost exclusively off the south coast of Iceland but as waters warmed, cod spawning spread northward until there were major spawning locations completely surrounding Iceland. Capelin, the major prey of adult cod, shifted their spawning from the south to the north coast, becoming scarce on the south coast that in turn resulted in a decrease in the condition of cod in the south, while those cod residing on the north coast were in good condition. The increased influx of Atlantic waters to the north of Iceland is believed to have lead to an increase in primary production off northern Iceland due to reduced stratification and higher nutrient concentrations, based on latter studies (Thorardottir, 1984; Gudmundsson, 1998). Zooplankton abundance is also significantly higher in warm years (i.e. more Atlantic waters) than in cold years (Astthorsson and Vilhjálmsson, 2002). Since *C. finmarchicus* constitutes 60–80% of the zooplankton biomass in spring, interannual variations mainly reflect variations in this species (Astthorsson and Vilhjálmsson, 2002). This increased production is believed to have contributed to the higher cod abundance during the warm period.

In the Barents Sea, during the 1920s and 1930s cod began appearing in high abundance and on Bear Island Bank a cod fishery was re-established there after an absence of almost 40 years (Blacker, 1957). Cod also spread northward off West Svalbard with sufficient abundance to support a fishery (Beverton and Lee, 1965) and eastward reaching Novaya Zemlya by 1929-1930 (Cushing, 1982). At this time there was a distributional shift in spawning with proportionately more cod spawning in the northern regions of Norway (Lofoten and Finnmark) compared to southern Norway at Møre (Sundby and Nakken, 2004). The stock size of Arcto-Norwegian cod peaked in the 1930s and 1940s (Hylen, 2002). Catch per unit effort (CPUE) was significantly higher in the period 1925–1960 than in the periods before or since and coincided with high recruitment (Godø, 2003). High recruitment was believed to be, in large part, a result of greater food availability (Sætersdal and Loeng, 1987; Ottersen and Loeng, 2000). The mean weight of the cod in Lofoten rose rapidly in the 1920s into the early 1930s and remained high before starting a general decline in the 1960s. The increase in mean weight between the pre-1920s period and 1930s–1960s was over 50%.

In summary, the increase of the West Greenland cod stock in the 1920s was caused by increase in the long-term temperature trend that, in turn, increased the zooplankton production in the Arctic-dominated ecosystem. Moreover, import of larvae and juveniles from the Icelandic cod was assumed to be a necessary condition for the increase of the West Greenland cod.

The role of import from neighbouring cod stocks in the recovery is an issue that also is described by Svedang (Annex 3, Extended abstract 9). It has been hypothesised that most juvenile cod at the eastern Skagerrak coast are recruited from offshore spawning areas mainly in the North Sea (Svedäng, 2003; Cardinale and Svedäng, 2004), from which they are passively transported (Munk *et al*., 1995, 1999). The following low abundance of adult of cod was suggested to be due to return migration of juvenile/ maturing fish at a certain size or age (Pihl and Ulmestrand, 1993). This theory was further supported by the fact that a relatively strong year class of cod in 2001 in the Skagerrak was genetically assigned to be originating from eastern North Sea cod populations, in contrast to the results in the year before when genetic analysis suggested local origin (Knutsen *et al*., 2003, 2004).

Recolonisation of areas depleted of cod stocks, such as along the Swedish Skagerrak coast (Svedäng, 2003), should be related to the general recruitment level and to dispersal rates. However, one alternative hypothesis is that juvenile fish do not remain where they once have settled, unless they are in close vicinity to their parental spawning grounds. It was thus conjectured that the temporal development in distribution of cod in various size classes after a major recruitment event, should be a reflection of the migratory behaviour of its offshore origin. Accordingly, recolonisation in such a case will be a much slower process than otherwise anticipated.

In summary, the examples above on the role of import and recolonisation from neighbouring cod stocks in recovery are challenging the prevailing views on genetic separation between Atlantic cod stocks. Novel views on marine metapopulations (Kritzer and Sale, in press) might throw new light on the interactions between neighbouring cod stocks.

The North Sea cod stock increased by a factor of 2.6 from 1963 to 1971 at the start of the “gadoid outburst”, which lasted to the mid 1980s. The increase in biomass coincided with an increase in fishing mortality and was due to increased recruitment over a number of years. The possible reasons for the increase and the circumstances in which it occurred were explored by a previous ICES/GLOBEC Workshop (Werner *et al*., 1999). Changes in the marine ecosystem, involving the timing, quantity and size composition of copepod production are the most likely explanation for the “gadoid outburst” (Beaugrand *et al*., 2003) and also contributed to the subsequent return of the cod biomass to its former level.

The E. Baltic cod stock increased by a factor of four from 1971 to 1983.

The Norwegian spring-spawning herring (NSSH), which has a recruitment pattern quite similar to those of the adjacent stocks of Arcto-Norwegian cod and haddock, may serve as a case study to show some of the circumstances and conditions under which recoveries can take place. The NSSH went through a collapse in the late 1960s, apparently as a combined effect of overfishing and decrease in the long-term sea temperature trend (Toresen and Østvedt, 2000). The biomass of the stock, which had been above 10m tons almost uninterruptedly since 1928, dropped below 1m tons in 1968, hit a minimum of 2000 tons in 1972 and increased fairly steadily to pass through the 1m ton mark again in 1987. The relative contributions of fishing and environment in this collapse are disputed (Fiksen and Slotte, 2002) and in particular whether the relationship between spawning biomass and recruitment changed over this period.

Some of the factors which assisted in bringing about the recovery of the stock were:

1) A moratorium on NSSH was established and suceeded in keeping fishing mortality low for a 12 year period from 1974. The moratorium was relatively easy to manage, because herring is caught mainly in directed fisheries and can generally be avoided in the bycatch of other fisheries. Also the distribution of the stock collapsed into a limited area along the coastal Norwegian shelf and with overwintering areas limited to a couple of fjords in Northern Norway.

2) In the early 1980s the long-term mean temperature in the Nordic Seas changed from a declining to an increasing trend. This may have been associated with an increasing trend in the productivity of the ecosystem.

3) During spring 1983 the environmental conditions were particularly beneficial for larval survival all along the Norwegian coast and in the Barents Sea, probably because of the strong influx of warm Atlantic water and high zooplankton abundances. Strong year classes of cod, haddock and herring were formed.

In summary, for the case of the NSSH, the effective fishing moratorium, the change in the long-term temperature trend and, fortuitously, one single year of extremely good larval survival in 1983 were key processes in the recovery.

2.6 ToR f) Comment on past projections of cod stock recovery, evaluate whether they were correct and draw conclusions concerning how future projections can be improved

Little attention was directed toward this ToR during the workshop. However, reference was made to the experience off eastern Canada, where moratoria imposed on several collapsed cod stocks in the early 1990s did not lead to the recoveries that were widely expected (Rice *et al*., 2003; Shelton *et al*., 2003, 2006; Chouinard and Swain, Annex 3, Extended abstract 5; Lilly, Annex 3, Extended abstract 6).

A clear, unambiguous summary of factors associated with the decline and recovery (or non-recovery) of these stocks is difficult because of differences among the various stocks. In general, the stocks declined during the 1960s and 1970s as a result of overfishing, especially by non-Canadian trawler fleets that targetted offshore over-wintering and spawning aggregations. With the declaration by Canada of a 200 nautical mile zone of Extended Fishery Jurisdiction in 1977, landings by distant water fleets declined. Stocks increased under reduced fishing mortality and good productivity (good recruitment and individual growth). The stocks declined again during the late 1980s and early 1990s as productivity declined and fishing mortality increased. The decline in productivity included a decline in recruitment, a decline in growth rate, and an increase in natural mortality, with the magnitude and relative importance of these changes varying among stocks. Some of these changes in productivity have been attributed to changes in the physical environment, including a decline in water temperature.

All stocks from the eastern Scotian Shelf northward were closed to directed fishing at some time between mid-1992 and early 1994. The responses of the stocks varied considerably. Some stocks, notably offshore northern (2J3KL) cod and eastern Scotian Shelf cod (4VsW), continued to decline after imposition of the moratoria and have shown no sustained signs of recovery. Other stocks, notably those in the northern and southern Gulf of St. Lawrence (3Pn4RS and 4TVn), did not decline to the same extent as the two just described but have remained at low levels of productivity. The only stock that rebounded strongly was that off southern Newfoundland (3Ps), but even that stock has experienced low recruitment during most years of the past decade.

The general expectation that moratoria would lead to recovery is probably not a projection in the sense implied by the ToR. Nevertheless, one can discuss why the general expection of recovery was not realized. As described in various overviews (Chouinard *et al*., 2003; Rice *et al*., 2003; Lilly and Murphy, 2004; Shelton *et al*., 2003, 2006) and elsewhere in the present workshop report, there has been a general decline in productivity and in some cases a continuance of fishing mortality from directed and bycatch fisheries. The decline in productivity includes a decline in recruitment (e.g. 3Ps cod), a decline in growth rate (e.g. southern Gulf of St. Lawrence cod) and an increase in natural mortality. The latter has been an important feature of the two stocks in the Gulf of St. Lawrence, and is particularly important for cod on the eastern Scotian Shelf and the offshore components of northern cod (although the possible contribution of fishing to the extremely high total mortality of offshore northern cod has not been clarified).

A general conclusion from the experience off eastern Canada is that humans may not have the ability to “rebuild” cod stocks that have declined to very low levels, at least not in the relatively short term of a decade or so. Stock productivity may be kept low by various natural phenomena, including depensation due to predation (Shelton and Healey, 1999; Bundy and Fanning, 2005), Allee effects (Frank and Brickman, 2000) and changed life history characteristics (Hutchings, 2005). In addition, it may not be practical or even possible to reduce the effects of fishing to zero.

2.7 ToR g) Evaluate the role of cod forage species (e.g. capelin) for variability in abundance and size-at-age of cod

The prey spectrum of cod is broad and changes as the cod grows. For juvenile and adult cod, the diet consists largely of fish and crustaceans. In many ecosystems, the most important prey are medium-sized planktivorous fish such as capelin, sand lance and herring, but juveniles of groundfish are important for cod in some areas such as Flemish Cap.

The role of prey in affecting cod abundance (through recruitment and mortality) and size-at-age is seen more clearly toward the northern end of the cod range, especially in cod-capelin ecosystems (notably Barents Sea, Iceland, Labrador-Newfoundland), and in other systems that have relatively few species (e.g. Baltic Sea)

2.7.1 Cod size-at-age and condition

Change in the abundance or availability of an important prey has been found to affect cod size-at-age and condition. For example, declines in capelin abundance have been correlated with reductions in growth rate of cod in waters around Iceland (Steinarsson and Stefánsson, 1996; Stefánsson *et al.*, 1998) and in the Barents Sea (Mehl and Sunnanå, 1991; Jørgensen, 1992), and with a reduction in somatic condition and liver reserves of cod in the Barents Sea (Jørgensen, 1992; Marshall *et al.*, 1999; Yaragina and Marshall, 2000). For the cod off Labrador and eastern Newfoundland, Krohn *et al.* (1997) reported that capelin biomass explained some of the variability in cod growth and condition, but other studies did not find significant relationships, and it has been difficult to distinguish between the effects of changes in capelin abundance and the direct or indirect effects of changes in the physical environment (Lilly Annex 3, Extended abstract 6).

In the Baltic Sea, changes in cod size-at-age are associated with changes in the biomass of prey (Gislason, 1999).

In contrast to the positive association often seen between biomass of pelagic fish and the growth and condition of cod, there has been a significant decline in condition of cod and other groundfish species on the Eastern Scotian Shelf (DFO, 2003; Choi *et al.*, 2004) at the same time as an increase in the biomass of pelagics. This is acknowledged to be perplexing (DFO, 2003). Bundy and Fanning (2005) hypothesize that the poor condition found in small cod is due to competition with increased populations of planktivorous fish, and propose that cod that are in poor condition when they are small remain that way when they become large.

In areas where the diversity of potential prey is higher (e.g. North Sea, Georges Bank), it appears that cod growth is less dependent on the abundance of any specific prey.

2.7.2 Cod abundance

There are several mechanisms by which changes in the abundance or availability of forage species might contribute to changes in recruitment and mortality of cod stocks.

2.7.2.1 Decreased recruitment via poor condition

It is recognized that poor condition can negatively affect spawning potential by decreasing the liklihood of maturing (Marteinsdottir and Begg, 2002), increasing the incidence of skipped spawning (Rideout *et al.*, 2005) and decreasing the reproductive output of those fish that do spawn (Lambert and Dutil, 2000). It is possible, then, that changes in prey abundance or availability may affect condition (especially liver index), which in turn may affect spawning success and thus recruitment, and may ultimately contribute to stock decline or recovery. An example of all steps in this mechanism occurring within a single ecosystem was not identified during the Workshop.

2.7.2.2 Increased mortality via poor condition

It has been demonstrated in laboratory studies that reduced ration will cause reduced condition and ultimately death. However, the question of whether a decline in cod condition has contributed to an increase in mortality of fish in the wild is difficult to address in the absence of findings of dead or moribund fish. Nevertheless, one can use the observations from laboratory studies to determine condition indices that are indicative of fish that might soon die. Fish exhibiting such low condition indices were found in the northern and southern Gulf of St. Lawrence (Lambert and Dutil, 1997; Schwalme and Chouinard, 1999) during the early to mid-1990s. Dutil and Lambert (2000) concluded that natural mortality from poor condition contributed to lower production by cod in the northern Gulf of St. Lawrence during that period.

The question for the present workshop is whether there are examples in which changes in prey abundance or availability have contributed to changes in cod condition (especially liver index), which in turn have affected rates of natural mortality and contributed to cod stock decline or recovery.

It is not clear whether the decline in cod condition in the Gulf of St. Lawrence noted above was related to a decline in abundance of prey. However, it has been hypothesized that the cooling shortened the feeding season of cod, and thereby contributed to a decline in condition (Dutil *et al*. 1999).

The decline in condition of cod on the eastern Scotian Shelf is not related to the abundance of pelagic prey, because species that were historically important prey for cod increased following the cod collapse (see above).

For cod off southern Labrador and eastern Newfoundland, it was hypothesized that the collapse was related to an increase in stress associated with a change in abundance and availability of capelin (Atkinson and Bennett, 1994). There may be insufficient data from the appropriate times and locations to test this hypothesis (Lilly, 2001). With respect to the lack of recovery of cod in the offshore of southern Labrador, it has been stated that the high mortality experienced by cod since the collapse is due to poor condition attending low capelin availability (Rose and O'Driscoll, 2000; but see Lilly, Annex 3, Extended abstract 6).

2.7.2.3 Increased mortality via predation

It has been hypothesized that when forage species such as capelin are in low abundance, then predators may feed to a greater extent on cod. It has also been hypothesized that cannibalism might increase within a cod population when prey abundance is low, and that this might reduce year-class strength.

2.7.2.4 Decreased recruitment via predation

It has been hypothesized that planktivorous fish might affect recruitment of cod by preying on or competing with the cod's early life stages (eggs, larvae and perhaps pelagic juveniles). For example, a negative relationship between the biomass of pelagic fish (herring and mackerel) and cod recruitment rate (number of recruits produced per unit of spawning biomass) has been shown for cod in the southern Gulf of St. Lawrence (Swain and Sinclair, 2000; Chouinard and Swain, Annex 3, Extended abstract 5). High prerecruit survival from the mid-1970s to the early 1980s coincides with a period during which pelagic biomass had been reduced by overfishing.

A variant of this mechanism is the cultivator effect, wherein a large predator cultivates its young by preying on species that are potential predators and competitors of its young. If the large predator becomes less abundant, then its prey becomes more abundant, via predator release, and then keeps the predator at a new low level by preying on the large predator's early life history stages. Such a mechanism has been hypothesized for cod and its planktivorous fish prey in the Baltic Sea (Köster and Möllmann, 2000) and on the eastern Scotian Shelf (Bundy and Fanning, 2005). It is notable that there was no increase in capelin off eastern Newfoundland after the collapse of cod, but polar cod was more abundant during the first half of the 1990s and little is known about sand lance, so it is possible that predation by forage fish has had some effect. However, temperature associated distribution changes seems more likely in the case of polar cod since they retracted northward with the arrival of the warm water although the cod still have not returned.

2.8 ToR h) Evaluate the role of cod predators (e.g. seals) for variability in abundance and size-at-age of cod

This ToR is interpreted to refer to the predators of juvenile and adult cod. These predators are upper trophic level, large (or large-gaped) species, notably piscivorous fish and marine mammals.

Predation is obviously an important component of natural mortality, especially for smaller cod, as has been illustrated by numerous diet studies and multispecies models. However, the role of predation in the dynamics of cod stocks has taken on increased emphasis with the recognition that mortality remained very high in several depressed cod stocks off eastern Canada after directed fishing was stopped. Several analyses (e.g. Sinclair, 2001) demonstrated that an increase in natural mortality started well before the fisheries were closed. For the cod stock in the southern Gulf of St. Lawrence, analyses suggest that the increase in natural mortality played a role in the collapse of the stock (Chouinard *et al*., 2005).

The cause of this elevated natural mortality remains unclear and contentious. Numerous studies have discussed the possibility that predation by grey and (or) harp seals is an important component of the high mortality of cod on the eastern Scotian Shelf (Fu *et al*., 2001; Bundy and Fanning 2005), in the southern and northern Gulf of St. Lawrence (Chouinard *et al*., 2005; Duplisea *et al*., Annex 3, Extended abstract 17) and on the southern Labrador and Northeast Newfoundland shelves (Lilly, Annex 3, Extended abstract 6). Formal cod stock assessment meetings have concluded that predation by seals has contributed to the slow or non-existent recovery of these stocks (Rice *et al*., 2003).

One of the numerous uncertainties associated with these analyses is that elevated mortality has been demonstrated not only for juvenile cod but also for adult cod (Bundy and Fanning, 2005; Chouinard *et al*., 2005; Lilly *et al*., 2005), whereas seal diet data generally reveal feeding on only small cod. It has been suggested by some (e.g. Chouinard *et al*., 2005) that the high mortality of adult cod might be a consequence of belly-feeding, a manner of feeding whereby the seal takes a bite from the cod's belly, leaving the head and muscle mass. Such predation, which would be undetected by the examination of stomach contents or scats, has frequently been observed in inshore waters of eastern Newfoundland (Lilly and Murphy, 2004). The prevalence of such feeding is exceedingly difficult to determine, especially in open water away from land.

Part of the reason for the increased attention to the role of seals and other marine mammals in the dynamics of cod stocks is the difference in direction of population trends. Many species of marine mammals were heavily exploited for centuries and declined to low numbers, but have increased in recent years under more restrictive management. This is particularly notable for harp seals and grey seals in the Northwest Atlantic. In contrast, exploitation of cod has increased in recent decades, and many stocks are at all-time lows. Seals and other marine mammals do not have a strong dependency on cod; their major prey are usually pelagic species of fish and squid. However, if these marine mammals continue to eat some cod while the cod are at very low abundance, then they may contribute toward keeping the cod in a "predator pit". In conjunction with other mechanisms of depensation, such predation by marine mammals may help maintain cod and their ecosystems in a state that is quite different from that which existed in the 1980s and before.

Determination of predator diet (Buren *et al.*, Annex 3, Extended abstract 18) and estimation of prey consumption (Stenson and Hammill, Annex 3, Extended abstract 19) are demanding in terms of data acquisition and analysis. For some geographic areas, there is relatively little study of the diet of some potential cod predators (e.g toothed whales and minke whales in the Northwest Atlantic), and even for those predator species that are being studied, there is generally less information than desired. Once the consumption of cod and other prey has been estimated, there still remains the difficult task of assessing the impact of that consumption (Duplisea *et al.*, Annex 3, Extended abstract 17). Depending on the choice of model, this generally requires substantial understanding of other components of the ecosystem, information on predator migration patterns (Rosing-Asvid, Annex 3, Extended abstract 16) and functional feeding responses, and knowledge of additional causes of prey mortality. It has been stated (e.g. NAMMCO, 2005) that good progress in this area will require a larger commitment to modelling.

The diets of many marine mammals are similar to that of cod. Thus, harp and grey seals may not only prey upon cod but compete with them for resources such as capelin and sand lance. Such competition has been cited as a possible reason for non-recovery of cod off eastern Newfoundland, but demonstration of competition is difficult (Link *et al.*, Annex 3, Extended abstract 15). Of interest in this regard is the hypothesis by Rosing-Asvid (Annex 3, Extended abstract 16) that seals fare better when cod abundance is low.

2.9 ToR i) Evaluate the role of climate mediated through cod predators and prey

Variability in climate influences many aspects of the ocean environment, and thereby affects recruitment, growth, mortality and distribution of cod and its predators and prey. Thus, climate may affect not only the abundance of the predators and prey with which cod interacts, but also the extent and duration of the overlap between cod and those other species. The potential for interaction seems almost limitless. A few examples related to cod decline and recovery are given.

Castonguay *et al.* (1999) found that cod in the northern Gulf of St. Lawrence were distributed more southerly and deeper in winter during the late 1980s and early 1990s, and that the latitudinal shift was correlated with the cooling at mid-depth that had started in the mid-1980s. They inferred that the cod had started to migrate earlier to overwintering grounds, and surmised that this might have shortened the feeding season and contributed to declines in size-at-age and condition. As noted above (under ToR g), the low condition may have lead to increased mortality. Note, however, that Comeau *et al.* (2002) explored the causes and implications of a similar change in timing of migration by cod in the southern Gulf of St. Lawrence, and concluded that earlier departure from feeding grounds within the Gulf may not necessarily have been a factor contributing to the slow recovery of that stock.

Off southern Labrador and eastern Newfoundland, there were numerous changes in the distribution and phenology of cod during the late 1980s and particularly the early 1990s (Lilly Annex 3, Extended abstract 6). Among these was a change in north-south distribution of both cod and capelin (Lilly, 1994). Some investigators interpret the change in cod distribution to be a shift, and postulate that this was in response to the decline in water temperature (deYoung and Rose, 1993; Rose *et al.,* 1994; Atkinson *et al.,* 1997; Rose *et al.*, 2000) or the southward shift in the distribution of capelin (Rose *et al*., 2000). It is thought by some that this shift increased the vulnerability of the cod to both Canadian and non-Canadian fleets (Rose *et al*., 1994; Atkinson, *et al*., 1997; Rose and Kulka, 1999). The shift in capelin distribution may also have reduced feeding success of those cod that remained toward the north, and may have contributed to a decline in condition and an increase in mortality (Lilly, 2001).

As noted under ToR h, there is considerable interest in the possibility that seal populations are hindering or preventing the recovery of several cod stocks off eastern Canada. Climate can mediate reproductive success and distribution of seals and alter their access to prey. Three examples follow. (1) It is possible that the extensive ice conditions of the 1980s and early 1990s promoted low seal pup mortality, and contributed to the growth of the seal populations. Conversely, poor ice conditions, such as obtained during several recent years, might lead to higher pup mortality and a decrease in the seal populations. (2) Harp and hooded seals migrate to eastern Canadian waters during winter/spring, and it is possible that the duration of their stay will be longer when the water is cold and sea ice extensive. If shelf waters off eastern Canada become warmer, the seals may spend less time in the area and prey to a lesser extent on cod. (3) During the winters of the late 1990s and early 2000s there were several instances when cod appeared near the surface very close to shore in eastern Newfoundland (Lilly *et al*., 1999). Harp seals were seen at the periphery of the aggregations and were sometimes seen belly-biting the cod. Dead cod were found lying on the bottom. Such events were not previously known to people who lived nearby, and it was speculated that the warm winters had lessened the coverage by shore-fast ice and had made the cod more vulnerable to the seals.

2.10 ToR j) Evaluate the relationship between the decline and recovery of cod stocks and changes in the marine ecosystems

2.10.1 Effects of Atlantic Multidecadal Oscillations (AMO) versus decadal-scale and interannual climate variations

Studies on ecosystem effects and climate effects on growth and recruitment in North Atlantic fish stocks, particularly Atlantic cod, have mainly focused on interannual to decadal-scale variations (e.g. Elizarov, 1963; Sætersdal and Loeng, 1987; Ellertsen *et al*., 1989; deYoung and Rose, 1993; Planque and Frédou, 1999). Studies on such time scales relate to the original hypothesis by Hjort (1914) where emphasis is put on the large year-to-year variations in year-class strength. However, decline and recovery of fish stocks are probably to a larger extent associated with longer-term and sustained changes in the ecosystem like the Atlantic Multidecadal Oscillations (AMO). Although, the AMOs are generally of much smaller amplitudes than the interannual to decadal-scale amplitudes they seem to have much more profound effects on fish stocks and the ecosystems (Drinkwater, 2006; Drinkwater, Annex 3, Extended abstract 2). Moreover, multidecadal variations have also a larger spatial extent than the decadal-scale and shorter-term variations. Multidecadal variations have a pan-Atlantic spatial extent, while the decadal-scale variations that often are associated with the pattern of the North Atlantic Oscillation are limited to regions within the North Atlantic. A general problem with documenting the effects of AMO on fish stocks and the ecosystem is that long enough time series are available in only a few regions.

The most well documented biological change that occurred during the first AMO warm event in the 20th century was the increased abundance of Atlantic cod off West Greenland. From the late 1910s to the early 1930s they not only increased in numbers but also spread gradually northward from near the southern tip of Greenland to Upernavik, a distance of over 1200 km (Jensen, 1939). The increased abundance led to the development of a cod fishery, which quickly replaced sealing as the main industry in West Greenland. The cod fishery yielded moderate landings through the 1930s, declined during the war years but rose dramatically through the 1950s reaching a peak at close to 5 x 10^5 t in the early 1960s before declining rapidly later that decade during a period of decreasing air and ocean temperatures. Cod catches have remained relatively low since the 1970s. The cod off West Greenland originated from Iceland due to a combination of increased transport of larvae from Iceland and better survival of larvae once they reached West Greenland waters. During the warming period of the 1920s cod catches in Icelandic waters rose rapidly peaking in the early 1930s. While increased fishing effort contributed to these record catches, there was very high recruitment in the 1920s, with the highest recruitment on record being in the early 1920s (Schopka, 1994).

In the Barents Sea, during the 1920s and 1930s cod began appearing in high abundance and on Bear Island Bank a cod fishery was re-established there after an absence of almost 40 years (Blacker, 1957). Cod also spread northward off West Svalbard with sufficient abundance to support a fishery (Beverton and Lee, 1965) and eastward reaching Novaya Zemlya by 1929–1930 (Cushing, 1982). At this time there was a distributional shift in spawning with proportionately more cod spawning in the northern regions of Norway (Lofoten and Finnmark) compared to southern Norway at Møre (Sundby and Nakken, 2004). The stock size of Arcto-Norwegian cod peaked in the 1930s and 1940s (Hylen, 2002). High recruitment was believed to be, in large part, a result of greater food availability (Sætersdal and Loeng, 1987; Ottersen and Loeng, 2000). The mean weight of the cod in Lofoten rose rapidly in the 1920s into the early 1930s and remained high before starting a general decline in the 1960s.

The climate changes that occurred during the warm period of the 1920s to the 1960s lead to significant ecosystem changes, including dramatic impacts on numerous cod stocks. Cod abundance increased through the northern North Atlantic especially in the Barents Sea, Icelandic waters and off West Greenland driven by a combination of higher recruitment and higher growth. The feeding areas as well as the spawning areas of the stocks shifted northward. The history of the Norwegian spring-spawning herring in 20th century, which was introduced in Section 2.5, is another prominent example of a fish stock whose biomass matches the major warming and cooling trends of the 20th century (Figure 9, Toresen and Østvedt, 2000).

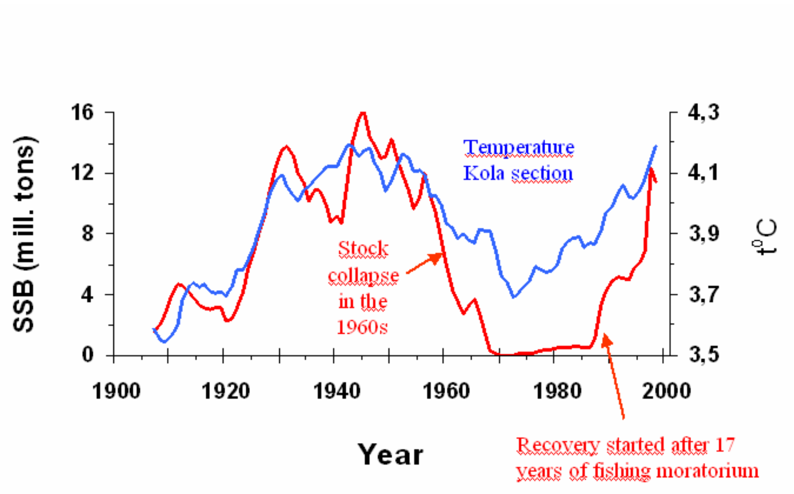

Figure 9. The relation between development of the SSB of Norwegian spring-spawning herring through the 20th century and long-term averaged sea temperature (after Toresen and Østvedt, 2000).

After 17 years of fishing moratorium the recruitment of the 1983 year class became the start of the new herring period. The year 1983 was an extraordinary year in Norwegian Sea – Barents Sea ecosystem with not only strong herring year class but strong cod and haddock year classes as well.

2.10.2 Ecosystem effects on the individuals stocks

Barents Sea

In the arctic and arcto-boreal regime of the North Atlantic Ocean temperature has long been recognized as an important factor for the productivity in fish stock. Ishevskii (1961, 1964) found positive correlations between temperature and recruitment of cod stocks in the Barents Sea and in the Northwest Atlantic region, and he noticed that temperature and recruitment seemed to vary inversely in the two regions. Sætersdal and Loeng (1987) analysed recruitment of the Arcto-Norwegian cod through the 20th century and showed that strong year classes tended to occur in periods of warm years and particularly at the beginning of the warm periods. They proposed that in warm periods the gonad production increased resulting in better recruitment. Ellertsen *et al*. (1989) analysed the time series 1946–1985 of year class strengths of Arcto-Norwegian cod based on virtual population analysis of 3-year-old fish. They found that year class strength was always low in cold years, but in warm years both good and bad year classes occurred. They concluded from this that a high temperature is a necessary but not sufficient condition for the formation of strong year classes. Ellertsen *et al*. (1989) proposed that the causal mechanism might be linked to the production of the main prey item for cod larvae, the *Calanus* nauplii, since the onset of the *Calanus* production was found to be strongly temperature dependent. .

Skjoldal *et al*. (1987) linked the variations in the zooplankton abundance in the western Barents Sea to the variations in the inflow of zooplankton-rich Atlantic water from the Norwegian Sea. Skjoldal and Rey (1989) showed that the large fluctuations in the zooplankton biomass in the Barents Sea in late spring during the period 1978–1985 were due to variations in the influx of Atlantic water from the Norwegian Sea. Helle and Pennington (1999) found a high positive correlation between the average zooplankton abundance in the western Barents Sea in June-July and the influx of Atlantic water in June from the Norwegian Sea to the Barents Sea.

Hence, a link between high temperature and advection of *Calanus*-rich water masses was established for the Barents Sea ecosystem. The increased inflow Atlantic water masses from the Norwegian Sea into the Barents Sea resulted in both higher temperatures and high abundances of *Calanus*-rich water masses. This was shown to result in good recruitment of cod, haddock and herring and generally increase the productivity and carrying capacity of the Barents Sea ecosystem.

The influence from higher trophic levels for the Barents Sea cod is poorly investigated. From northern Norwegian waters we know that herring schools may consume larger amounts of pelagic cod eggs (Melle, 1985). On the other hand, we also know that small ctenophores are consumers of cod eggs and larvae (Båmstedt *et al.,* 1994; Martinussen and Båmstedt, 1999). Small larvae in poor condition will probably have more difficulties to avoid attack from these small ctenophores, while the bigger and well fit larvae will generally be more able to avoid them according to the hypothesis by Houde (1989) that bigger larvae have better survival. Ctenophores and probably other small jelly plankton are important predators on the larval stages of fish off the coast of Norway in addition to krill and pelagic fish, but there is no documentation on their quantitative effects as predators.

Experimental work by Kjesbu *et al*. (1996) shows that larger and older females tend to have a longer spawning period than smaller and younger fish. Larger females tend to produce a relatively greater number of eggs, i.e. the number of eggs produced per gram body weight increases with increasing length (Marteinsdottir and Thorarinsson, 1998). Repeat spawners also produce eggs that have a wider range of vertical distribution than recruit spawners, thus causing broader horizontal dispersion (Kjesbu *et al*., 1992).

Labrador Sea

Similar temperature - cod recruitment relationships to that found for Barents Sea cod have been indicated for the other Atlantic cod stocks at the lower temperature range. The Northern cod is one of the Atlantic cod stocks living at low temperatures. Elizarov (1963) found a positive correlation between temperature and catches of cod in the region. deYoung and Rose (1993) demonstrated a similar response of cod recruitment to low temperature as for the Greenland cod and the Arcto-Norwegian cod. They related the temperature effect to changing spawning locations of the fish in warm and cold years, and suggested that a southward shift in the distribution of spawning cod in cold years led to a reduced recruitment because of lower retention of the eggs and larvae in the southern region. The cool ocean climate that developed at the Labrador Shelf after 1988 was followed by the collapse in the Northern cod. Although it was claimed that overfishing alone was the cause of the collapse (Myers *et al*., 1996), it cannot be rejected that the cool climate was an important additional factor. Taggart *et al*. (1994) found that the recruitment variability in the 1980s was in part determined by environmental conditions, but pointed out that the causal relationship is unclear since the thermal environmental conditions are correlated with most of the other climate parameters.

The causal mechanism proposed in the Barents Sea that the effect of high temperature on cod recruitment is a proxy for the advection of *Calanus*-rich water masses (e.g. Sundby, 2000) has not been confirmed for the cod stocks in the Northwest Atlantic. However, it cannot be rejected that there the cod recruitment - temperature relation might also be a proxy for the supply of Calanus-rich water masses, but there are no similar zooplankton time series to explore this.

The large population of marine mammals in the Labrador Sea is thought to have an important influence on the ecosystem structure and function (Stenson and Hammill, Annex 3, Extended abstract 19). This has lead to the view that seals can have a negative impact on commercial fish stocks, including Atlantic cod. Over the last decade several Atlantic groundfish stocks have collapsed while many marine mammal populations, particularly seals, have shown marked increases leading to suggestions that seals were involved in the failure of the fishery. Although it is now considered that seals played no, or only a minor role, in the collapse of Canadian groundfish stocks in the early 1990’s, they may play a more important role in slowing the recovery of certain Atlantic cod stocks.

Gulf of St. Lawrence

For the southern Gulf of St. Lawrence cod stock, increased catches starting in 1950 resulted in higher exploitation rate and caused the stock to decline until it reached a low level in the mid 1970s (Chouinard and Swain, Annex 3, Extended abstract 5). The stock rebounded rapidly without a moratorium on the fishery. The recovery of the late 1970s was fuelled largely by exceptional recruit-per-spawning stock biomass ratio during that period.

Analyses have shown that the high recruitment rates in the mid to late 1970s appear to be associated with the collapse due to fishing of pelagic fish stocks (both herring and mackerel) in the southern Gulf at that time. Herring and mackerel are thought to negatively impact recruitment of cod through predation on eggs and larvae. There also appears to be a small negative effect of warm temperatures in the spring and early summer on cod recruitment.

As cod abundance and biomass recovered in the late 1970s, this was accompanied by a decline in growth rate. The decline appears to have been caused by size-selective mortality in the fishery, a negative relationship with density and some effect of temperature. Cod biomass peaked in the mid 1980, then started to decline and collapsed by the early 1990s. The decline coincided with a rise in fishing mortality but was accentuated by an increase in natural mortality starting in the mid 1980s. Changes in natural mortality correspond to changes in the abundance of grey seals in the southern Gulf of St. Lawrence. Grey seal abundance in the southern Gulf is estimated to have increased from approximately 20 000 animals in the 1970s to about 55 000 animals in recent years, a near three-fold increase.

The lack of recovery for southern Gulf of St. Lawrence cod since the moratorium is due to continued poor productivity, particularly high natural mortality and low growth. Besides fishing, it thus appears that for southern Gulf of St. Lawrence cod, changes in the marine ecosystem have contributed to declines and recovery and lack of recovery of the stock. However, the changes implicated are primarily related to the abundance of predators of cod at the early (egg and larvae) and adult stages as opposed to be related to variation in climate.

Iceland

For the Icelandic cod Astthorsson *et al*. (1994) analysed the time series from 1971 to 1992 and concluded that neither the abundance indices nor the mean lengths of 0-group cod were correlated with temperature. On the other hand, they showed that there was a significant correlation between the zooplankton biomass in southwestern Icelandic waters and the 0-group index of cod indicating a direct link between cod recruitment and zooplankton abundance.

North Sea

Ecosystem effects in relation to the North Sea cod stock were investigated by the Workshop on Gadoid Stocks in the North Sea during the 1960s and 1970s (Heath and Brander, 2001). Changes in the timing, abundance and size composition of Calanus and other planktonic prey probably resulted in major changes in the productivity of the ecosystem for cod between the early 1960s and the late 1990s (Beaugrand *et al*. 2003)

For the North Sea the extensive time series on zooplankton from the Sir Alistair Hardy Foundation document the long-term decrease of *C. finmarchicus* after the mid 1960s and particularly after the 1980s (Reid *et al*. 2003). The decrease is highly correlated with the decline in North Sea cod SSB after the gadoid outburst in the early 1960s. Rothschild (1998) analysed the relationships between abundance of zooplankton and year-class strengths of North Sea cod and herring, including also the variations in fishing mortality. He found that large year classes of cod co-occurred with either high abundances of *Calanus* or *Paracalanus/Pseudocalanus*. He also found that high abundance of both *Calanus* and *Paracalanus/Pseudocalanus* rarely occurred. In years with low abundance of *Calanus* or *Paracalanus/Pseudocalanus* good recruitment of cod occurred only once while in all the other ten years with low zooplankton abundance bad cod recruitment occurred. Moreover, there are indications that the reduction in other North Sea fish stocks is linked to the decline abundance of *C. finmarchicus* (ICES, 2005e). Temperature in the North Sea has increased over the same period of time. Hence, there are strong indications that the general reduction in fish stocks of the northern North Sea is linked to the general decrease of *C. finmarchicus* in the ecosystem.

2.10.3 Concluding remarks

The role of zooplankton for growth and recruitment in Atlantic cod

For the major cod stocks of the Northeast Atlantic, i.e. the Arcto-Norwegian cod in the Barents Sea, the Icelandic cod and the North Sea cod there has been documented that the abundance of *Calanus* spp has strong impact on growth and recruitment. Since one of the two core production areas of *C. finmarchicus* is located in the Norwegian Sea, advection of *C. finmarchicus* onto the surrounding shelves inhabited by the cod stocks is considered to be an important mechanism for supplying zooplankton food to larval and early juvenile cod (Sundby, Annex 3, Extended abstract 10). Moreover, it is assumed that the large biomass supply of *C. finmarchicus* also influenced adult cod indirectly as food for planktivore pelagic fish.

The increased influx of Atlantic water to the Nordic Seas and the correspondingly increased temperature in the Northeast Atlantic have adversely influenced the recruitment of Atlantic cod in the Barents Sea and in the North Sea. In the Barents Sea the increased influx of Atlantic water has increased the advection of Calanus-rich water masses to the Barents Sea. In the North Sea the increased flux of Atlantic water through the Norwegian Trench has suppressed inflow of Norwegian Sea Intermediate Water which is rich in overwintering *C. finmarchicus* (Sundby, Annex 3, Extended abstract 10).

In the Northwest Atlantic there are no sufficient time series on zooplankton that could indicate a similar mechanism between advection of Calanus-rich water masses and Atlantic cod recruitment. However, the other of the two core production areas of *C. finmarchicus* is located in the oceanic region in the Subpolar Gyre to the south of Greenland and east of Newfoundland. Therefore, potentially, the *C. finmarchicus* might play a similarly important role for the historically large cod stocks in the Northwest Atlantic, i.e. the West Greenland cod and the Northern cod. Time series on *C. finmarchicus* in the Labrador Sea could have enlightened the issue.

The role of upper trophic levels in controlling Atlantic cod growth and recruitment

Marine mammals have the potential to influence the abundance of cod stocks, particularly in the Arctic habitats of Atlantic cod. Although there is no strong evidence that marine mammals are a major cause of declines in cod stocks, there is an indication of that marine mammals could play a significant role in keeping the collapsed cod stocks down and decrease the possibilities of recovery, particularly in the Northwest Atlantic. Marine mammals might presently play such a role in Northern cod. In overwintering areas in the eastern part of Gulf of St. Lawrence seals to a large extent have occasionally fed on cod. Also at the Scotian Shelf marine mammals are important predators on cod.

Pelagic fish may be important predators on cod eggs. High recruitment rates in the Gulf of St. Lawrence in the mid to late 1970s appeared to be associated with the collapse due to fishing of pelagic fish stock, i.e. herring and mackerel. For the Barents Sea cod no similar relationship has been yet found, but it has been documented that herring can feed intensively on the pelagic cod eggs in the main spawning areas of Lofoten.

3 Suggestions for future work and recommendations

The effect of size-selective mortality on size-at-age should be further investigated covering more stocks.

The examination how the age structure and geographical substructure of the spawning stock affects resilience to climate change should be extended to cover as many other stocks as possible, e.g. by comparing the correlation between recruitment and temperature with the mean age of the female spawning stock.

It is recommended that the Working Group on Cod and Climate Change consider a publication of the workshop results as an ICES Cooperative Research Report and/or submit a paper to the proceedings of the 24th Lowell Wakefield Fisheries Symposium on Resiliency of Gadid Stocks to Fishing and Climate Change to be held in Anchorage, October 31–November 3, 2006.

A summary of the recommendations is provided in Annex 4.

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Annex 2: Agenda

May 9

13:00-14:00 Welcome and Introduction - housekeeping, purpose, history

Local host (George Lilly)

Conveners (Brian Rothschild, Kai Wieland, Svein Sundby, George Lilly)

Welcome remarks by Julian Goodyear, Regional Director of Science, Fisheries and Oceans Canada, Newfoundland and Labrador Region

Keith Brander – Remarks on background to this workshop

14:00-15:30 Presentations and Discussion in Plenary

Presentations on major issues

Keith Brander: An overview and comparison of the declines which have taken place in cod stocks (the possible role of changes in weight-at-age)

Ken Drinkwater: Cod responses to the Atlantic Multidecadal Oscillation

Brian Rothschild, Henrik Sparholt, and Keith Brander: Notes on similarities and differences among cod populations of the North Atlantic ocean.

Niels Daan: A generalized stock-recruitment relationship for the Northeast Atlantic cod stocks

15:30-16:00 Refreshment break

16:00-17:30 Presentations and Discussion in Plenary

Regional Overviews

Ghislain Chouinard and Doug Swain: Contrasting recovery rates of southern Gulf of St. Lawrence cod between the 1970s and 1990s: the roles of fishing, climate and ecosystem change

George Lilly: The decline and non-recovery of northern (2J3KL) cod, with brief remarks on cod in 3Ps and 3NO

Kai Wieland, Marie Storr-Paulsen and Kaj Sünksen: Fishery and environmental aspects relevant for the decline and recovery of the Atlantic cod (*Gadus morhua*) stock in Greenland offshore waters

Geir Ottersen, Dagø O. Hjermann, and Nils Chr. Stenseth: Long-term (1913-2004) changes in the age-structure of Arcto-Norwegian cod strengthens climate-recruitment link

Henrik Svedäng: Decline and recovery of cod along the eastern Skagerrak coast in relation to population and offshore recruitment

Svein Sundby, Paul Budgell, Morten D. Skogen, Eva Falk, Mari Myksvoll Skuggedal, and Francisco Rey: The long-term decrease of cod recruitment in the North Sea – the mechanistic links to ocean climate, water mass characteristics, nutrient conditions and the large-scale dynamics of *Calanus finmarchicus*

Fritz Köster: Eastern Baltic cod recovery - The importance of species interactions Baltic cod (presentation given by Kai Wieland)

Antonio Vázquez: The collapse of the Atlantic cod (*Gadus morhua*) stock on Flemish Cap

Fisheries Induced Evolutionary Change

Katja Enberg: Fisheries induced evolutionary change and recovery potential of cod stocks

Doug Swain: The possible role of evolutionary responses to fishing in the non-recovery of the collapsed southern Gulf cod stock

Predator-prey interactions

Jason Link, Bjarte Bogstad, Henrik Sparholt, and George Lilly: The role of cod in the ecosystem, with emphasis on the effect of predators and prey on cod (from draft chapter from cod book)

Aqqalu Rosing-Asvid: Interactions between harp seals and Atlantic cod off west Greenland

Daniel Duplisea, Mike Hammill and Red Méthot: Harp seal predation on Northern Gulf cod: fitting historical data and projecting cod recovery under various seal hunt scenarios

Alejandro Buren, Mariano Koen-Alonso and Garry Stenson: Predator-prey interaction between harp seals and Atlantic cod: An exploration of sources of variation

Garry Stenson and Mike Hammill: Quantifying prey consumption by harp seals

May 10

08:30-10:30 Plenary: Finish presentations

10:30-11:00 Refreshment break

11:00-12:30 Plenary: Finish presentations

12:30-13:30 Lunch

13:30-15:30 Plenary session: Finish presentations

15:30-16:00 Refreshment break

16:00-17:30 Plenary session: addressing Terms of Reference

May 11

08:30-10:30 Plenary session /Break out groups: addressing Terms of Reference

10:30-11:00 Refreshment break

11:00-12:30 Plenary session /Break out groups: addressing Terms of Reference

12:30-13:30 Lunch

13:30-15:30 Plenary session /Break out groups: addressing Terms of Reference

15:30-16:00 Refreshment break

16:00-17:30 Plenary session /Break out groups: addressing Terms of Reference

May 12

08:30-09:00 Plenary

- Discussion of potential for external publication (s) resulting from the meeting

- Review the state of the report

10:30-11:00 Refreshment Break

11:00-12:30 Further review of the report and closing discussion

12:30-13:30 Lunch

13:30-18:00 Writing continues (for those who wish)

Annex 3: Extended abstracts of presentations

The following table lists the extended abstracts by first author and in the sequence in which they appear below. The table also indicates which of the Terms of Reference is addressed by each abstract. An eleventh column has been added for “adaptive change”.

	a	b	c	d	e	f	g	h	i	j	adaptive change
Brander	1	1	1	1	1						
Drinkwater			1		1					1	
Rothschild	1	1									
Daan	1	1									
Chouinard			1		1		1	1	1	1	
Lilly		1	1	1	1	1	1	1		1	
Wieland	1	1			1						
Ottersen		1		1	1						
Svedang	1				1						
Sundby	1		1							1	
Köster		1	1		1		1	1	1	1	
Vazquez		1	1							1	
Enberg	1	1	1	1	1						1
Swain		1	1	1	1					1	1
Link							1	1			
Rosing-Asvid								1			
Duplisea								1			
Buren								1			
Stensen								1		1	
TOTAL	7	10	9	5	10	1	4	8	2	8	2

Extended abstract 1

The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970

Keith M. Brander

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This paper was produced as part of the preparation for the Workshop on Decline and Recovery in order to (i) bring together the data on changes in biomass, fishing mortality, recruitment and weight-at-age in a common format (ii) describe changes in biomass and weight-at-age which have taken place (iii) describe some of the characteristics of decline and recovery and propose some working definitions of terms such as “prolonged period of decline”, “collapse” and “recovery”. The data set and a working paper describing it was made available on the ICES/GLOBEC website five months before the workshop in order that all workshop participants and others who wished to contribute ideas and working papers could make use of it. A full version of the paper was submitted to the ICES Journal and will be published as an essay.

When the data for fifteen stocks (seven from each side of the N Atlantic plus Greenland) were assembled and plotted it became apparent that there were consistent patterns of change in both biomass and weight at age and the paper goes on to consider what the patterns may indicate concerning the causes of change in biomass and in particular the direct and indirect role of change in mean weight-at-age. There are two principal proposals which arise:

1) Further analysis of the direct and indirect effects of changes in weight-at-age on stock decline and recovery requires tropho-dynamic modelling.
2) Prolonged periods of decline in biomass have in most cases been preceded by periods of decline in in mean weight-at-age. Change in mean weight-at-age should be monitored for the information it gives on future productivity and reproductive output of the stock.

Methods

Information on many characteristics of North Atlantic cod life histories and population processes has recently been assembled and published in a standard format for seventeen stocks, together with extensive reference lists (ICES, 2005a). Data on fifteen of these stocks are presented here, with some additional information from primary sources, which are either cited in ICES (2005a) or here.

Trends in population biomass for each cod stock are represented by total biomass. This is the product of population number-at-age and weight-at-age, where the former is derived from catch-at-age using virtual population analysis and the latter from sampling of commercial and research survey catches.

Trends in weight of individual cod are represented by stock weight-at-age averaged over five age groups, beginning in each case with the age at which the fish attain 1 kg in weight. This range was chosen to represent the most abundant and best sampled ages in the catch, i.e. those large enough to exceed the size over which gear selection occurs, but excluding higher ages, which are influenced by small number effects. The range of ages used in estimating total biomass and mean individual weight for each stock is given in columns 5 and 6 respectively of Table 1 and the % of total biomass which the age groups included in the mean weight represent is in column 7. Data sources, in which details of sampling and methods can be found are given in column 8. The ICES assessment reports can be accessed at http://www.ices.dk/iceswork/workinggroups.asp (codes for individual stocks are shown in Table 1). Weight-at-age (state) is not intended to “represent” growth (rate) in this analysis, but changes in weight-at-age provide evidence of changes in growth. The time series of biomass and weight-at-age are shown in Figure 1. A seven-year moving window analysis of the time series of total biomass and mean weight is used to identify “prolonged periods of decline”, which are defined as periods in which the variable declined in at least five of the seven years within the window.

The quality and completeness of the time series was erratic prior to 1970, therefore almost all the data used are for subsequent years. Although the time series are referred to as “data”, they are in fact model output. Changes to the virtual population analyses, which are in many cases updated annually, alter the estimates of numbers and stock biomass, although for earlier years such retrospective changes are small and do not affect the major trends.

An overview and comparison of the declines which have taken place in cod stocks

Total landings of North Atlantic cod (*Gadus morhua*) declined from over three million tons in 1970 to less than one million tons in 2000 due to changes in total stock biomass, for which the term “collapse” has frequently been used (Harris, 1998). The downward trend has been particularly marked in the NW Atlantic, where fisheries for cod on most of the Canadian shelf have been stopped or severely restricted since the early 1990s, with the aim of allowing the stocks to recover. There are as yet few signs of recovery in most Canadian stocks. The declines which have occurred in the NE Atlantic stocks, while serious, have not been as extreme as those in the NW Atlantic and cod fisheries have continued, with restrictions on total catch and some seasonal and area closures.

Trends in total biomass and mean weight-at-age since 1970 are shown in Figure 1. The first and last years of the "prolonged periods of decline" in total biomass and weight-at-age, which were identified using the moving-window time-series analysis, are given in Table 2 and the periods of decline in biomass also marked in Figure 1 by a sequence of open boxes along the x-axis.

The six cod stocks in Canadian waters all experienced a prolonged period of decline which began in the mid 1980s and ended in the mid 1990s. The decline in biomass in these six stocks was in every case preceded by a decline in the mean weight-at-age. The lag between the decline in biomass and the decline in weight-at-age was five years for four of the six stocks, two years for the S. Grand Bank stock and eight years for the S. Gulf of St Lawrence. The greatest decline in biomass took place in the S Grand Bank stock, where the total biomass in 1995 was 3% of the 1984 level. The smallest decline was in the S Newfoundland stock, which fell to 26% between 1985 and 1993. The decline in weight-at-age was in every case much smaller than the decline in biomass (from 34 to 80% of the original level).

The Canadian cod stocks share other common patterns of change in total biomass and weight-at-age. Both declined until about 1975, followed by a substantial increase to the early or mid 1980s. Weight-at-age increased in all Canadian stocks after 1995, but total biomass only increased in some stocks. The depth-averaged 5 year mean of temperature at Stn 27 on the Newfoundland shelf is shown in Figure 1 and shares some of the trends described for weight-at-age and total biomass. The southernmost stock in the NW Atlantic is the shared stock on Georges Bank. It underwent a prolonged period of decline in total biomass 1988–1995, but not in weight-at-age.

The offshore cod stock at Greenland is included in Tables 1 and 2, but lacks a complete, consistent time series since 1992 because the biomass is too small to assess. This stock had a prolonged period of decline 1966–1975 (to 5% of its starting level), which was preceded by a decline in weight-at-age (lagged by three years).

With the exception of the Celtic Sea, NE Atlantic cod stocks also declined after 1970, but the declines do not share a common pattern and are much smaller than those among the Canadian stocks. In the NE Atlantic there have also been a number of periods of rapid increase in total biomass. For example, the stock at Faroe declined to 19% over the period 1984–1991, but increased quickly to the 1984 level by 1996. On both sides of the N Atlantic, changes in mean weight-at-age are smaller in the warmer water stocks (Georges Bank, North Sea, Irish Sea and Celtic Sea) and there are no prolonged periods of decline in weight-at-age in any of these areas, or in the Baltic.

Evaluate the relative roles of fishing and climate in causing declines in abundance

There is considerable interest in establishing the causes of the declines which have taken place, in order to learn how to avoid such changes in future, to provide appropriate advice for ongoing management of stocks on which fishing continues and to make forecasts of the likelihood and timescale of stock recovery (Rice *et al.*, 2003; Shelton *et al.* 2006). All North Atlantic cod stocks have declined in total biomass since 1970, with the exception of the Celtic Sea. Overfishing is a major cause of decline in every case, but probably not the only cause.

A period of prolonged decline in weight-at-age began between 1978 and 1982 in all Canadian cod stocks (Table 2) and was probably due to an adverse change in the productivity of the stocks (Dutil *et al.*, 1999; Drinkwater, 2002). This must have had an immediate, proportional effect on biomass, but the effect is not detectable either because it was too small and/or because it was obscured by other changes (e.g. in stock numbers). The decline in biomass in these six stocks began two to eight years later and was much greater than proportional to the weight-at-age change.

Evaluate the causes of observed changes in rates of survival, growth and maturity, including a tropho-dynamic perspective

Could a change in weight-at-age cause a lagged decline in stock biomass? Two explanations and proposals for further modelling can be put forward, in fulfillment of the third aim of the paper. First, as growth changes, the allocation of energy to routine metabolism, somatic growth and reproduction changes (Nisbet *et al*., 2000), resulting in non-linear changes in the reproductive output, by altering age and size at maturity, specific fecundity and egg viability. Dynamic energy budget models would be suitable for exploring this process (Nisbet *et al*., 2000). Second, when weight-at-age changes, the effect of fishing on the stock is affected for a number of reasons. For example a total allowable catch (TAC) intended to harvest a defined proportion of the stock will only do so if the weight-at-age has been correctly predicted. Unanticipated decline in weight-at-age will cause higher than intended fishing mortality (more, smaller fish are caught). Furthermore fishermen are known to dump poor condition fish (high-grading), resulting in additional mortality (Kulka, 1997). Even before the underlying processes are revealed, it seems worthwhile to monitor persistent changes in mean weight-at-age, since a decline may provide early information of increased risk of stock decline.

All stocks have experienced periods of increasing total biomass, which are unlikely to have been caused by fishing and are generally attributed to one or more years of good recruitment. However in many cases (Figure 1) the stock increases coincided with increasing weight-at-age, suggesting that here too changes in individual growth and productivity played a role.

Changes in mean weight-at-age are generally attributed to changes in growth rate due to three main types of cause (i) “environmental” factors, the principal one being ambient temperature (ii) food availability (including density dependent effects) and (iii) selective effects of fishing (Krohn *et al*., 1997; Swain *et al*., 2003), but it can be difficult to disentangle these, because their effects can be direct or indirect and they interact with each other. For example, temperature has a direct effect on growth rate and also an indirect effect by altering the production of food organisms (ICES, 2002). Another reason why it is difficult to assign causes with confidence is the poor quality of field information on the contributing factors; for want of more precise, directly observed information, various proxies are used. Interannual changes in temperature may be represented by mean bottom temperature at a fixed station or by a value for the area occupied by cod during an annual fishing survey (i.e. ambient temperature is unknown); population biomass is used to represent density dependent effects (i.e. intensity of competition for food is unknown) and selective effects of fishing are inferred from sizes backcalculated from otolith increments (i.e. actual selection by fishing activity is unknown) (Sinclair *et al*., 2002).

Observed changes in weight-at-age have been attributed to all of the above causes and to combinations of them in different stocks. The depth averaged temperature at Stn 27 on the Newfoundland shelf (Figure 1) is an indicator of major changes in the thermal environment of the Canadian shelf, with widespread consequences for the ecosystems (Frank *et al*., 2005). The *prima facie* evidence of patterns of change in weight-at-age and total biomass, which are similar to this temperature pattern, point to a causal connection. Temperature is known to affect growth of cod and evidence from experiments and the field shows that the effect of temperature change is progressively greater at low temperatures (Bjornsson and Steinarsson, 2002; Brander, 2003; Folkvord, 2005). This may explain why the warm-water stocks (Georges Bank, North Sea, Irish Sea and Celtic Sea) show less variability in weight-at-age than the cold-water stocks. More detailed studies of the growth changes in individual Canadian cod stocks support the existence of a temperature effect, but also effects of prey availability

(Krohn *et al*., 1997), density dependence and a common pattern of residuals, which may be due to size-selective mortality (Swain *et al*., 2003). Other published work (Dutil *et al*., 1999; Rätz and Lloret, 2003) showed that decline in biomass was also accompanied by decline in fish condition and the authors considered the implications for productivity and management.

Unlike the NW Atlantic, where the oceanographic and biological environment of the Canadian shelf is dominated by changes in the Labrador Slope Current, the NE Atlantic stocks do not show common patterns of change in weight-at-age. A second major difference between the NE and NW Atlantic cod stocks is that the former all occupy areas with mean temperatures above 4°C, whereas the latter are all below 4°C, with the exception of Georges Bank. For some NE Atlantic stocks there is evidence that temperature causes changes in weight-at-age (Ottersen and Loeng, 2000; Brander, 2000), but it is difficult to distinguish direct temperature effects from the associated effects on production or dynamics of forage species, such as capelin (Michalsen *et al*., 1998). Interannual variability in capelin abundance seems to play a major role in changes in weight-at-age in the Arcto-Norwegian and Icelandic cod stocks and is important in the NW Atlantic too (Rose and O'Driscoll, 2002). Weight-at-age changes at Faroe, which are particulary closely coupled with changes in total biomass (see Figure 2) have been linked to changes in plankton production (Steingrund and Gaard, 2005). The Eastern Baltic is the only stock with a significant negative relationship between weight-at-age and stock abundance, however, this has been ascribed to the closely coupled predator-prey relationships between cod and its principal prey species, sprat and herring, rather than to density-dependence (Gislason, 1999).

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Table 1 Stock names and area codes. Areas occupied by each stock are taken from Myers *et al.* (2001). Mean bottom temperatures are from Brander (1995) and Myers *et al.* (2001). Age ranges used in estimating total biomass and mean weight-at-age. % of total biomass is the fraction of total biomass which comes from the age range used to estimate mean weight-at-age.

Cod Stock	NAFO or ICES code	Area (km^2)	Temp. ^{o}C	Age range biomass	Age range weight	% of total biomass	Data sources and ICES assessment WG codes
S Labrador	2J3KL	253492	0	3-13	5-9	76	(Bishop *et al*. 1993); (Lilly *et al*. 2003); (Lilly and Murphy, 2004)
S. Grand Bank	3NO	121246	1.75	3-13	5-9	80	(Healey *et al*. 2003)
S. Newfoundland	3Ps	70510	2.5	3-13	4-8	68	(Brattey *et al*. 2003)
N Gulf	3Pn4RS	89041	1	3-13	5-9	85	(Fréchet *et al*. 2003)
S. Gulf	4TVn	118343	1.75	3-15	5-9	81	(Chouinard *et al*. 2003)
E. Scotian Shelf	4VsW	102428	3.75	1-15	4-8	80	(Mohn *et al*. 1998)
Georges Bank	5Z	102596	8	1-10	1-5	77	(Hunt and Hatt, 2002); (O'Brien *et al*. 2002)
Greenland offshore	NAFO1 ICES XIV		1.6	3-10	3-7		NWWG (ICES, 1996)
Arcto-Norwegian	I,II	592610	4	3+	4-8	79	AFWG (ICES, 2005b)
Iceland	Va	237031	5.8	3+	3-7	81	NWWG (ICES, 2005c)
Faroe	Vb1	36236	7.4	2+	2-6	85	NWWG (ICES, 2005c)
E. Baltic	IIId, 25-29	216833	5	2-7	3-7 [1]	95	WGBFAS (ICES, 2005c)
North Sea	IIIa,IV,VIId	539823	8.6	1-10	2-6	88	WGNSSK, (ICES, 2006a)
Irish Sea	VIIa	48263	10	1-6	1-5	97	WGNSDS (ICES 2006b)
Celtic Sea	VIIe-f	155358	11	1-6	1-5	96	WGSSDS (ICES 2006c)

Table 2 Year ranges are the first and last years of “periods of prolonged decline” identified using seven year moving-window time-series analysis. A “periods of prolonged decline” is defined as a period during which biomass or weight-at-age declined in at least five out of seven consecutive years. % decline in total biomass and mean weight-at-age is the value in the last year of the “period of prolonged decline” divided by the value in the first year as a %.

Cod Stock	**Total biomass**		**Mean weight**	
	Years	**% decline**	**Years**	**% decline**
S Labrador	1985-95	5%	1980-88	64%
S. Grand Bank	1984-95	3%	1982-94	72%
S. Newfoundland	1985-93	26%	1980-94	80%
N Gulf	1983-94	6%	1978-92	62%
S. Gulf	1986-93	20%	1978-88	34%
E. Scotian Shelf	1985-93	10%	1980-92	44%
Georges Bank	1988-95	27%	none	none
Greenland offshore	1966-75	5%	1963-69	63%

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[1] For the E Baltic the youngest age (3 yr old) is less than 1kg

Arcto-Norwegian	1993-2000	44%	1992-99	76%
Iceland	1987-94	49%	1977-83	76%
Faroe	1984-91	19%	1984-91	66%
E. Baltic	1983-92	20%	none	none
North Sea	1980-93	33%	none	none
Irish Sea	1987-96	38%	none	none
Celtic Sea	none	none	none	none

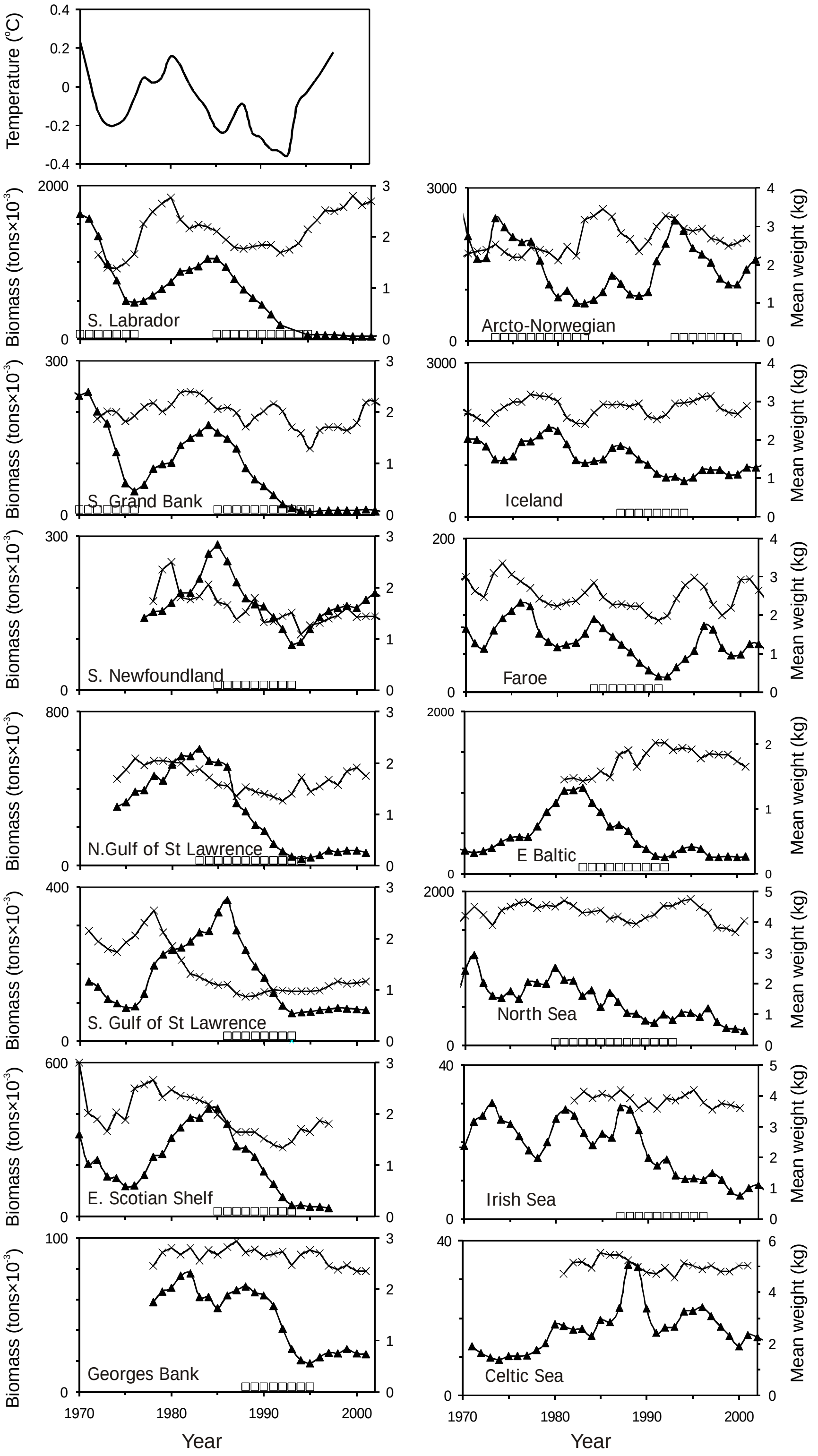

Figure 1 Trends in total biomass (black triangles represent tons × 10^{3} on left axes) and mean weight-at-age (crosses represent kg on right axes) for North Atlantic cod stocks. The open squares along the X axis represent periods of prolonged declinein total biomass. Data sources can be found in ICES (2005). The Canadian shelf stocks are the upper six on the left. The top panel on the left shows the depth averaged 5 year means of temperature at Stn 27 on the Newfoundland shelf (Colbourne and Anderson, 2003).

Extended abstract 2

The cod response to the Atlantic multidecadal oscillation

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Sea surface temperatures in the North Atlantic vary on a variety of time scales. Many recent studies have highlighted the approximate decadal oscillations that show strong association with the North Atlantic Oscillation (NAO). There is also a strong Atlantic Multidecadal Oscillation (AMO) with an approximate 80-year period (Sutton and Hodson, 2005). Following a relatively cool period in the early 1900s, there was rapid warming in the 1920s through the 1930s and warm conditions prevailed through to the 1960s when temperatures declined (Figure 1). The following cool period extended until 1990 when temperatures rose again. In response to the AMO there have been large ecosystem changes. Indeed, the early ecosystem changes, especially in commercial fish stocks, were noted in response to the warming in the 1920s and led to a Symposium on Climate Change in ICES in 1949 and would have been held much earlier if not for the World War II. They documented many of the ecosystem changes, which were followed by excellent reviews by Beverton and Lee (1965), Cushing and Dickson (1976) and Cushing (1982). This presentation deals mainly with the cod response during the warm period of the early 1900s and is derived from the recent review of the ecosystem changes by Drinkwater (2006).

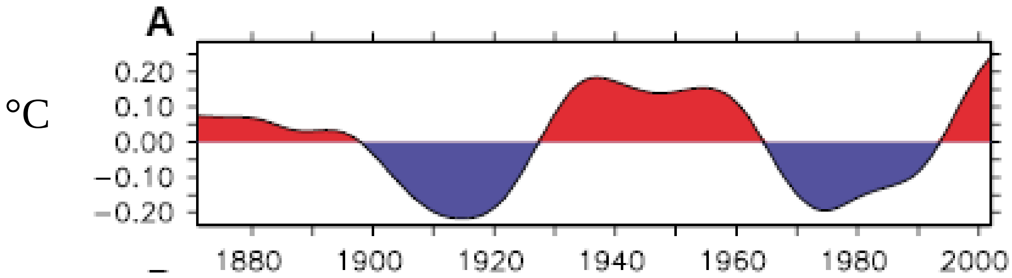

Figure 1. The AMO based on sea surface temperature anomalies in the North Atlantic Ocean (taken from Sutton and Hodson, 2005).

The warming period of 1920s-1960s existed throughout most the northern North Atlantic and includes both air and sea temperatures, the latter extending to subsurface depths down to 200 m and more. The area of warming covers most of the region inhabited by cod with the exception of the southeast coast of Canada and the northeastern United States. Highest temperatures were in the more northern areas. Through the 1940s and 1950s temperatures varied but generally remained relatively high. Thereafter, there was a rapid cooling trend with the exact timing of the decline varying spatially, the Northeast Atlantic declining slightly earlier than in the Northwest. The high temperatures recorded during the warm period from 1930–1960 match, and in some cases exceed, the present day warming. A marked reduction in sea-ice extent that accompanied the warming in the Barents Sea, around Iceland and off West Greenland. There were also increases transports in several warm ocean currents, e.g. (1) eastward flowing Irminger Current south of Greenland towards the Labrador Sea; (2) Atlantic water to the west and north of Iceland; (3) the branch of the North Atlantic Current to the west of Svalbard, known as the West Spitzbergen Current, and the inflow of Atlantic waters to the Barents Sea.

The most well documented biological change that occurred during the warm event was the increased abundance of Atlantic cod off West Greenland. From the late 1910s to the early 1930s they not only increased in numbers but also spread gradually northward from near the southern tip of Greenland to Upernavik, a distance of over 1200 km (Jensen, 1939). The increased abundance led to the development of a cod fishery, which quickly replaced sealing as the main industry in West Greenland. The cod fishery yielded moderate landings through the 1930s (< 10^5 mt), declined during the war years but rose dramatically through the 1950s reaching a peak at close to 5 x 10^5 t in the early 1960s before declining rapidly later that decade (Figure 2) during a period of decreasing air and ocean temperatures. Cod catches have remained relatively low since the 1970s. The cod off West Greenland originated from Iceland due to a combination of increased transport of larvae from Iceland and better survival of larvae once they reached West Greenland waters. Zooplankton samples (1950–1985) show abundance, dominated by *Calanus finmarchicus*, was much greater during the warmer 1950s and very early 1960s compared to remaining relatively cool years (Pedersen and Rice, 2002). These authors found that approximately 25% of the interannual variability in cod larval abundance could be accounted for by abundance indices of zooplankton.

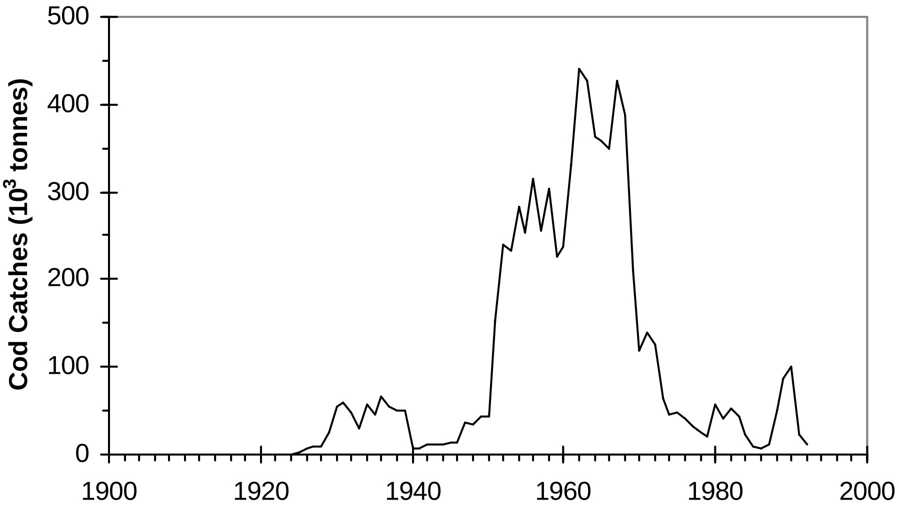

Figure 2. The annual catches of cod off West Greenland.

On the other side of the Labrador Sea, Tåning (1953) suggested that cod off Newfoundland expanded northward to northern Labrador, but he did not discuss the evidence for such a claim. However, catches of cod off Labrador and northern Newfoundland showed no large changes during the warm period compared to the early 1900s.

During the warming period of the 1920s cod catches in Icelandic waters rose rapidly peaking in the early 1930s at almost 6 x 10^5 t. While increased fishing effort contributed to these record catches, there was very high recruitment in the 1920s, with the highest recruitment on record being in the early 1920s (Schopka, 1994). Prior to the 1920s warming, cod spawned almost exclusively off the south coast of Iceland but as waters warmed, cod spawning spread northward until there were major spawning locations completely surrounding Iceland. Capelin, the major prey of adult cod, shifted their spawning from the south to the north coast, becoming scarce on the south coast that in turn resulted in a decrease in the condition of cod in the south, while those cod residing on the north coast were in good condition. The increased influx of Atlantic waters to the north of Iceland is believed to have lead to an increase in primary production off northern Iceland due to reduced stratification and higher nutrient concentrations, based on latter studies (Thorardottir, 1984; Gudmundsson, 1998). Zooplankton abundance is also significantly higher in warm years (i.e. more Atlantic waters) than in cold years (Astthorsson and Vilhjálmsson, 2002). Since *C. finmarchicus* constitutes 60–80% of the zooplankton biomass in spring, interannual variations mainly reflect variations in this species (Astthorsson and Vilhjálmsson, 2002). This increased production is believed to have contributed to the higher cod abundance during the warm period.

In the Barents Sea, during the 1920s and 1930s cod began appearing in high abundance and on Bear Island Bank a cod fishery was re-established there after an absence of almost 40 years (Blacker, 1957). Cod also spread northward off West Svalbard with sufficient abundance to support a fishery (Beverton and Lee, 1965) and eastward reaching Novaya Zemlya by 1929-1930 (Cushing, 1982). At this time there was a distributional shift in spawning with proportionately more cod spawning in the northern regions of Norway (Lofoten and Finnmark) compared to southern Norway at Møre (Sundby and Nakken, 2004). The stock size of Arcto-Norwegian cod peaked in the 1930s and 1940s (Hylen, 2002). Catch per unit effort (CPUE) was significantly higher in the period 1925–1960 than in the periods before or since and coincided with high recruitment (Godø, 2003). High recruitment was believed to be, in large part, a result of greater food availability (Sætersdal and Loeng, 1987; Ottersen and Loeng, 2000). The mean weight of the cod in Lofoten rose rapidly in the 1920s into the early 1930s and remained high before starting a general decline in the 1960s. The increase in weight between the pre-1920s period and 1930s–1960s was over 50%.

In summary, the climate changes that occurred during the warm period of the 1920s to the 1960s lead to significant ecosystem changes, including dramatic impacts to numerous cod stocks. Cod abundance increased through the northern North Atlantic especially in the Barents Sea, Icelandic waters and off West Greenland driven by a combination of higher recruitment and higher growth. Stocks also shift their distribution northward, in the case of West Greenland over 1200 km and off West Spitzbergen 500 km. Spawning shifted northward and in some areas, such as West Greenland and Iceland, new spawning sites were established farther north than previously observed. The changes in fish populations had significant economic impacts, especially in West Greenland where there was a shift from a seal-dominated economy to one dependent upon cod. Where warm Atlantic waters replaced the cold Arctic waters or became relatively more important, primary and secondary production, especially *Calanus finmarchicus*, appears to have increased and this is consistent with a bottom-up driven increase in cod production.

As temperatures declined in the northern North Atlantic during the 1960s, ecological conditions often returned to their previous state. Cod off West Greenland collapsed with economic hardships but were replaced by shrimp. By the time of the change in the environmental conditions in the 1960s, expanding fisheries due to more extensive use of trawlers, the development of large long-distance foreign fishing fleets, and the general increase in the number of fishermen after the last world war, lead to significant impacts on fish populations. Thus, there has been much debate as to whether the observed decline in several fish species, such as cod in the 1960s, was mostly due to fishing or to climate. It is clear that both played a significant role.

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Extended abstract 3

Notes on similarities and differences among cod populations of the North Atlantic Ocean

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Time series of SSB, R, and F were examined for five cod stocks: southern Grand Bank (3NO), Iceland-Greenland (ICEG), North Sea (NSEA), Faeroe Plateau (FARP), and Northeast Arctic (NEA). Comparisons were facilitated by normalizing the data in standard deviation units.

There was a general downward trend in SSB. This downward trend occurred in the presence of increased fishing mortality. Fishing mortality during the latter part of the time series often exceeded 1.0. The SSB for the NEA stock was negatively correlated with the SSB of the other stocks. The SSB for the NSEA stock was positively correlated with the 3NO, ICEG, and the FARP stock.

While the decreases in stock were coupled with increased fishing mortality over the c. fifty year period, decadal scale variation reflected a complex interaction between fishing mortality and environmental variability.

Not all stocks were coupled with fishing mortality (Figure 1). A linear relationship between standardized SSB and standardized fishing mortality is a measure of production. The expected negative relation was obtained for three of the stocks. However, the slope of the line was equivalent to zero for the FARP and 3NO stocks, indicating that fishing mortality did not affect the abundance of these stocks.

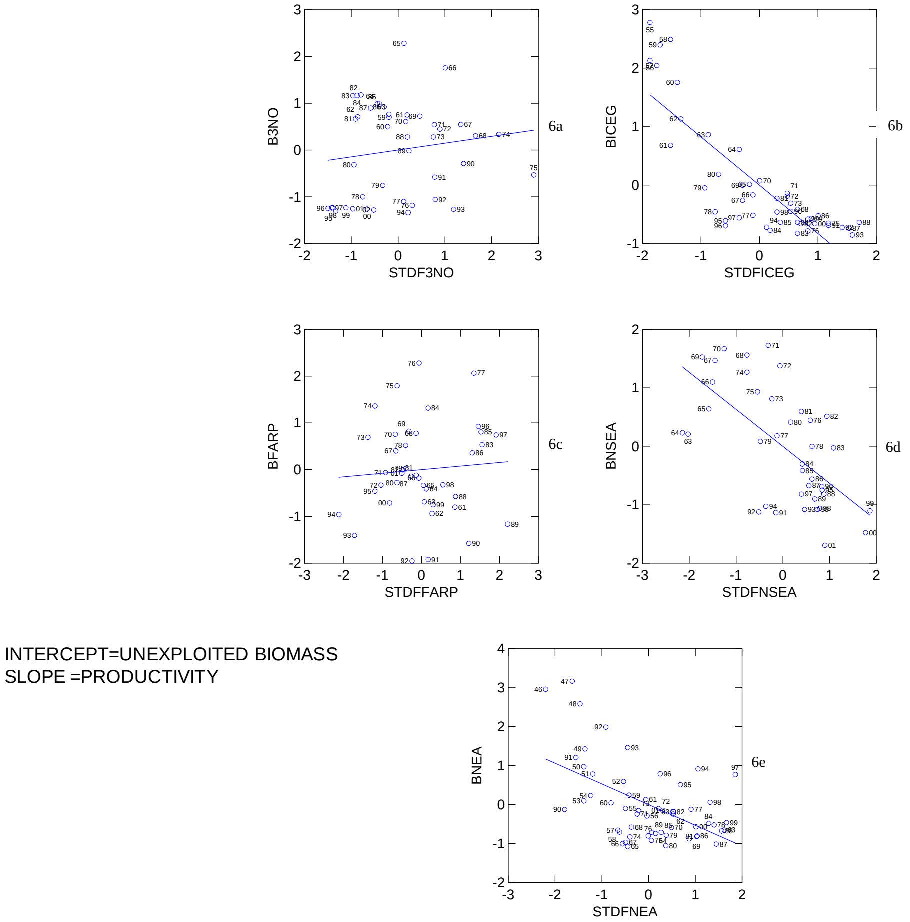
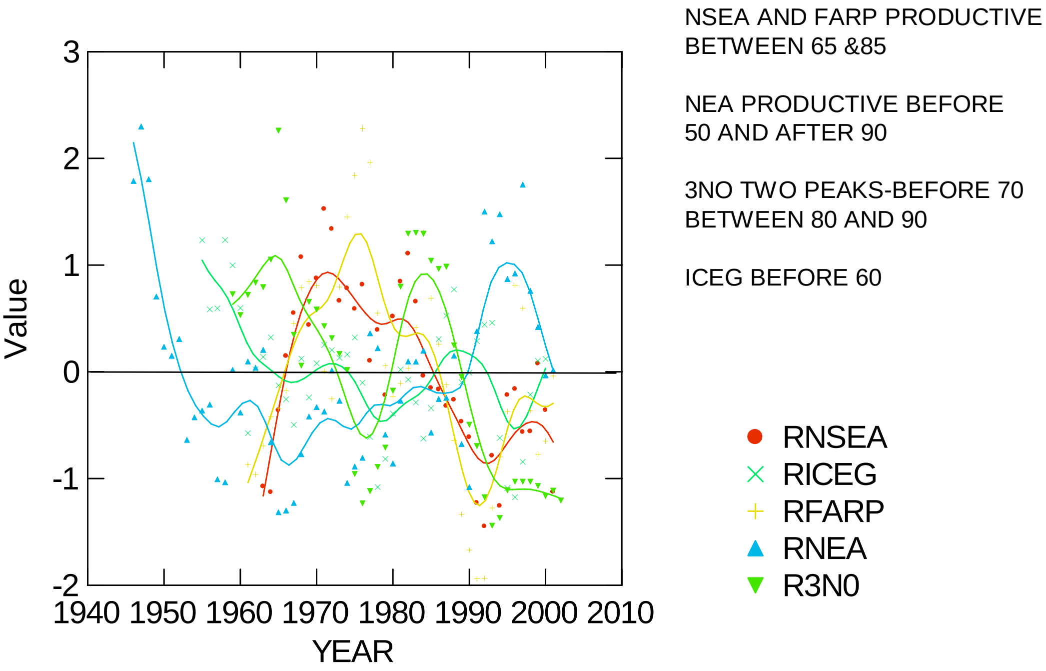


Figure 1. Apparent production of the five stocks suggested by a linear fit to the data. The intercept can be thought of as a measure of unexploited biomass, and the slope can be thought of as a measure of productivity.

The residuals from the linear fit can be interpreted as environmental variation. These residuals are plotted in Figure 2, which shows that there is temporal coherence among the residuals. These indicate productive and unproductive periods. The strong correlation between the FARP and NSEA is interesting in the light of the presentation by Sundby *et al.*

(Annex 3, Extended Abstract 10), indicating that the flux of zooplankton into FARP and NSEA have a common origin.



NSEA AND FARP PRODUCTIVE BETWEEN 65 &85

NEA PRODUCTIVE BEFORE 50 AND AFTER 90

3NO TWO PEAKS-BEFORE 70 BETWEEN 80 AND 90

ICEG BEFORE 60

Figure 2. Residuals of biomass data from linear fit of biomass to fishing mortality as displayed in Figure 3.

The dynamical changes in SSB and F reflect fishery-independent mini-collapses. This is shown in Figure 3. The events labeled E reflect a decrease of the stock after it reaches a maximum. The downturn occurs at relatively low fishing mortality. The increase in fishing mortality occurs after the decrease in stock, not before. In other words, the cod stock reaches a carrying capacity at low fishing mortality. When the carrying capacity decreases, fishing mortality increases. It is significant that fishing mortality increases *after* the stock declines, not before.

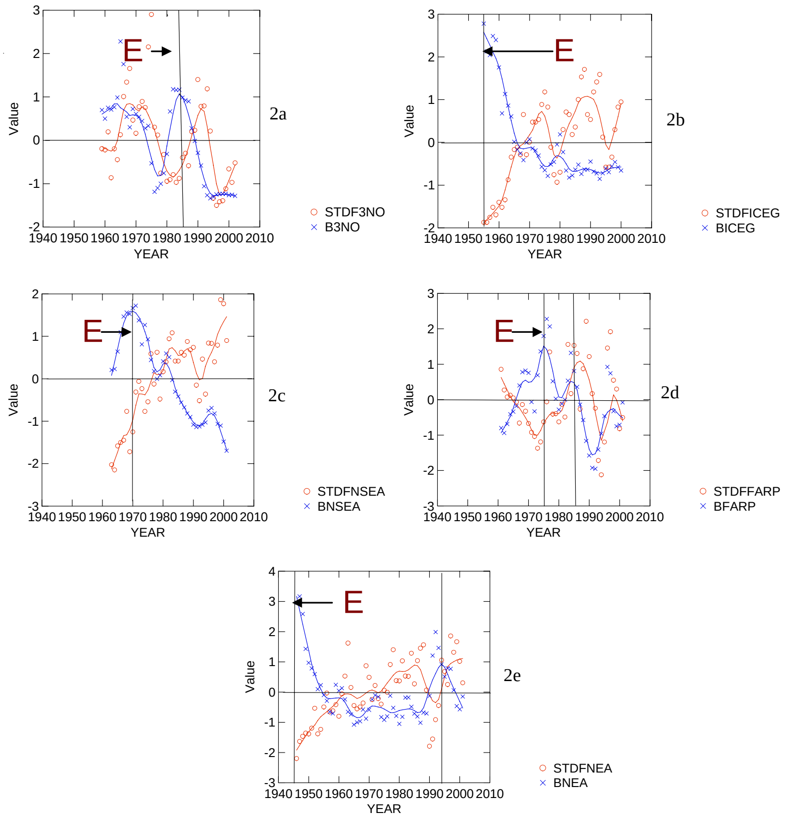


Figure 3. Time series of STDF and B showing decoupling events for each stock. The vertical line represents a peak abundance, and the horizontal line represents "average" fishing mortality and abundance. Note that there are both decoupled events and coupled events. The coupled events are where the interactions occur in a normal way (e.g., 1985, FARP and 1995, NEA).

The SR relationships generally reflect both depensation and compensation (Figure 4).

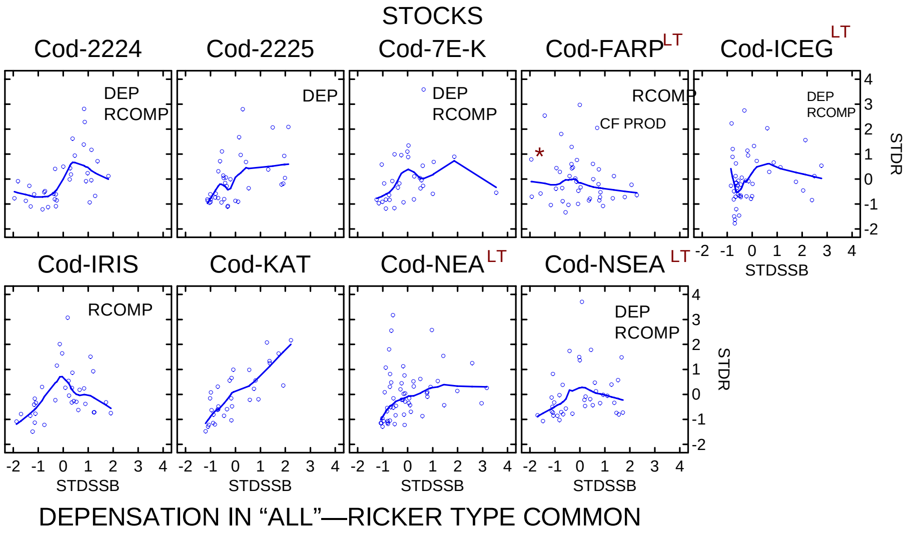


Figure 4. Relation between normalized recruitment (STDR) and spawning stock biomass for several cod populations. A concave lower left-hand limb reflects depensation, while a convex upper right-hand limb reflects Ricker-type compensation. Most stocks indicate depensation (DEP) while only some stocks indicate Ricker compensations (RCOMP).

It is interesting to observe that the stocks not only generally exhibit depensation and Ricker-like compensation, they also reflect that large recruitments can occur at low stock sizes (see particularly NEA and ICEG). The idealized setting suggests that recruitment is controlled by depensatory and compensatory mechanisms. However, the residuals are driven by the environment, and it appears for some stocks that the coupling between the deterministic model and the data is least effective when the stock is at a relatively low level.

Extended abstract 4

A generalized stock-recruitment relationship for the Northeast Atlantic cod stocks

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Standard stock assessment procedures include plots of recruitment (R) versus spawning stock biomass (SSB) to guide the setting of reference points for management. However, the functions used for different stocks may vary and the parameter estimates have wide confidence limits, because time series are relatively short, variation in R is high and the range over which SSB has varied may be restricted. Thus, the available S/R plots may overemphasize differences among stocks. As an alternative approach, one could assume that all stocks are subject to a common S/R relationship and that all observations are expressions of that relationship, even though the parameterization may vary. The goal of this contribution is to plot all S/R observations for 9 Northeast Atlantic cod stocks (North Sea, West of Scotland, Irish Sea, Kattegat, Baltic-South, Baltic-North, Faroe Plateau, Iceland and Arcto-Norwegian) and to determine their relative position in recent years.

The underlying assumption made was that the S/R relationship is characterized by a dome-shaped curve. As a first step, all R and SSB observations were standardized by division by the mean and a 3rd-order polynomial (forced through zero) was fitted to each individual stock (Figure 1). Only for the Kattegat stock no dome could be defined. To be able to include these estimates, a common dome was estimated for the combined Kattegat-Baltic South data set. Clearly, the average conditions relative to the dome have varied considerably among stocks. Next all observations by stock were standardized relative to their dome by dividing all R and SSB observations (by stock) by the R/SSB pair characterizing the highest point on the dome. This allows all observations to be included in a common dome-shaped stock recruitment relationship for Northeast Atlantic cod (Figure 2).

The figure also shows the average R/SSB pairs during the most recent 5 years. While the SSB for the Faroe Plateau and Arcto-Norwegian cod appears to be beyond the dome and in good shape, the recent situation for all other stocks indicates that SSB and R have been considerably reduced below the dome. This suggests that the recruitment dynamics of these stocks are largely controlled by depensatory effects, and corresponding imminent dangers of further decline under continued fishing.

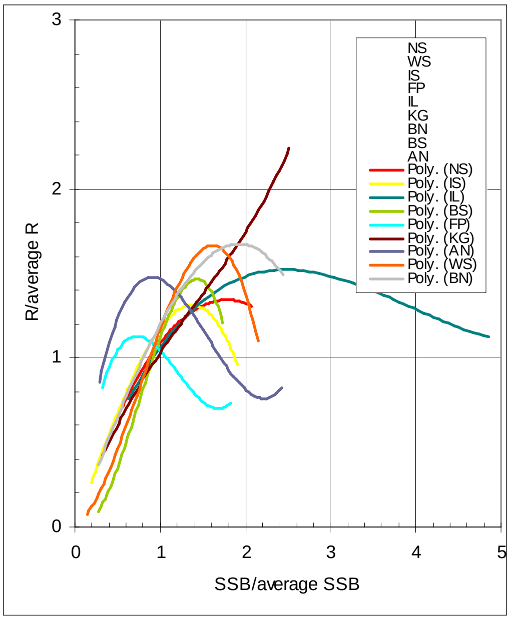
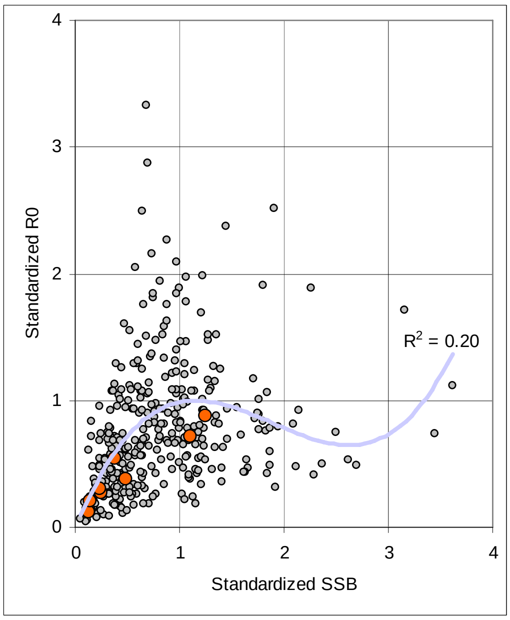


Figure 1. Fitted 3rd order polynomials (forced through the origin) to the stock recruitment observations for individual stocks (standardized by division by the mean). NS: North Sea; WS: West of Scotland; IS: Irish Sea; FP: Faroe Plateau; IL: Iceland; AN: Arcto-Norwegian; KG: Kattegat; BS: Baltic South; BN: Baltic North.



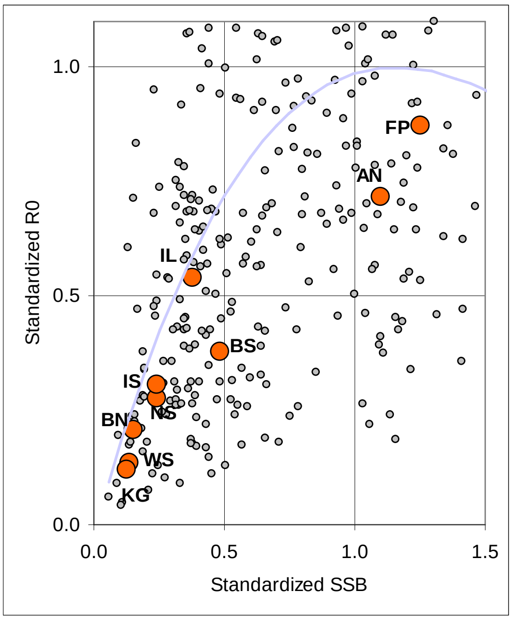


Figure 2. Standardized stock recruitment plot for 9 Northeast Atlantic cod stocks with fitted 3rd order polynomial forced through the origin. Lower panel: detail allowing the average R and SSB observations during the most recent 5 years.

Extended abstract 5

Contrasting recovery rates of southern Gulf of St. Lawrence cod between the 1970s and 1990s: the roles of fishing, climate and ecosystem change.

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The southern Gulf of St. Lawrence cod stock declined to low levels in the early nineties because of high exploitation rates. Despite the closure of the fishery for several years and limited catches recently, the stock has not recovered (Chouinard *et al.*, 2005) (Figure 1). The stock experienced a similar decline in the mid-1970s but rebounded rapidly without a moratorium on the fishery. The main cause for the lack of recovery in the recent period is the reduced productivity of the stock (Rice *et al.*, 2003; Chouinard *et al.*, 2003). The presentation summarized the findings of analyses (see references) of the roles of fishing, climate and ecosystem change on the components of production (growth, recruitment, natural and fishing mortality) that explain the reduced productivity.

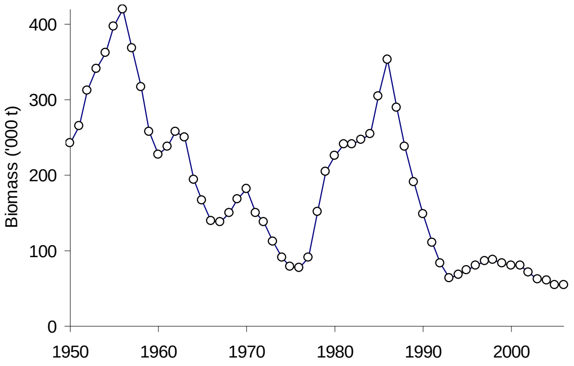


Figure 1. Spawning stock biomass ('000 t) for southern Gulf of St. Lawrence cod.

Growth rates in the recent period are much lower than those of the 1970s (Figure 2). While causes for the decline in growth appear to be linked in order of importance to size-selectivity of the fishery, density and a small effect of temperature (Sinclair *et al.*, 2002a, 2002b; Swain *et al.*, 2003), a significant portion of the explained variation could not be attributed to a single variable((Figure 3). Despite a closure and low catches in the fishery, reduced density and near-average temperature conditions recently, size-at-age has not recovered. This may imply a fishery-induced evolutionary change in this cod population.

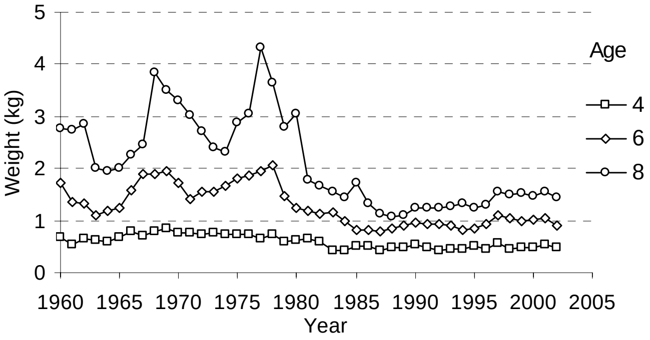
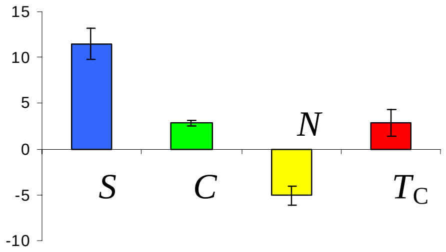


Figure 2. Weight at age 4, 6 and 8 for cod in the southern Gulf of St. Lawrence in the period 1960–2002.

a)



b)

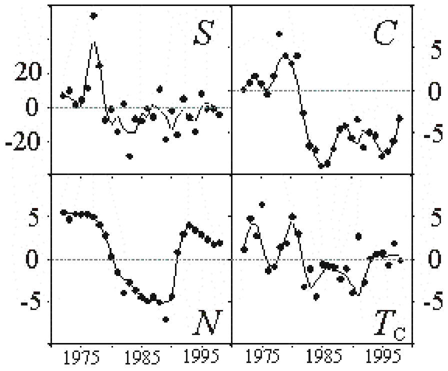


Figure 3: Parameter estimates of model including direct size selection (S), cumulative size selection (C), population density (N) and occupied temperature on mean length for cod of ages 5-11 (a) and effect on the annual mean predicted L∞ (b) (adapted from Sinclair *et al.*, 2002a)

Ecosystem and environmental factors potentially affecting the recruitment rate of southern Gulf cod have been examined (Swain and Chouinard, 2000; Swain and Sinclair, 2000; Swain *et al.*, 2000). A negative relationship between pelagic fish (herring and mackerel) biomass and the number of cod recruits produced per unit of spawning biomass has been shown for this population (Figure 4). The effect is thought to be the result of predation by pelagics on cod eggs and larvae. There also appears to be a small negative effect of warm temperatures in the spring and early summer. No relationship is evident between recruitment rate and spawning stock characteristics (e.g., age diversity, proportion of old spawners, spawner size). Pelagic fish stocks in the southern Gulf were depressed in the mid-1970s and the low cod biomass produced an exceptionally high number of recruits. However, in the 1990s, while cod spawning biomass was at similar low level to that observed in the 1970s, pelagics were highly abundant and the recruitment rate has only been about average.

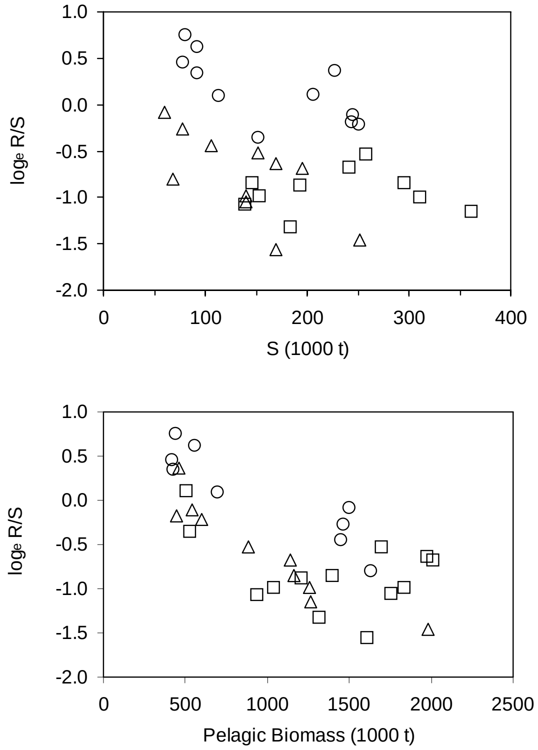


Figure 4. Relationships between cod recruitment rate and (A) cod spawning stock biomass S or (B) pelagic fish biomass in the southern Gulf of St. Lawrence. Different symbols are used for different levels of pelagic fish biomass (A) or cod spawning stock biomass (B) (low – circles; medium – squares; high – triangles). Data are for 1963–1994 and are estimated by SPA.

Analyses have indicated that natural mortality increased in the mid-1980s (Sinclair, 2001). The amount of biomass lost due to the increased natural mortality is estimated to be between 12 to 20 kt annually during the period 1994–2005 and cannot be attributed to unreported catches. There is no evidence of an increase in mortality due to diseases or toxins although it is noted that the parasite load for cod in this stock is considered high compared to other stocks. Condition index of cod did not decline in the 1980s. A correspondence between grey seal population abundance in the southern Gulf of St. Lawrence and natural mortality of adult cod was uncovered (Chouinard *et al.*, 2005) (Figure 5). While this correspondence is not consistent with seal diet information which suggest that predation is mostly on juveniles, seal diets are based primarily on the presence of hard parts in seals stomachs and this could be explained if seals frequently do not consume the heads of large cod.

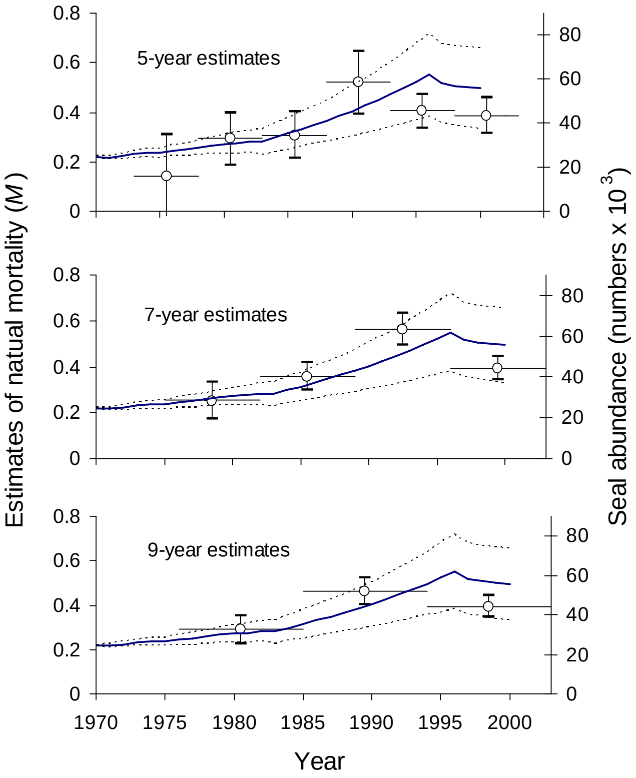


Figure 5. Estimated natural mortality for periods of 5 (top), 7 (middle) and 9 years (bottom) from the calibration of sequential population analysis and trends in grey seal population with confidence interval (solid lines). Error bars for estimates of *M* and confidence intervals for grey seal population estimates are +/- 2 SE.

Finally, while the limited fishery that has been conducted since the late 1990s is not the main factor preventing recovery (Figure 6), however, it is further delaying rebuilding given the poor productivity of the stock (Shelton *et al.*, 2006).

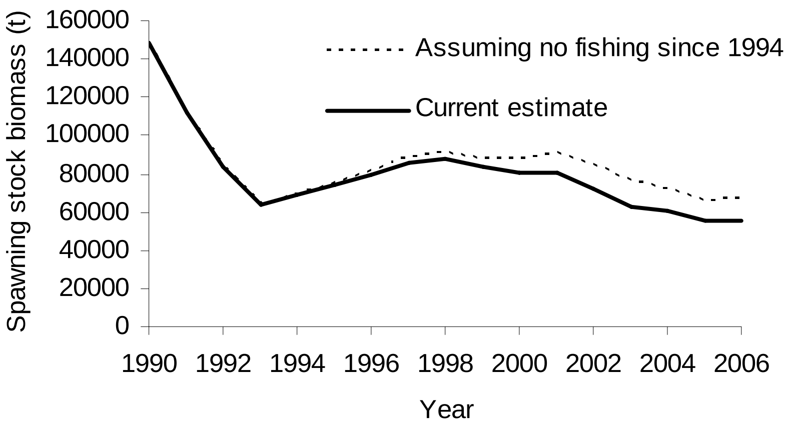


Figure 6. Current estimate of spawning stock biomass (solid) and estimated assuming (dashed) that no fishery had taken place since 1994.

Comparison of these factors in the mid-1970s and recently indicates that conditions for a recovery were exceptionally favorable in the earlier period. The lack of recovery of southern Gulf cod recently is primarily caused by changes in productivity of the stock particularly growth and natural mortality. Given the less favorable conditions, a rapid recovery could not be expected after the moratorium in 1993 and rebuilding of the stock will likely be protracted unless there are significant changes in the parameters affecting productivity.

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Extended abstract 6

The decline and non-recovery of northern (2J3KL) cod, with brief remarks on cod in 3Ps

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Introduction

The northern (2J3KL) cod stock off southern Labrador and eastern Newfoundland was closed to directed commercial fishing on 2 July 1992. Within two years, moratoria were imposed on all other cod stocks in Atlantic Canada from the eastern Scotian Shelf northward. The stocks on the eastern Scotian Shelf (4VsW), the southern Grand Bank (3NO) and the offshore of 2J3KL have remained closed. The inshore populations of northern cod were reopened for 5 years but then closed. The stocks in the northern (3Pn4RS) and southern (4TVn) Gulf of St. Lawrence were reopened, reclosed, and reopened. Among the stocks that were reopened, only the stock off southern Newfoundland (3Ps) has remained continuously open.

These differences in management reflect, to some extent, differences in stock dynamics, or more correctly, in the understanding or perception of stock dynamics. (For some stocks, there are strong disagreements between the status as reported by scientific assessments and the status as understood by fish harvesters based on their own experience and observations.) Some stocks, notably offshore northern cod and eastern Scotian Shelf cod, continued to decline after imposition of the moratoria and have shown no sustained signs of recovery. Other stocks, notably those in the northern and southern Gulf of St. Lawrence, did not decline to the same extent as the two just described but have remained at low levels of productivity. The only stock that rebounded strongly was that off southern Newfoundland. However, even that stock has experienced low recruitment during most years of the past decade, and this has contributed to a recent decline in biomass, which in turn has triggered a reduction in quota.

Thus, there are many similarities in the dynamics and management of cod populations of Atlantic Canada since about the mid-1980s (and even earlier), but there are also many differences, and while it is important to seek similarities and common causes, it is also important to recognize and understand the differences. Note that large differences can occur over short distances. The rapid growth of the 3Ps stock following its closure contrasts dramatically with the continuance of decline followed by non-recovery in the adjacent 2J3KL stock to the northeast and the 4VsW stock across the Laurentian Channel to the southwest.

The one factor that most strongly links the cod populations of Atlantic Canada from the eastern Scotian Shelf northward is the cooling that occurred in the Labrador Sea and adjacent waters during the 1980s and early 1990s. In addition, most of the ecosystems within which these stocks are embedded have experienced large changes in biota, including decreases in abundance of most groundfish, increases in abundance of smaller species (shellfish off eastern Newfoundland and pelagic species on the eastern Scotian Shelf) and increases in the abundance of seals.

This overview briefly reports some observations regarding the decline and recovery (or non-recovery) of the cod stocks off Newfoundland and Labrador. There are no new analyses. The issues are so broad and the literature so large, that all aspects must be treated superficially and some perilously so. Emphasis is placed on the northern (2J3KL) cod, but there is some discussion of the stock off southern Newfoundland (3Ps).

This note will start with a short overview of the fishery and population dynamics of 2J3KL cod, followed by a brief discussion of changes in the physical environment. It will then attempt to address most of the workshop Terms of Reference. Much of the information is extracted from stock assessment reports and literature summaries (Lilly and Murphy, 2004; Lilly *et al.*, 2005; DFO, 2005a).

Fishery and population dynamics

Historically, many of the cod in the northern (2J3KL) cod stock migrated from overwintering areas offshore to feeding areas inshore, where they were exploited by the traditional inshore fixed-gear fishery. Reported landings increased dramatically in the late 1950s and 1960s as non-Canadian fleets exploited the dense offshore overwintering aggregations (Figure 1). Landings declined rapidly during the 1970s. Canada declared a 200 nautical mile zone of Extended Fishery Jurisdiction in 1977. Landings rose again during the 1980s as the inshore fishery experienced greater success and Canadian trawlers replaced the non-Canadian trawlers on the offshore grounds. However, landings declined rapidly in the early 1990s and a moratorium on directed commercial fishing was declared in July 1992.

Research surveys showed that the stock continued to decline for 2 years after the start of the moratorium (Figure 2). By the mid-1990s, it was apparent that the offshore populations were barely detectable. At the same time, it was recognized that there were aggregations of cod in the inshore in Div. 3L and southern Div. 3K. These inshore populations appeared to be more productive during the 1990s than populations in the offshore. A small fishery directed at these inshore populations was introduced in 1998 but closed indefinitely in 2003 (Figure 1).

Prior to the collapse of the stock, mathematical reconstruction of the population based on the reported catches (sequential population analysis or SPA) was the main tool used to estimate the size of the stock as a whole and to provide a basis for projections. The models indicated that the 3+ biomass declined from about 3 000 000 t in the early 1960s to about 500 000 t in the late 1970s (Figure 3). The stock recovered partially to just over 1 000 000 t by the mid-1980s, but declined again during the late 1980s. The actual time course from the mid-1980s onward is somewhat uncertain, but the stock clearly reached an extremely low level by about 1994. The spawner stock biomass (SSB) collapsed from about 1 500 000 t in the early 1960s to about 125 000 t in the late 1970s, and then increased to 400–500 000 t through most of the 1980s (Figure 4). The SSB declined rapidly after 1988 or 1999. Patterns in recruitment and mortality are shown in Figures 5 and 6.

The use of SPA was discontinued in the early 1990s (for reasons, see Lilly *et al.*, 2003). From the late 1990s to the present, information on stock status has been provided for the offshore and inshore separately.

In the offshore, the major source of information has been the bottom-trawl surveys. These surveys have shown that the biomass has remained extremely low (Figure 2), recruitment has been low (Figure 7) and mortality has been extraordinarily high (Figure 8). Additional information has come from hydroacoustic studies in specific areas.

For the inshore, monitoring has been conducted since 1995 by limited test-fishing conducted by fish harvesters using commercial gears (sentinel surveys) and by hydroacoustic studies in one specific inlet (Rose, 2003). In 2003, SPA was reintroduced but applied to data collected in the inshore since the mid-1990s. In 2005, the area to which SPA was applied was further limited to a central portion of the inshore where resident populations were understood to reside. This model indicated that the 3+ biomass and spawner biomass increased to a peak in about 1997–1998, declined during the period of the fishery (1998–2002), and started to increase after reimposition of a closure (Figures 3 and 4). Trends in recruitment and fishing mortality are shown in Figure 5 and 6.

Environmental trends

The marine environment off Labrador and eastern Newfoundland has experienced considerable variability since the start of standardized measurements in the mid-1940s (Colbourne and Anderson, 2003; Colbourne *et al.*, 2005; Petrie *et al.*, 2005). A general warming phase reached its maximum by the mid-1960s. Beginning in the early 1970s there was a general downward trend in ocean temperatures, with particularly cold periods in the early 1970s, early to mid-1980s and early to mid-1990s (Figure 9). Ocean temperatures started to warm in 1995 and have generally been above normal for a decade, with some indices reaching near-record levels in recent years.

Attention has frequently (e.g. Drinkwater, 2002, 2005) been drawn to the conclusion by Petrie *et al.* (1992) that conditions at Station 27 (in the inner branch of the Labrador Current off St. John's) represent low-frequency temperature variability throughout the area from southern Labrador to the southern Grand Bank. While this is accepted, it must also be recognized that indices from different areas, seasons and portions of the water column must vary somewhat. This is immediately apparent in Figure 9. Note, in particular, that the annual depth-averaged temperature at Station 27 reflects annual variability in the temperature of the near-surface waters much more than does the CIL cross-sectional area, and in this respect 1991 stands out as a particularly cold year.

There have also been changes in ice cover, salinity, stratification and other aspects of the physical oceanography (Colbourne *et al*. 2005; Petrie *et al*. 2005).

ToR b. Evaluate the relative roles of fishing and climate in causing declines in abundance.

It has generally been assumed that the initial decline of the 2J3KL cod stock in the 1960s and 1970s was due entirely to overfishing, but there was so little fishery-independent information at the time that it would be difficult to test other hypotheses. There is considerable controversy regarding the cause(s) of the second collapse. Many studies (e.g. Hutchings and Myers, 1994; Hutchings, 1996; Myers *et al.*, 1996) have concluded that the collapse was caused entirely by fishing activity, which would include reported landings (Figure 1), unreported landings and discards.

There has, however, been much attention to the role of the physical environment. Several authors have pointed to various ways in which the decline in water temperature might have contributed to the collapse, either directly by reducing productivity (Mann and Drinkwater, 1994; Drinkwater, 2002, 2005; Parsons and Lear, 2001) or indirectly by affecting distribution (Rose *et al*. 2000). See Lilly (2001), Rice (2002) and Lilly and Murphy (2004) for additional details.

The relative importance of fishing and environment is difficult to determine. Certainly, fishing played a very large role. After the extension of fisheries jurisdiction, the intent was to fish conservatively so as to promote stock growth, but in retrospect it is clear that fishing mortality was consistently underestimated and stock size consistently overestimated during the 1980s (Sinclair *et al.*, 1991; Shelton, 2005). A major change in scientific perception of stock size occurred in 1988–1989 (Baird *et al.*, 1991; Bishop and Shelton, 1997). This change implied a large reduction in total allowable catch (TAC), but the reduction in TAC was only partially implemented because it was feared that the consequences for the industry would be too severe. Fishing mortality was allowed to escalate (Figure 6) and in the words of Shelton (1998) turned "what might have been a severe stock decline under a fixed fishing mortality rate into a collapse". Note that the actual extent to which fishing mortality increased remains uncertain (see ToR c).

It is helpful, when discussing the collapse of 2J3KL cod, to distinguish between events before 1989 and events after 1989. Athough it was recognized in 1988-1989 that the stock had been overestimated, assessments by DFO (Baird *et al.*, 1991; Bishop and Shelton, 1997) and an independent review committee (Harris, 1989, 1990) indicated that there was still a considerable quantity of cod in the sea in 1989. In 1989 the review panel wrote (Harris, 1990; p. 64):

"The rather stable level in the biomass since 1984 … is supported by the commercial catch index and the (research vessel) data. It also accords reasonably well with the trends in inshore catches during this same period. All this brings us to the view that the state of the stock measured by the biomass trends does not support a conclusion that anything drastic or threatening has occurred to the northern cod stock to date."

There then followed, during 1990–1994, a rapid disappearance of cod from research vessel surveys, both bottom-trawl surveys in the spring and autumn (Figure 2) and hydroacoustic studies in spring/summer off southern Labrador (Anderson and Rose, 2001) and eastern Newfoundland (Rose and Kulka, 1999). The rapid decline in bottom-trawl survey indices could not be accounted for by reported landings (Bishop and Shelton, 1997; Shelton and Lilly, 2000). Either the fish were not as abundant as indicated by the standard treatment of the survey data (see critique by Hutchings, 1996) or the fish were initially abundant and then rapidly disappeared. In the latter case, there are again two possibilities; these fish died of natural causes (e.g. predation, starvation) or they were caught and not reported. The latter possiblity would include large quantities of fish being discarded as juveniles (Myers *et al.*, 1997) and large quantities being caught and under-reported by non-Canadian fleets on the Nose of Grand Bank in Division 3L (Rose *et al.*, 2000).

The extent to which scientific assessment contributed to the collapse remains in debate. If stock size had not been overestimated through the 1980s, then TACs would presumably have been lower, the stock presumably would have grown more than it did, and the stock might have been less susceptible to adverse environmental conditions (assuming, of course, that the environment did play a role in the collapse). In addition, the change in scientific perception of stock status in 1988–1989 was so large and sudden that politicians were concerned about the socioeconomic costs of reducing the quota severely as implied by the revised estimate of stock size. Quotas were reduced, but not sufficiently to keep fishing mortality from escalating.

The big question, as noted above, is the extent to which fishing mortality escalated. If fishing was the sole cause of the disappearance of the fish, then fishing mortality must have been extraordinarily high (greater than an instantaneous rate of 2.0 per year). See discussion of natural mortality under ToR c.

ToR c. Evaluate the causes of observed changes in rates of survival, growth and maturity, including a tropho-dynamic perspective

Many changes in population vital rates (recruitment and mortality) and biological characteristics (length and weight at age, weight at length, age and size at maturity) have been documented for 2J3KL cod. Exploration of these properties is complicated by several factors.

1) There are geographical differences in the temporal trends of these properties and the physical and biological factors that might affect them.

2) There have been differences since at least the mid-1990s between populations in the offshore and populations in the inshore.

3) Assessment meetings have not accepted a sequential population analysis (SPA) for the stock as a whole since the early 1990s. This makes it impossible to use model output to compare population productivity in the stock as a whole before, during and after the final collapse, and to compare model output from 2J3KL cod with model output from other cod stocks for the period since the early 1990s.

Recruitment

Year-class strength, as estimated by SPA, peaked in the early 1960s and then declined to a low level by 1970–1971 (Figure 5). There followed three periods of moderately good recruitment. The last of these (the 1986 and 1987 year-classes) is of great interest. These year-classes seemed moderately strong at ages 2 and 3 (Figure 7) and were caught in large numbers in the inshore fishery in 3L during the early 1990s, but they seemed to disappear rapidly (Shelton and Lilly, 2000) and made only a very small contribution to SSB. Perception of the strength of these year-classes, especially the 1987 year-class, varies considerably depending on the data and models that are chosen (Figures 5 and 7). All year-classes since the early 1990s have been very weak.

There is expectation that recruitment in 2J3KL cod might be positively influenced by warm temperatures, because the stock is at the northern limit of the species' range in North America (Planque and Frédou, 1999), but there have been conflicting reports of whether such a relationship can be detected (deYoung and Rose, 1993; Hutchings and Myers, 1994; Taggart *et al.*, 1994; Planque and Frédou, 1999). Drinkwater (2005) found a positive relationship between recruitment and temperature data from a monitoring site (Station 27) off eastern Newfoundland. (Details of the recruitment series and temperature index used were not provided.)

A reported relationship between recruitment and salinity (Sutcliffe *et al.*, 1983) was subsequently supported (Myers *et al.*, 1993) and later rejected (Hutchings and Myers, 1994; Shelton and Atkinson, 1994) as data for additional years became available.

The very weak recruitment in the offshore of 2J3KL since the early 1990s (Figure 7) is an important component of the lack of recovery of offshore populations and the stock as a whole. This low recruitment to ages 2–3 may be due to a number of factors including the production of relatively few eggs and larvae, which in turn might be a consequence of the very small number and small individual size of spawners, and poor survival of eggs, larvae, pelagic juveniles or demersal juveniles.

Because there has been so little monitoring of any of the cod's early life history stages, there seem to be few prospects for exploring this further.

It has been observed that the abundance and composition of phytoplankton and zooplankton have changed between the 1980s and more recent years (Johns *et al.*, 2003), but the extent to which this might be affecting growth and survival of larval and pelagic juvenile cod is not known.

The information that bears most directly on this issue comes from pelagic net surveys conducted during 1994–1999 (Colbourne and Anderson 2003). It was found that the biomass of zooplankton and the abundance of pelagic cod on Grand Bank were very low in 1994, but that they increased as the waters warmed during the mid- to late 1990s. The abundance of pelagic juvenile cod did not increase until 2 years or so after the zooplankton started to increase. This is interpreted as evidence that the cold conditions of the early 1990s were inhibiting recruitment of cod, and that warm conditions were necessary but not sufficient for improved recruitment. Good feeding conditions were also necessary. An improvement in year-class strength in the late 1990s compared to the mid-1990s was also observed in the bottom-trawl surveys, but these year-classes were much weaker than the weakest year-classes of the 1980s (Figure 7).

It is important to note that the quick population growth of the stock in 3Ps and inshore populations in 3KL, following the cessation of fishing in 1993 and 1992 respectively, was based largely on year-classes that were already in the population at the time that fishing was stopped. In 3Ps, the 1989 and, to a lesser extent, the 1990 year-classes were important contributors. These year-classes appear to have been only moderately strong when young, but they were protected from directed fishing for four years (1993–1996), grew very well and were largely responsible for the increase in fish availability that lead to the reopening of directed fishing in 3Ps in 1997. In 3KL, sentinel surveys and other sampling revealed that the 1989 and particularly the 1990 and 1992 year-classes were relatively strong in the inshore by the mid-1990s, and both the sentinel data and the SPA indicate that growth of the inshore populations to a peak in 1997–1998 (Figure 3,4) was based largely on the 1990 and 1992 year-classes. The strength of these year-classes cannot be compared with earlier year-classes in the inshore. However, they do appear to have been stronger than any year-classes since. Note that the 1990 and 1992 year-classes were weak in the offshore of 2J3KL.

A general conclusion from these observations is that the cessation of directed fishing can have a positive benefit by protecting year-classes that are already in the population. This was clearly the situation in 3Ps and inshore 3KL. However, such a result does not always follow, as illustrated by events in the offshore of 2J3KL. The 1988 and 1989 year-classes, which were initially as strong as, or almost as strong as, the year-classes of the mid-1980s (Figure 7), continued to decline after the imposition of the moratorium and almost disappeared by 1994.

Natural mortality

The natural mortality rate assumed for all SPA modelling of the 2J3KL stock as a whole has been 0.2 per year. As noted above, it is difficult to account for all the cod that disappeared from the system without invoking either a considerable increase in non-reported fishing mortality or an increase in natural mortality. A similar controversy surrounds the American plaice stock off Labrador and northeastern Newfoundland (SA 2 + Div. 3K), which declined to a very low level through the 1980s and early 1990s, a period during which reported catches were low (Morgan *et al*., 2002). Most other species of demersal fish, including many of no commercial value, declined dramatically through the same period (Atkinson, 1994; Gomes *et al*., 1995). It has been stated that fishing was the cause of all these declines (Haedrich and Fischer, 1996; Haedrich and Barnes, 1997; Haedrich *et al*., 1997). However, the available data consist of indices of stock abundance and very rough estimates of removals by the fishery. Without information on catchability of the survey trawl, it is not possible to estimate the number of fish in the water each year, and with little or no information on discards and no information on incidental fishing mortality, it is not possible to determine the number of fish killed by the fishery. Under such circumstances, it remains somewhat a matter of faith to attribute the declines entirely to fishing and to reject the possibility of an increase in natural mortality.

Note as well that total mortality rate, as estimated from catch rate at age in the autumn bottom-trawl surveys (Figure 8), remained very high after directed fishing was stopped (Lilly *et al*., 2005). Has this high total mortality been caused by the activities of fleets directing for other species, or is it primarily natural? If it is natural, at what point did natural mortality increase? Did it increase only after the stock became greatly reduced in abundance, or did it increase during the early 1990s, or even before? In this context, it is important to note that the common assumption about natural mortality (M=0.2) has been changed for SPA modelling of some groundfish stocks in Atlantic Canada. For American plaice on Grand Bank (3LNO), the SPA model “that provided the best fit to the data included a natural mortality of 0.6 on all ages from 1989 to 1996 and 0.2 otherwise” (NAFO 1999). Such an approach was not adopted for 2J3KL cod (see Shelton and Lilly, 2000), but an increase in M was adopted for SPA modelling of cod in the northern Gulf of St. Lawrence, in the southern Gulf of St. Lawrence and on the eastern Scotian Shelf. For each of these cod stocks, M was increased from 0.2 to 0.4 starting in 1986. It must be recognized, of course, that these increases in M provide a way of accounting for various possibilities, including true natural mortality (such as deaths associated with adverse environmental conditions, predation and disease), deaths caused by the fishery but unrecorded and changes in catchability in fishery-independent indices.

The question of whether there was an increase in natural mortality in the late 1980s and early 1990s, and whether any such increase was related to environmental factors, is of great importance to understanding the dynamics of Atlantic cod and other demersal fish (Lilly, 2002; Rice, 2002). The possible influence of cold water is of considerable interest because of an apparent coincidence between the rapid disappearance of cod from research surveys (Figure 2) and the low temperature (Figure 9) and extensive ice cover of the early 1990s. While it seems unlikely that significant numbers of fish died as a direct consequence of exposure to cold water, there is still insufficient evidence to reject the possibility that the cold water and extensive ice cover led to a reduced duration of feeding opportunity, which itself led to poor body condition and death (Dutil and Lambert, 2000; Lilly, 2001).

The reason for the continuing high total mortality in the offshore (Figure 8) remains unclear. It could be that the fishing that has continued for other species is causing sufficient removals (landings and discards) and unseen mortality of cod to keep the cod populations from rebounding. However, recorded landings and discards appear very small relative to the survey estimates of biomass (Lilly and Murphy, 2004). It is also possible that natural mortality is very high. Such high natural mortality could be caused by inadequate quantity or availability of suitable prey (see ToR g) or by intensive predation (see ToR h).

There is evidence that natural mortality of adults was unusually high in the inshore during the late 1980s and early 1990s. An analysis of tag returns during the inshore fishery of 1998–2002 revealed that fish tagged in southern 3K disappeared much faster than could be accounted for by the catch and an assumed natural mortality of 0.2 per year (Lilly *et al*., 2003). The same phenomenon occurred in 3L, but to a lesser extent. When an inshore SPA was first attempted in 2003, the level of natural mortality applied was 0.5 (Lilly *et al*., 2003). Upon further consideration, the level was dropped to 0.4 for the SPA in 2005 (Lilly *et al*., 2005).

Growth and condition

The sampling of commercial landings has shown that mean weight-at-age increased during the late 1970s and early 1980s and then declined during the remainder of the 1980s and early 1990s (Lilly *et al*., 2005). Sampling of catches during autumn bottom-trawl surveys indicates that the extent of the decline varied with Division: there was a strong decline in 2J, a lesser decline in 3K and little or no decline in 3L (Figure 10). Size at age has been shown to decline with environmental temperature (Krohn *et al*., 1997; Shelton *et al*., 1999).

Size-at-age has improved since the early to mid-1990s, but remains below values observed in the late 1970s. Note that comparisons can be made only for young cod, because extremely few cod older than age 5 have been caught during the offshore surveys. The small sample sizes for even age 5 probably contribute importantly to the high among-year variability in point estimates since the mid-1990s. Note as well that commercial weights-at-age are available for years since the early 1990s, but these are not directly comparable to data obtained prior to 1992 because of substantial changes in the relative contributions of the various gear types and changes in the location and timing of catches from each gear (Lilly *et al*., 2005).

Changes in weight-at-age can result from changes in either length-at-age or weight at length (condition). Condition can be expressed in various formulations. Here it is presented as Fulton's index ($W/L^3 * 10^5$), where W is either the gutted weight of the fish or the liver weight in kg, and L is the length in cm. The trend in condition has differed among Divisions (Lilly *et al*., 2005). In 2J, both gutted condition and liver index declined in the early 1990s. During the second half of the 1990s, gutted condition returned to approximately normal, whereas the liver index improved but did not fully recovery. In 3K, gutted condition declined during the early 1990s and improved during the latter half of the 1990s. Liver index changed little during the 1990s. In 3L, gutted condition remained relatively unchanged over time whereas liver index increased considerably in the early 1990s and has since declined to an intermediate level.

To explore more thoroughly the changes in condition during the 1980s and early 1990s, condition was computed for cod aggregated over a wider size range than used in the computations reported above. The results (Figure 11) show that as liver index declined in 2J, it increased in 3L. Additional exploration has shown that there have even been differences in pattern between different areas within a Division (Lilly, 1996).

The changes noted above in size-at-age and condition have been attributed to changes in stock size, temperature and the abundance of capelin (see references in Lilly 2001), but many of the studies provide insufficient explanations because they fail to account for the spatial variability in the trends.

Maturity

The proportion mature at age increased among young female cod during the early 1990s and has fluctuated since (Figure 12). When data collected prior to the initiation of stratified-random surveys in 1978 are included in the analyses, it can be demonstrated that the female age at 50% maturity was generally between 6 and 7 among cohorts produced in the mid-1950s and about 6 among those produced from the late 1960s to the early 1980s, but declined dramatically thereafter to a low of 5 for the 1989 cohort. Age at maturity has remained low but variable (5–6) for the 1990–2000 cohorts (Lilly *et al.*, 2005).

Olsen *et al.* (2005) demostrated that maturation reaction norms shifted toward earlier ages and smaller sizes during the 1980s and particularly the early 1990s, providing evidence of rapid evolutionary change that was interpreted to be the consequence of strong selection by the fishery. They also demonstrated that these changes appeared to be halted and even showed signs of reversal upon closure of the fisheries.

Distribution

The ToR does not refer to distribution, but one cannot assess changes in population dynamics of 2J3KL cod during the late 1980s and early 1990s without considering changes in distribution. These changes included a delay in timing of the inshore migration (Davis, 1992), a movement toward the shelf break in the autumn (Lilly, 1994) and to deeper water during the winter (Baird *et al.*, 1992), and a change in north-south spatial distribution as deduced from catches during autumn research bottom-trawl surveys (Lilly, 1994; Atkinson *et al.*, 1997), winter research acoustic studies (Baird *et al.*, 1992) and winter-spring commercial fisheries (Kulka *et al.*, 1995; Wroblewski *et al.*, 1995). With respect to the north-south changes, particularly the disappearance from the north, there is controversy as to whether the changes reflect differences in timing of the disappearance of different groups of fish (e.g. Hutchings, 1996), or whether there was a redistribution of fish (Rose *et al.*, 1994, 2000).

These distribution changes have contributed to difficulties in assessing the extent and causes of changes in size-at-age, condition and mortality, and may have contributed to those changes.

ToR d. Evaluate the consequences for stock resilience of decreases in mean weight and length and age/size diversity

Size-at-age

There was a decline in mean weight at age during the 1980s and early 1990s, especially toward the north (Figure 10). This decline included both a decline in length at age and a decline in weight at length (condition). Thus, the contribution of individual growth to stock productivity declined during the 1980s and especially during the early 1990s.

Drinkwater (2002) states that approximately 30–50% of the decline in the spawning stock biomass from the early 1980s to the early 1990s was due to reduced weights-at-age. It is not clear what the reader is to infer from this. The weight-at-age did decline considerably, but did this decline contribute to the underestimation of fishing mortality and to the setting of quotas that, in retrospect, were too high?

The severe declines in weight-at-age that occurred in the early 1990s, notably in the north, quickly reversed, so that values after the mid-1990s were not dissimilar to those in the mid-1980s. There have been few suggestions that reduced growth rate is a contributer to the lack of recovery in this stock.

Condition

The extent to which the severe decline in condition during the early 1990s, especially in the north, contributed to stock collapse remains unclear. It might have contributed to an increase in natural mortality (see ToR c) and an increase in the rate of dumping by fish harvesters

(Drinkwater, 2002), but there appears to be little information to inform either of these possibilities.

There is also uncertainty about the extent to which poor condition is contributing to the lack of recovery. Studies of cod condition and feeding in specific areas and seasons have been interpreted as indicating that cod have not been faring well in certain areas (Rose and O’Driscoll, 2002). In contrast, the routine monitoring of cod size-at-age and condition during autumn bottom-trawl surveys has not identified a problem in recent years (Lilly *et al*., 2005).

Age/size diversity

The extent to which a severe reduction in age/size diversity has contributed to the lack of recovery is not known. The spawner biomass of cod in the offshore of 2J3KL is extremely small, and this in itself is expected to result in a low possibility of a good year-class. There are numerous word models and laboratory studies that support the contention that reduced size/age structure will further reduce the likelihood of successful reproduction, but it is exceedingly difficult to test whether the reduced age/size diversity has actually been contributing to lack of recovery in the offshore of 2J3KL.

It may be noted that there was a considerable reduction in age/size diversity by the mid-1990s in the inshore populations of 3KL and in the 3Ps stock. Age/size diversity increased from the mid-1990s onward in both these areas, but this has not prevented a decline in recruitment in the 3Ps stock.

Modelling the consequences of changes in life history parameters

Hutchings (2005) conducted simulations to explore the consequences of a reduction in age at maturity, coupled with additional factors such as reduced reproductive success in first time spawners and increased mortality upon attainment of maturity. He found that a reduction in age at maturity might reduce annual population growth, and concluded that fishing-induced changes in life history traits might in themselves generate slow or negligible recovery.

ToR e. Document and comment on historic evidence of previous cod stock recoveries and the environmental and fisheries circumstances in which these occurred

For 2J3KL cod, it will be instructive to compare environmental and fisheries circumstances during recovery from the first collapse (late 1970s to mid-1980s) to circumstances during the second and deeper collapse (late 1980s to mid-1990s). The contrast between these two periods is of great significance to an understanding of the collapse of cod stocks in Atlantic Canada (Rice *et al*., 2003).

SPA output is of limited use in comparing the two time periods. The SPA models indicate that total (3+) biomass reached a low of about 500 000 t in 1975–1977 (Figure 3) and spawner biomass reached a low of about 130 000 t in 1977 (Figure 4). At what time were comparable levels reached during the second collapse? This remains unclear because of the poor fit between model output and the index from the research vessel surveys in the late 1980s and early 1990s, as described above. SPA models without adjusted catch indicate that total biomass dropped below 500 000 t during 1989 and SSB dropped below 130 000 t during 1990, whereas comparable dates from the SPA model in which unreported catch was added (Shelton *et al*. 2006) would be 1991 and 1992. Although the time course of the second collapse remains uncertain, the stock clearly dropped quickly through the floor established in the late 1970s and kept on going.

Fisheries circumstances

The collapse during the 1960s and 1970s was caused primarily by the intensive offshore fishing by non-Canadian fleets, although there was undoubtedly a contribution from technological changes in the inshore fishery during the 1950s and 1960s. The number of participants in the inshore fishery had declined during the 1970s (Schrank, 2005). Inshore landings declined to a minimum in 1974 but started to increase even before declaration of Canada's 200 mile fisheries zone in 1977. Nevertheless, the declaration of the zone displaced the non-Canadian fleets, and a low in offshore landings occurred in 1978. The stock started to increase and fishing mortality declined for a few years, even though total landings were increasing.

The optimisim generated by declaration of the 200 mile limit lead to a wave of Canadian expansion in the catching sector and the processing sector (Schrank, 2005). When it became clear in 1988–1989 that stock size was significantly smaller than had been indicated by previous assessments, the Harris review panel in its interim report recommended that the quota be reduced, but not to the extent implied by the new estimate of stock size. This was because "the sudden reduction in catch levels designed to reduce the F value to the $F_{0.1}$ level of approximately 0.20 would be altogether too drastic a measure in view of the social and economic repercussions of such action. A not unreasonable compromise position, we believe, would be reduce the fishing mortality from its current level to a point approximately half-way to the $F_{0.1}$ level …" (Harris, 1989; p. 38).

Thus, fisheries circumstances were very different during the two collapse-recovery periods. During the late 1970s, a substantial reduction in offshore effort and landings was accomplished with no social or economic repercussions to Canada, whereas in the late 1980s a substantial reduction in landings would have entailed substantial socioeconomic consequences. The reduction that was implemented in 1989 did have important consequences, but these were minor compared to the consequences of the moratorium imposed just a few years later.

Environmental circumstances

As noted above, there was a cool period that lasted from the early 1970s to the mid-1990s, with particularly cold periods in the early 1970s, early to mid-1980s and early to mid-1990s. Comparisons among different sections of this period of about 25 years will yield somewhat different results depending on the environmental index being used (Figure 13). Nevertheless, the period immediately after declaration of the 200 mile limit was characterized by normal or above-normal temperatures, whereas the period starting in 1987 was characterized by somewhat cooler temperatures for a few years followed by cold temperatures in 1990 or 1991 (depending on index). The winter and spring of 1991 were particularly severe.

The early 1990s was a period of dramatic contrast between the cod off Labrador-Newfoundland and the cod in the Barents Sea. The intensification of the positive phase of the North Atlantic Oscillation that produced the cold conditions off Labrador-Newfoundland contributed to warmer waters and increased inflow of water rich in zooplankton in the Barents Sea. The northern cod off Labrador-Newfoundland collapsed while the Northeast Arctic cod in the Barents Sea thrived, despite high fishing mortality. This further supports the contention that the collapse of northern cod was not caused by fishing alone.

Role of specific year-classes

The recovery following declaration of the 200 mile limit was built largely on the moderately strong 1973–1974 (and 1975) year-classes. These year-classes had been spawned prior to the declaration of the 200 mile limit, were subjected to reduced fishing mortality compared to year-classes that had preceded them, and contributed to an increase in total biomass and particularly spawner biomass.

In contrast, the moderately strong year-classes of 1978–1982 were subjected to increasing fishing mortality through the 1980s, despite the intention to fish conservatively.

The big question is what happened to the 1986–1987 year-classes. As noted above, these two year-classes appeared to be moderately strong in the survey indices, but they disappeared from the survey catches very quickly in the early 1990s and contributed very little to spawner biomass.

Recruitment, size-at-age, condition and age/size structure

Information on recruitment, growth, and condition is provided under ToR c. A detailed comparison between these population and biological characteristics in 1977–1983 with those in 1987–1993 has yet to be conducted.

It has been stated that a reduction in size/age structure contributed to a reduction in resiliency. For example, Drinkwater (2002) compared the age structure of the catches in 1962 and 1991, and concluded that removal of the larger, older fish by heavy fishing pressure made the stock more susceptible to a series of weak year-classes. Of interest in the present context is a comparison between the age/size structure in the late 1970s, a period after which there was a recovery, and that during the late 1980s, a period after which there was a deeper decline and no recovery. Such a comparison has yet to be conducted.

Natural mortality

The biggest question, and the one that might be the most difficult to answer, is whether there was a difference in natural mortality between the two time periods. The coincidence between the severe cold of the early 1990s and the rapid decline in survey indices suggests that the cold water and extensive ice cover may have been a contributing factor. However, there is no evidence that there was increased mortality associated with the cold around 1972–1974 and 1983–1985.

Prey

If one focuses on the biomass of capelin in the ecosystem, then it is of interest that there may have been considerably less capelin during the late 1970s than during the late 1980s. However, many aspects of capelin biology, including their accessability to hydroacoustic surveys, changed dramatically in the early 1990s, particularly in 1991, the year of particularly severe cold and ice cover.

Predators

Changes in the predator field are not well-documented. However, there is good evidence that the harp seal population increased from the early 1970s to the mid-1990s.

ToR f. Comment on past projections of cod stock recovery, evaluate whether they were correct and draw conclusions concerning how future projections can be improved

The projections that might be of most relevance to this workshop are those that were undertaken after the first decline and during the second decline (the collapse). Much has been written about these projections, the extent to which they were overly optimistic, and the consequences that followed.

After the first decline of the 2J3KL cod stock and Canada’s declaration of a 200 mile zone of Extended Fishery Jurisdiction in 1977, there was hope and optimism that the stock could be rebuilt. Projections by government scientists (Pinhorn, 1979), as presented to a government-industry seminar, indicated that the total allowable catch (TAC) “… could be as high as 350 000 tons by 1985… These projections were made on the assumption that the number of new fish entering the commercial stock (recruitment) … would be the average of that observed over recent years including the strong year-classes of the 1960s. … It was stressed very strongly that, if recruitment in future was lower than average, then the stock would rebuild more slowly than projected” (Lear and Parsons, 1993). The expulsion of distant-water fleets from most of the continental shelf and the projection of rapid increase in the cod stock created an "optimism bubble" (Schrank, 2005) that generated a tremendous wave of expansion in the fishing industry and contributed to overcapacity in harvesters, vessels and processing plants (Schrank, 2005; Vilhjálmsson *et al.*, 2005). The stock did grow, but much less than projected. It has repeatedly been noted that the projected recruitment did not take into account the much reduced level of spawner biomass. In addition, there is no mention of the weights-at-age used in the projections, but we now know that weights-at-age declined in the 1980s as the environment cooled (see above). Furthermore, fishing mortality was consistently underestimated (see ToR b), with the result that removals were higher than they should have been under the policy in place at the time.

By the summer of 1992 it was clear that the 2J3KL cod stock had declined considerably. Accompanying the declaration of the moratorium was a "Backgrounder" document that stated that there had been a sudden decline in the stock since 1990 and that no single factor could be identified as the main cause of the decline. It noted, however, that the increase in mortality was consistent with extreme environmental conditions in 1991. It also noted that assessment groups had not made any catch projections past 1992. Nevertheless, there followed a graph (reproduced by Lear and Parsons, 1993; their Figure 10) with a projection showing spawning stock biomass increasing in two years to a level approaching or exceeding the long term average. The only information accompanying the figure was that the projection assumed a return to normal natural mortality rates. The projected rapid growth in SSB was clearly dependent on high survival, growth and maturation (at age 7) of the 1986 and 1987 year-classes, which had appeared moderately strong in the research surveys and had contributed to high landings in the 1990 inshore fishery, especially in 3L. This projection has been ridiculed by many, and is frequently referred to as an example of bad science providing bad advice. However, perhaps critics should bear in mind that the rapid recovery was not an expectation of scientists who participated in the assessments. After all, the assessment meetings in 1992 had not made projections to 1993 because of uncertainties in the assessment. Whatever the source of the projection, it is now clear that it was far off the mark. Mortality remained high. The stock did not recover. The social and financial costs of waiting for a recovery were tremendous (e.g. Vilhjálmsson *et al.*, 2005)

It is noteworthy that reports from formal stock assessment meetings continued to be very pessimistic in 1993 (Bishop *et al.*, 1993) and that this pessimism was picked up in the early reports of the Fisheries Resource Conservation Council (FRCC), a new independent body created in 1993 to advise the Minister on quotas and other management measures. In a letter to the Minister of Fisheries and Oceans in August, 1993, the FRCC (1993) provided the following summary of stock status and advice regarding management of 2J3KL cod.

"Based upon the stock assessment report by scientists in the Department of Fisheries and Oceans, as well as the Report of the Scientific Council of NAFO, the situation of the 2J3KL cod (Northern Cod) stock can be characterized as follows:

> 1. The Stock continues to decline and is in a very depressed state, believed to be at the lowest level of abundance experienced during the 20th century.
>
> 6. Stock recovery in the near future is unlikely and substantial recovery of the spawning biomass is unlikely before the year 2000 at the earliest. At this stage, there are no reasons to be optimistic about stock recovery even then.
>
> 7. Realistic projections about stock rebuilding are impossible until we better understand the reasons for the decline and until the various stock indicators reverse their downward trends."

The absence of any sustained sign of recovery in the offshore populations by 2005, 13 years after declaration of the moratorium, illustrates that fishing has not been the only factor governing stock dynamics. It is possible that factors other than fishing contributed to the collapse, and that at least some of those factors are still operating. It is also possible that once the stock had declined to a very low level, for whatever reason, then factors other than fishing have assumed greater importance. The latter possibility must be tempered by the possibility that the fishing that has continued for other species is causing sufficient removals (landings and discards) and unseen mortality of cod to keep the cod populations from rebounding. However, recorded landings and discards appear very small relative to the survey estimates of biomass.

The factors that might be preventing recovery were explored during the 2003 assessment meeting (Rice and Rivard, 2003; Rice *et al*., 2003) and reviewed by Lilly and Murphy (2004; their Appendix 4).

The Term of Reference requires us to "draw conclusions concerning how future projections can be improved". To do so would be trite. Problems with long-term projections are well-known, and considerable effort has gone into improving the statistical methodology so as to take uncertainty into account. In addition, many fisheries scientists in Atlantic Canada are now highly reluctant to produce long-term projections, with good reason. The two examples described above are well-known to the industry and the public in general, and are frequently cited (along with the collapse of northern cod) as reasons why people should pay little attention to fisheries scientists.

Any prediction of the long-term status of 2J3KL cod would presumably want to take global warming into account. Vilhjálmsson *et al*. (2005) and Drinkwater (2005) have discussed the possibility that cod off Labrador and eastern Newfoundland will become more abundant and expand back to the north. However, as noted by Vilhjálmsson *et al*. (2005; p. 740): "The simple scenario of a gradual change back to a cod-capelin system under moderate warming conditions is uncertain. This is because the influence of oceanographic variability in the past is not clear, and because it is likely that the dynamics of some species are now dominated by a different suite of factors than was the case in the past. It is highly likely that the ecosystem off northeastern Canada changed substantially as a consequence of fishing during the first four centuries after the arrival of European fishers, changed even further with the increasingly intensive fishing of the 20th century, and has changed dramatically from the 1960s onward. The magnitude of these changes is such that it would be difficult to predict accurately the future state of this ecosystem even without the added complications of climate change. Thus, the system could remain in its current state, could revert to some semblance of an historic state (or at least the state of the early 1980s), or could evolve toward something previously unseen."

With respect to changes that might be caused by global warming, there is at this time little information on the manner in which global warming will affect the specifics of water temperature, ice coverage, stratification and many other factors of interest for predicting the dynamics of cod off northeastern Canada (Lilly and Carscadden, 2002; Drinkwater, 2005). For examples of our inability to predict oceanographic conditions on the Labrador and Newfoundland Shelves, we have only to look back over the past few decades. Who predicted the cold conditions over the Labrador and Newfoundland Shelves that accompanied intensification of the positive phase of the NAO in the last three decades of the 20th century, and particularly the severe cold and ice-cover of the early 1990s? Just when fisheries biologists were becoming convinced of the significance of the relationship between a high NAO index and cold conditions over the Labrador and Newfoundland Shelves, and were talking about incorporating such information into projections, the relationship broke down for a few years as the centre of the pressure systems moved to the east. This too was not predicted. (If it was, it was not made known to fisheries biologists.) See Drinkwater (2005) for additional information regarding uncertainty associated with predicting the effect of climate change at regional scales, and Vilhjálmsson *et al*. (2005) for some discussion associated with predictions specific to the Labrador and Newfoundland Shelves. Given the high degree of uncertainty associated with predicting regional climate change, and the dramatic changes that have occurred in the Labrador/Newfoundland ecosystem, one must ask whether anything is to be gained from long-term predictions regarding distribution, abundance/biomass and phenology of cod in this area. One might also ask whether industry and government need such predictions, given (i) the likelihood that any resurgence of cod will be obvious (from surveys and bycatches) well before an offshore fishery becomes sustainable and (ii) the fact that the industry has demonstrated an ability to adjust to different species as opportunities arise.

ToR g. Evaluate the role of cod forage species (e.g. capelin) for variability in abundance and size-at-age of cod

Much of the following information has been extracted from a section on the cod of eastern Newfoundland and Labrador in Link *et al*. (in prep).

Capelin has historically been the major prey of medium-sized cod off southern Labrador and eastern Newfoundland. Assessment of the contribution of capelin to individual growth and population dynamics of 2J3KL cod is hindered by the absence of a reliable long-term index of capelin abundance/biomass. It is generally accepted that capelin were abundant during the early 1970s, declined during the late 1970s and increased during the 1980s. Many aspects of capelin biology, including their availability to offshore fisheries and hydroacoustic surveys, changed dramatically during the early 1990s, with most changes being especially pronounced in 1991 (Carscadden *et al*. 2001).

Size-at-age

Despite the expectation that linkages among species would be strong in a system with few abundant members, it has proved difficult to find evidence of such links. Neither Akenhead *et al*. (1982) nor Millar *et al*. (1990) found a significant relationship between cod growth and capelin biomass. It was felt by several authors (Akenhead *et al*., 1982; Shelton *et al*., 1991) that measurement error may be high, given the complexities and limitations of quantifying fish abundances and vital rates, and that the potential for Type II error was high. Krohn *et al*. (1997) did find, however, that with the inclusion of data from the early 1990s, capelin biomass explained some of the variability in cod growth and condition.

It may be noted that capelin abundance/biomass appears to have been low during the late 1970s (Lilly, 1991, 1994), and the quantity of capelin found in cod stomachs during autumn surveys was also low (Lilly, 1991; Taggart *et al*., 1994), and yet cod growth was good at that time.

Cod Mortality

The role of capelin in the collapse of cod during the early 1990s remains unclear. Estimates of capelin biomass from offshore hydroacoustic surveys declined dramatically from 1991 onward, and the capelin changed their autumn distribution toward the southeast (Lilly, 1994; Carscadden and Nakashima, 1997). It has been suggested that these changes, together with changes in the timing of capelin migrations, made the capelin less accessible to cod, thereby contributing to low condition and possibly an increase in mortality of the cod (Atkinson and Bennett, 1994; Lilly, 2001). However, it may be noted that most of the cod remaining during the latter stages of the collapse seemed to have undiminished access to capelin, at least in the offshore during the autumn (Lilly, 1994; Taggart *et al*., 1994; O’Driscoll *et al*., 2000).

The role of capelin in the non-recovery of cod is also controversial. Rose and O’Driscoll (2002) concluded from studies of cod condition and feeding in specific areas and seasons that cod was not faring well in certain areas, and that this was due to low availability of capelin. In contrast, the routine monitoring of cod during autumn research surveys in the offshore and the observations of fish harvesters in the inshore have not identified any problems with cod growth or condition (Lilly *et al*., 2005).

ToR h. Evaluate the role of cod predators (e.g. seals) for variability in abundance and size-at-age of cod

The following information has been extracted from a section on the cod of eastern Newfoundland and Labrador in Link *et al.* (in prep).

The predators of cod tend to change as the cod grow (Lilly, 1987; Pálsson, 1994; Bundy *et al.*, 2000). Very small cod are eaten by squid, various demersal fish (such as sculpins) and some seabirds. Larger juveniles have many predators: demersal fish, most notably larger conspecifics and Greenland halibut; harp seals and hooded seals (*Cystophora cristata*); certain toothed whales, such as harbour porpoise and pilot whales (*Globicephala melaena*); and probably minke whales. Large cod seem to have few natural predators, but seals can prey upon them by belly-feeding, a mode of predation whereby the seal takes a bite from the cod's abdomen, consuming the liver and some of the other abdominal organs, but generally leaving the rest of the carcass and the head (Lilly *et al.*, 1999).

The predator that has attracted most attention is the harp seal (Bundy *et al.*, 2000; Hammill and Stenson, 2000). There was speculation that seals contributed to the collapse of the cod stock (Atkinson and Bennett, 1994), but it is generally thought that their contribution was small. However, the total mortality of cod in the offshore has remained very high since the moratorium on directed fishing in 1992, and analyses of tagging data have revealed that adult cod in the inshore experienced high mortality in addition to that caused by the reopened fishery in 1998-2002 (Lilly *et al.*, 2003). It is possible that the seals could be maintaining cod in a "predator pit" (Shelton and Healey, 1999). It has been concluded by some (DFO, 2003; Rice *et al.*, 2003), based on the large size of the harp seal population, the known predation by harp seals on cod, and the paucity of information pointing to other factors, that predation by harp seals is a contributing factor to the high mortality of cod. It must be emphasized, however, that there is very little information on harp seal diet in the offshore, where most of the seal foraging is thought to occur. The little information available for hooded seals indicates that they too could be important predators on cod (McLaren *et al.*, 2001).

There has also been concern regarding the role of harp seals as competitors of cod. Harp seals are estimated to have consumed about 3 million tons of food per year in the northern cod stock area during the late 1990s (Hammill and Stenson, 2000; Stenson and Perry, 2001). Most of this food was pelagic planktivores, notably capelin, so the potential for competition with cod exists. However, cod and seals share capelin and other planktivores (Arctic cod, sand lance, herring) with numerous additional predators, including other demersal fish, several species of baleen whales, and birds (Bundy, *et al.* 2000; Carscadden, *et al.* 2001). The complexity of the food web, and our rudimentary understanding of its dynamics, makes it very difficult to assess the effect on cod resulting from specific changes in the abundance of seals.

ToR i. Evaluate the role of climate mediated through cod predators and prey

There was a change in the autumn distribution of capelin during the early 1990s. It has been suggested that the change in capelin distribution was part of the reason for a change in cod distribution, and that the change in distribution of the cod resulted in their being more accessible to trawlers (Rose *et al.*, 2000, but see Hutchings, 1996). The extent to which the low water temperatures and extensive ice cover of the early 1990s contributed to changes in distribution of both cod and capelin, and to the accessibility of capelin to cod, remains unclear, in part because of the paucity of information during seasons other than autumn.

ToR j. Evaluate the relationship between the decline and recovery of cod stocks and changes in the marine ecosystem

Much of the following information has been extracted from a section on the cod of eastern Newfoundland and Labrador in Link *et al.* (in prep).

As noted above, the collapse of the 2J3KL cod stock in the early 1990s was but the most prominent in a series of profound changes within the Newfoundland-Labrador ecosystem. Among these were severe declines in most other demersal fish, including species that were not targeted by commercial fishing (Atkinson, 1994; Gomes *et al.*, 1995); a surge in snow crab and especially northern shrimp (Lilly *et al.*, 2000); an increase in the abundance of harp seals from fewer than 2 million individuals in the early 1970s to more than 5 million in the late 1990s (Healey and Stenson, 2000); and numerous changes in the biology of capelin, the dominant forage fish in the area (Carscadden *et al.*, 2001).

The role of cod within an ecosystem may become more apparent when cod biomass declines, as happened off Labrador and eastern Newfoundland. The surge in snow crab and particularly northern shrimp is consistent with a release from predation pressure from cod (Lilly *et al.*, 2000; Bundy, 2001; Worm and Myers, 2003) and other demersal fish, but it is difficult to separate the influence of predator release from the effects of environmental change. It may also be noted that there is no evidence that capelin or any other finfish increased following the cod collapse.

There has been a change in the pattern of human exploitation of this ecosystem; the hunting of charismatic species has declined or stopped, such that the population of harp seals is steady at a level much higher than in the 1970s and some whale populations are probably increasing, whereas the exploitation of finfish increased and most species of groundfish are at low levels. It is possible that reduced hunting and continued fishing will tend to keep the ecosystem in its present state.

Additional comment on the role of policy toward fisheries management

When a stock has declined to a very low level, its management is complicated by several factors that are of much less importance when the stock is in good condition. These include bycatches in ongoing fisheries directed at other species, a difference between fish harvesters and the formal assessment process with respect to understanding or perception of stock size, and social concerns. Three examples are provided for 2J3KL cod.

(1) Although directed fishing for cod has not been allowed in the offshore of 2J3KL since the moratorium was imposed in 1992, bycatches of cod have continued in fisheries directed at other species. Relatively large cod have been taken in otter trawls and gillnets targeting groundfish (especially Greenland halibut) and small cod have been caught and discarded by shrimp trawlers. The catches taken by these fisheries appear to be small compared to the biomass estimated from the research bottom-trawl surveys (Lilly and Murphy, 2004). However, there is no information on catchability at length for the survey trawl that has been used since 1995, so there is no estimate of the actual abundance of cod at length at the time of each survey. In addition, there is inadequate information on the magnitude and size range of catches (landings and discards) taken in the offshore by the various fleets, including the non-Canadian fleets fishing outside the 200 mile limit. Under such circumstances, it is difficult to estimate fishing mortality. This also means that it is difficult to assess the level of natural mortality, and hence the contribution of predators and prey to the non-recovery.

(2) Differences between fish harvesters and formal government assessments in the understanding or perception of the status of cod stocks has for many years been a prominent feature of the public discussion and fisheries management surrounding the cod stocks off eastern and western Newfoundland. An example is provided for the cod off eastern Newfoundland. The Fisheries Resource Conservation Council (FRCC) was established in 1993 as an independent body to advise the Minister of Fisheries and Oceans on quotas and other management matters. The FRCC reviewed stock status documents produced through the formal assessment process, and also took into account information and recommendations provided by the fishing industry. Its mandate included taking social and economic

considerations into account. For a summary of FRCC recommendations regarding management of 2J3KL cod, see Lilly *et al*. (2003). In 1997 and 1998 the FRCC was told by fish harvesters that the 2J3KL stock was in (much) better shape than indicated in DFO status reports. With income support programmes coming to an end, the FRCC recommended first a test fishery (1998) and then a small commercial fishery (1999). As noted above, this inshore fishery continued through 2002. During this 5-year period, catch rates in both the commercial fishery and the sentinel surveys plummeted. A sequential population analysis (SPA) conducted in 2003 on inshore data alone indicated that the inshore populations had declined by 50% (see above). Local knowledge had been considered superior to scientific information, and social concerns had taken precedence over biological concerns. The consequence was a substantial decline in inshore populations. Similar but perhaps less severe consequences followed DFO's acceptance of the FRCC advice for the two cod stocks in the Gulf of St. Lawrence (Rice *et al*., 2003) and the cod stock off southern Newfoundland.

(3) DFO has a policy under which participants in a fishery will, over time, become more effectively involved in the assessment and management of the fishery, a process termed "shared stewardship" (DFO, 2005b). Many fish harvesters in eastern Newfoundland believe that the assessment process is still underestimating the size of the 2J3KL cod stock. They also state that the stock is sufficiently large to support a small inshore fishery, that directed fishing will enhance the quantity and quality of information available for assessing the stock, and that compliance with regulations and other aspects of conservation will be improved if fishing is permitted. In addition, fish harvesters state that fishing should be permitted on a depressed stock as long as the stock is growing. It appears that the inshore fishery of eastern Newfoundland and southern Labrador will be reopened to a small directed fishery in 2006 so as to move forward with the shared stewardship initiative. (Added note: A small directed commercial and recreational fishery for the inshore of southern Labrador and eastern Newfoundland was announced in June 2006 (DFO, 2006).)

Decisions regarding the quantity of cod to be taken by directed and bycatch fisheries, and the level of risk to cod stock recovery that will be considered acceptable, are matters of policy developed by DFO in consultation with the fishing industry and other clients. However, in the context of factors affecting stock recovery, it must be acknowledged that fishing severely depleted populations must retard recovery (Shelton *et al*., 2006), and under circumstances of low stock productivity, adverse environmental conditions, faulty information, or excessive optimism, such fishing may even reverse gains that have been made (Rice *et al*., 2003).

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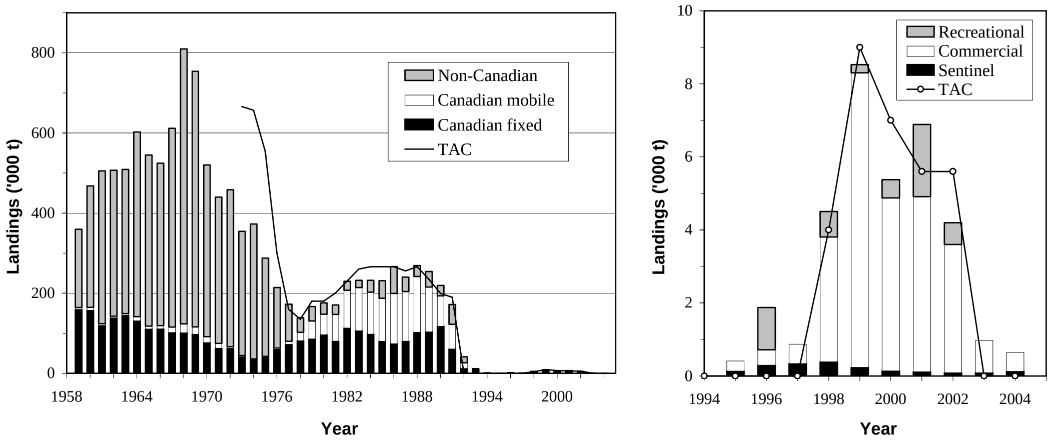

Figure 1. Total allowable catches (TACs) and landings (thousands of tons) from the 2J3KL cod stock in 1959–2004. The left panel illustrates landings by non-Canadian and Canadian fleets, with the latter divided into mobile gear (offshore) and fixed gear (mainly inshore). The right panel shows 1995–2004 in more detail, with the landings subdivided into food/recreational fisheries, index/commercial fisheries (including bycatch) and sentinel(test) fisheries. (from Lilly *et al.*, 2005)

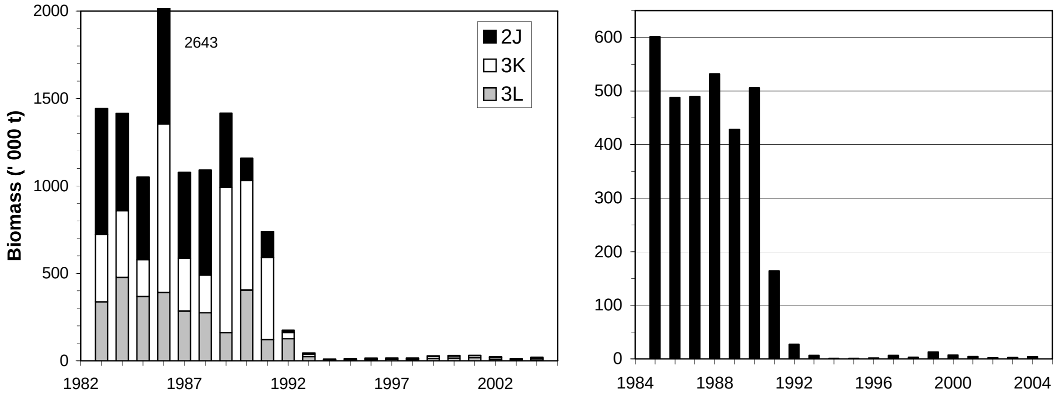

Figure 2. Offshore biomass indices from bottom-trawl surveys in 2J3KL during autumn (left panel) and 3L during spring (right panel). (from Lilly *et al.*, 2005)

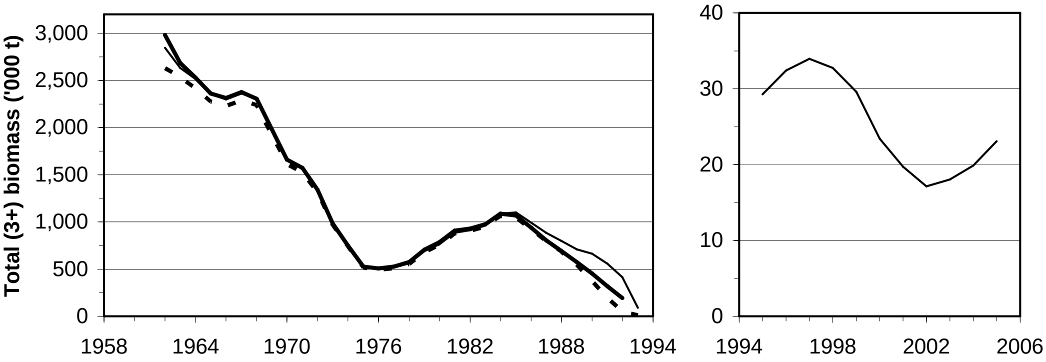

Figure 3. Trend in total (3+) biomass (thousands of tons) of 2J3KL cod as estimated by sequential population analyses (SPA). In the left panel, the solid bold line shows the biomass from the 1993 assessment (Bishop *et al.*, 1993, reconstructed by P. Shelton, DFO, St. John's, NL, pers. comm.), the dashed line shows an "illustrative" model with no alteration of catch (Lilly *et al.*, 1998) and the thin solid line shows a model with sufficient unreported catch added to allow the model to fit the pattern in the survey index (Smedbol *et al.*, 2002; Shelton *et al.*, 2006). The right panel shows biomass of fish from an SPA based on catches and indices from the central inshore area (Lilly *et al.*, 2005).

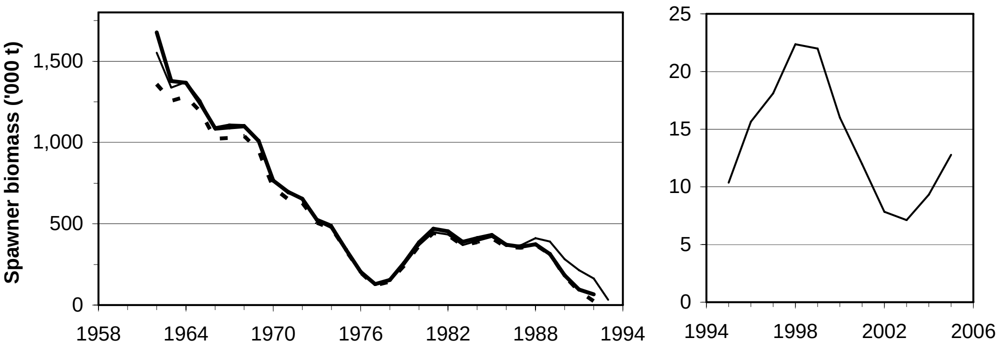

Figure 4. Trend in spawner stock biomass (SSB, thousands of tons) of 2J3KL cod as estimated by various SPAs. Lines as in Figure 3.

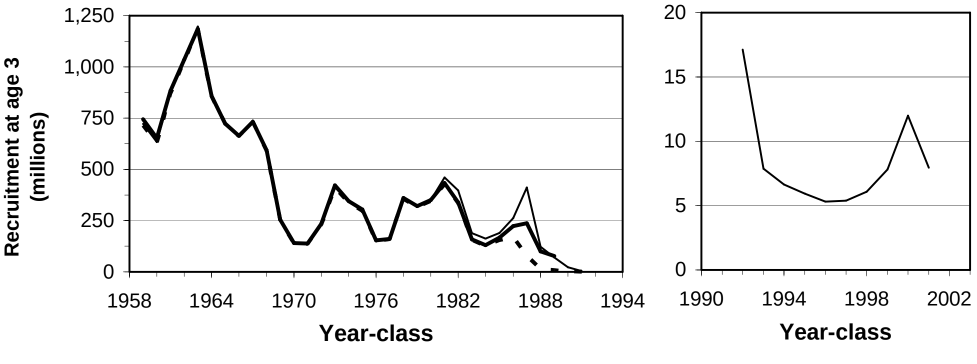

Figure 5. Trend in recruitment at age 3 (in millions) of 2J3KL cod as estimated by various SPAs. Lines as in Figure 3.

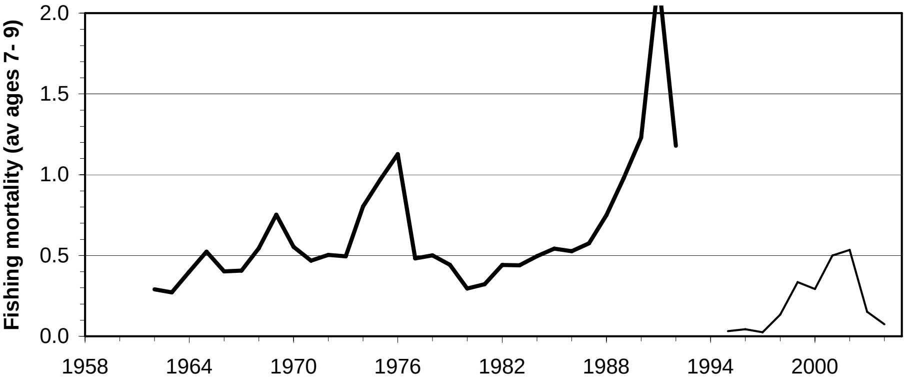

Figure 6. Fishing mortality, averaged over ages 7–9, in the 2J3KL cod stock, as estimated by SPA. The heavy line is from the whole stock SPA from the 1993 assessment (Bishop *et al.*, 1993) and the light line is from the central inshore SPA (Lilly *et al.*, 2005).

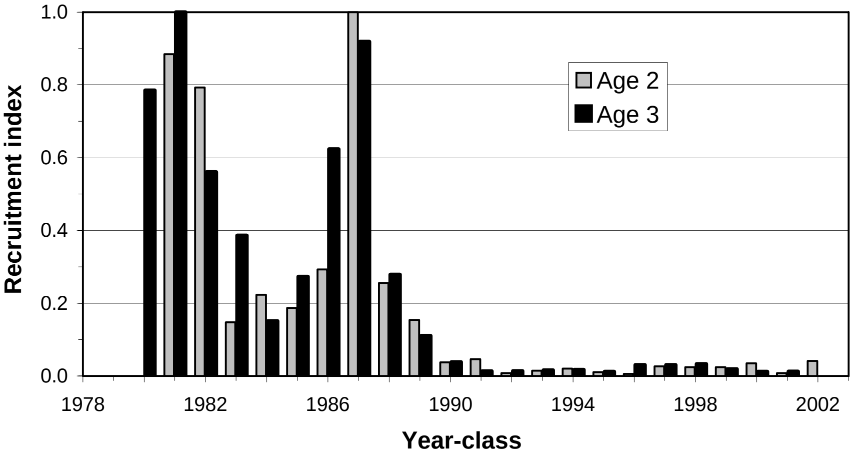

Figure 7. Relative sizes of the 1980–2002 year-classes in the offshore of 2J3KL, as measured by the mean catch per tow at ages 2 and 3 during the autumn offshore bottom-trawl surveys. Number per tow has been scaled to a maximum of 1 within the time-series for each age. (from Lilly *et al.*, 2005)

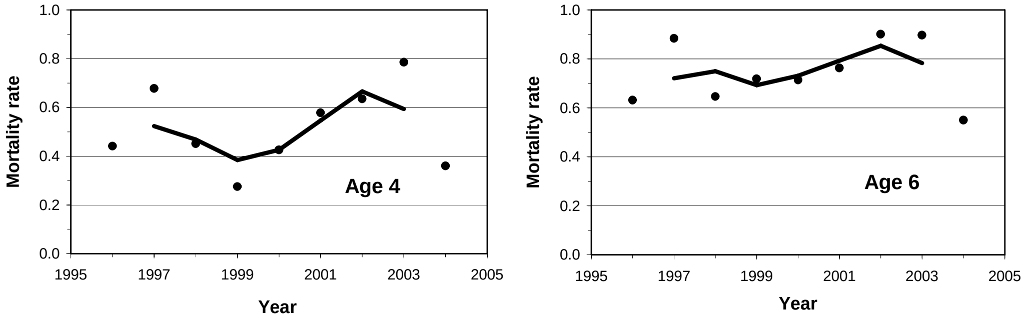

Figure 8. Age specific mortality calculated from mean catch per tow at age during the autumn bottom-trawl surveys in the offshore of 2J3KL. As an example, in the age 4 panel, the value of 0.7 in 1997 is the mortality experienced by the 1993 year-class from age 3 in 1996 to age 4 in 1997. The line is a 3-year moving average. (from Lilly *et al.*, 2005)

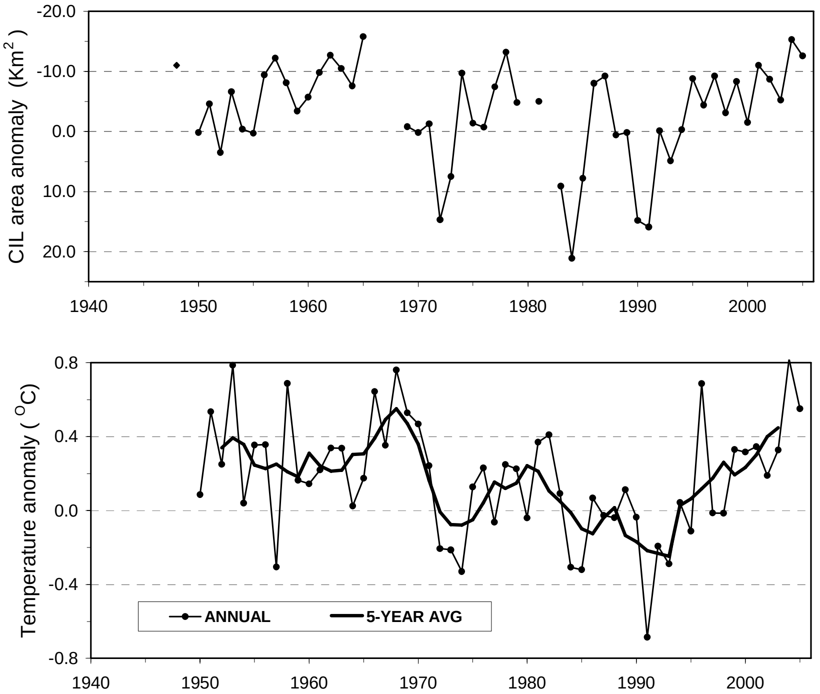

Figure 9. **Two indices of temperature from the Newfoundland Shelf. The upper panel shows anomalies from the cross sectional area of the Cold Intermediate Layer (CIL) during summer occupations of a transect off Cape Bonavista. The CIL is defined by the upper and lower 0° C isotherms. The larger the area, the more cold water on the shelf. Note that the ordinate axis is reversed. The lower panel is the temperature anomaly of the annual depth-averaged temperature at Station 27 off St. John's. It reflects changes in near-surface temperatures much more than does the CIL. (modified and updated from Colbourne *et al.*, 2005; additional data provided by Eugene Colbourne, DFO, St. John's, NL, Canada, pers. comm.)**

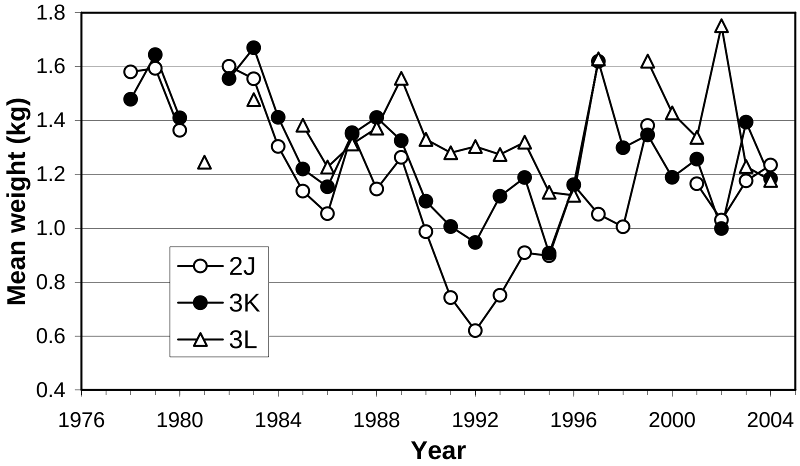

Figure 10. **Mean weight (kg) at age 5 of cod sampled during autumn offshore bottom-trawl surveys. (from DFO, 2005a)**

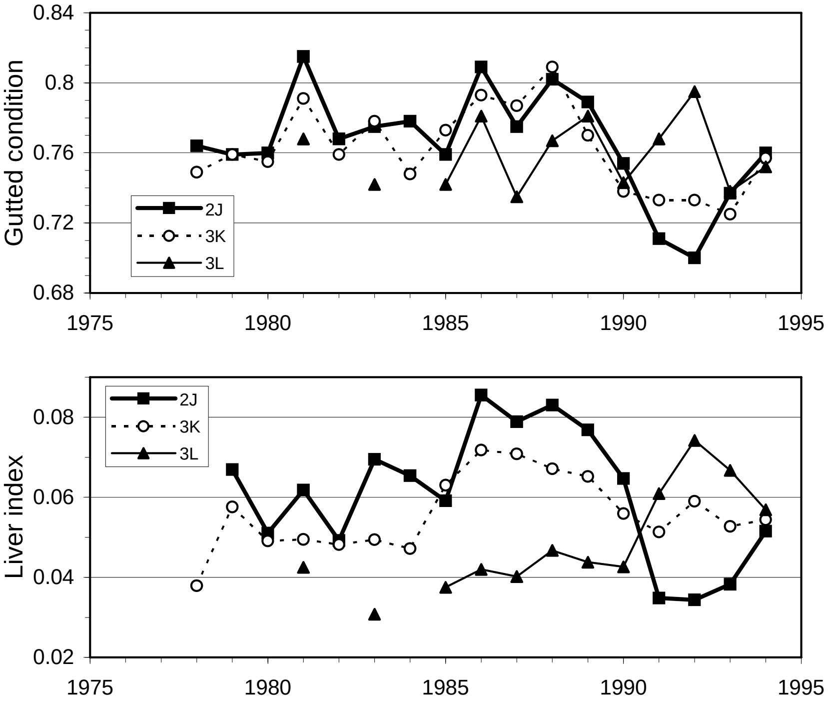

Figure 11. Fulton's condition index computed from gutted weight (above) and liver weight (below) for cod of 45–62 cm sampled during autumn bottom-trawl surveys in Divisions 2J, 3K and 3L in 1978–1994. (from Lilly, 2001)

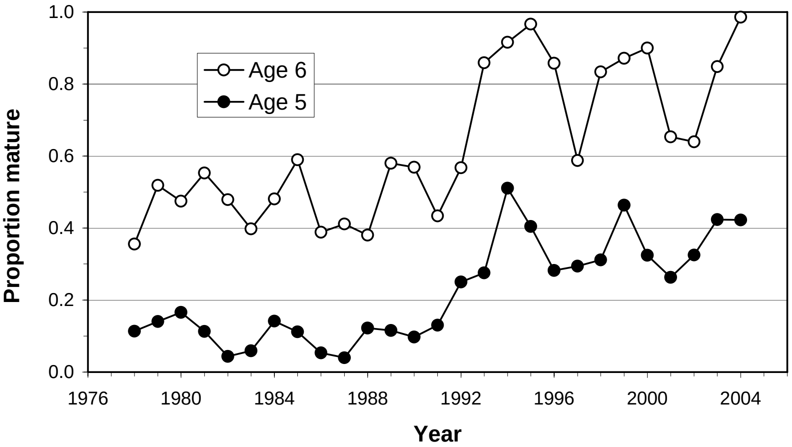

Figure 12. Percentage of females mature at ages 5 and 6 as predicted from modeling the maturity data from autumn offshore bottom-trawl surveys. (from DFO, 2005a)

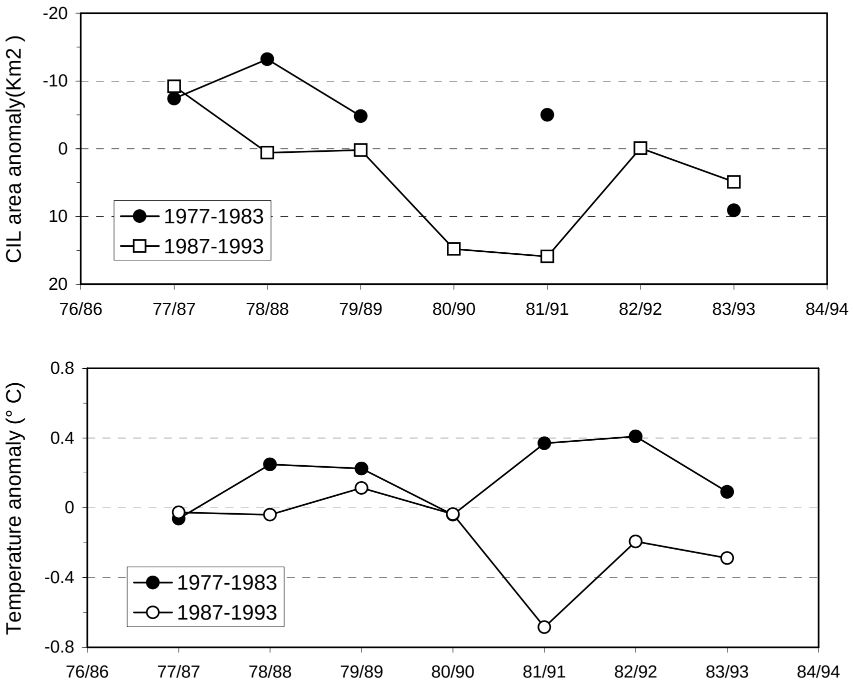

Figure 13. A comparison of temperature on the Newfoundland Shelf during two time-periods (1977–1983 and 1987–1993), as determined from the two indices shown in Figure 9.

Extended abstract 7

Fishery and environmental aspects relevant for the decline and recovery of the Atlantic cod (*Gadus morhua*) stock in Greenland offshore waters

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Cod have not been seen in Greenland prior to about 1910. Thereafter, cod became rather abundant within a decade extending its distribution in West Greenland waters from about 59° to 73 °N (Jensen, 1939). The occupation of Greenland waters started in the end of a cold period and commenced when a maximum in air temperature was observed (Figure 1). Since then, spawning populations has been established, both at East and West Greenland, which provided good recruitment during the 1950s and 1960s.

From a maximum of about 4 mill t in 1949, stock biomass at West Greenland declined to 110 000 t in 1975, despite a regular occurrence of good recruitment (Figure 2). After intermediate increases of biomass to levels of 250 000 t and 640 000 t in 1978 and 1987, respectively, the stock collapsed in the beginning of the 1990s. At that time, the mean latitude of the catch and survey biomass indicated a pronounced southward shift of the distribution (Figure 3). Sea temperature off West Greenland increased in the mid 1990s towards record high values (Figure 3), but a weak sign of a potential recovery has been detected first several years thereafter (Figure 1).

For West Greenland, two prolonged periods of decline in total biomass can be distinguished, i.e. 1950 to 1975 and 1987 to 1995, for which the proportion of biomass found their end amounted to 2.7 and less than 1 % of the initial value, respectively. During both of the two periods, fishing mortality (or exploitation rate (catch/survey biomass)) increased considerably and the mean latitude of the catch (or survey biomass) decreased. No general relationship between mean latitude of the distribution and sea temperature was found, but the two variables were significantly correlated for the years 1987–1992. The latter suggests that decreasing temperature has accelerated a homing migration of maturing fish towards East Greenland (and further to Iceland) of those year-classes, which are assumed to have originated mainly from Iceland (see e.g. Storr-Paulsen *et al*., 2004). Results from multiple linear regression analysis indicate that fishing mortality together with emigration (but neither temperature on its own nor recruitment failure) has been the ultimate cause for the decline in stock biomass in both periods (Table 1).

Once spawning fish had almost disappeared from the previous spawning areas of West and East Greenland in the late 1970s, recruitment became more or less solely dependent on larval transport from Iceland. This has obviously been the pre-requirement for the stock recovery observed in the mid 1980s and since the end of the 1990s (Figure 4, Table 2), depletion of the spawning stock in East and West Greenland might have caused a possible delay in the response of recruitment when warm conditions returned.

Simulation experiments have shown that inter-annual variation in particle transport across Denmark Strait is remarkably low (Logeman *et al*., 2004). These findings are supported by the observation that a high proportion of pelagic 0-stages have regularly found in East Greenland shelf waters in Icelandic surveys covering both Icelandic and East Greenland areas (ICES, 2002). Hence, in addition to effects related to the size and the age structure of the Icelandic spawning stock, low pre-recruit survival in Greenland waters may have prevented a more pronounced recovery of the cod stock at Greenland in the most recent years. However, results from preliminary analyses indicate that neither changes in stock size of polar cod (Figure 5) off West Greenland nor the geographical extension and the increase in effort in the fishery for northern shrimp (Figure 6) had an significant effect on the recruitment of Atlantic cod in Greenland waters. Other factors involved may include predation by seals and zooplankton production. It should, however, be noted that the data available for an analysis of pre-recruit survival of cod in Greenland waters are rather limited and a comparison of recruitment with environment variables is difficult due to the inference of an unknown (but presumable substantial) and varying proportion of recruits from Iceland in the recruitment time series derived from surveys or VPA assessments for Greenland offshore waters (Figure 7).

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Table 1. Stock parameters, catch and temperature for periods of decline in Atlantic cod stock size off West Greenland (VPA data: Buch *et al.*, 1994; Survey data incl. bottom temperature: Fock *et al.*, 2006; Catch data: Sünksen *et al.*, 2006; Surface temperature: Ribergaard, 2006).

Period: **1950 - 1975** VPA data (Biomass, SSB, Recruitment)

	Biomass (kt)	SSB (kt)	Catch (kt)	$F_{Age\ 5\ to\ 12}$	Recruitment at age 3 (10^3)	Mean latitude (°N)	Temperature (°C) Surface	Temperature (°C) Bottom
Range	108.4 - 4076.5	45.9 - 3092.7	39.4 - 425.3	0.06 - 0.94	10.6 - 631.5	61.1 - 65.2	0.3 - 3.2	n.a.
Average	1614.636	955.791	242.380	0.43	163.521	64.036	1.71	n.a.
Average annual change	-158.723	-121.874	-5.522	0.04	-24.457	-0.047	-0.01	n.a.

Significant factors for biomass change in multiple regression: **Fishing mortality, Mean latitude of catch**

Period: **1987 - 1995** Survey data (Biomass, SSB, Recruitment, Mean latitude; E': catch/survey biomass)

	Biomass (kt)	SSB (kt)	Catch (kt)	E' (%)	Recruitment at age 3 (10^3)	Mean latitude (°N)	Temperature (°C) Surface	Temperature (°C) Bottom
Range	0.1 - 638.6	0.0 - 60.7	0.0 - 70.3	0.0 - 116.6	0.0 - 692.6	60.6 - 63.2	0.8 - 2.2	2.8 - 4.0
Average	180.130	15.078	17.027	20.48	89.262	61.766	1.34	3.41
Average annual change	-79.816	-4.205	-0.492	3.38	-86.569	-0.146	-0.09	0.06

Significant factors for biomass change in multiple regression: **Recruitment, Mean latitude of survey biomass** *(significant when period is reduced to 1987-1992)*

Table 2. Stock parameters, catch and temperature for periods of increase in Atlantic cod stock size off East and West Greenland combined (Survey data incl. bottom temperature: Fock *et al.* 2006; Catch data: Sünksen *et al.* 2006; Surface temperature: Ribergaard 2006).

Period: **1984 - 1987** Survey data (Biomass, SSB, Recruitment)

	Biomass (kt)	SSB (kt)	Catch (kt)	E' (%)	Recruitment at age 3 (10^3)	Temperature (°C) Surface	Temperature (°C) Bottom
Range	45.3 - 690.2	21.4 - 55.7	6.0 - 22.4	1.2 - 113.2	1.0 - 710.6	1.0 - 2.2	2.7 - 4.2
Average	233.159	36.809	11.956	47.85	180.154	1.84	3.70
Average annual change	214.96	11.42	-7.589	-37.31	176.734	0.41	0.36

Significant factors for biomass change in multiple regression: n.a. (insufficient number of observations)

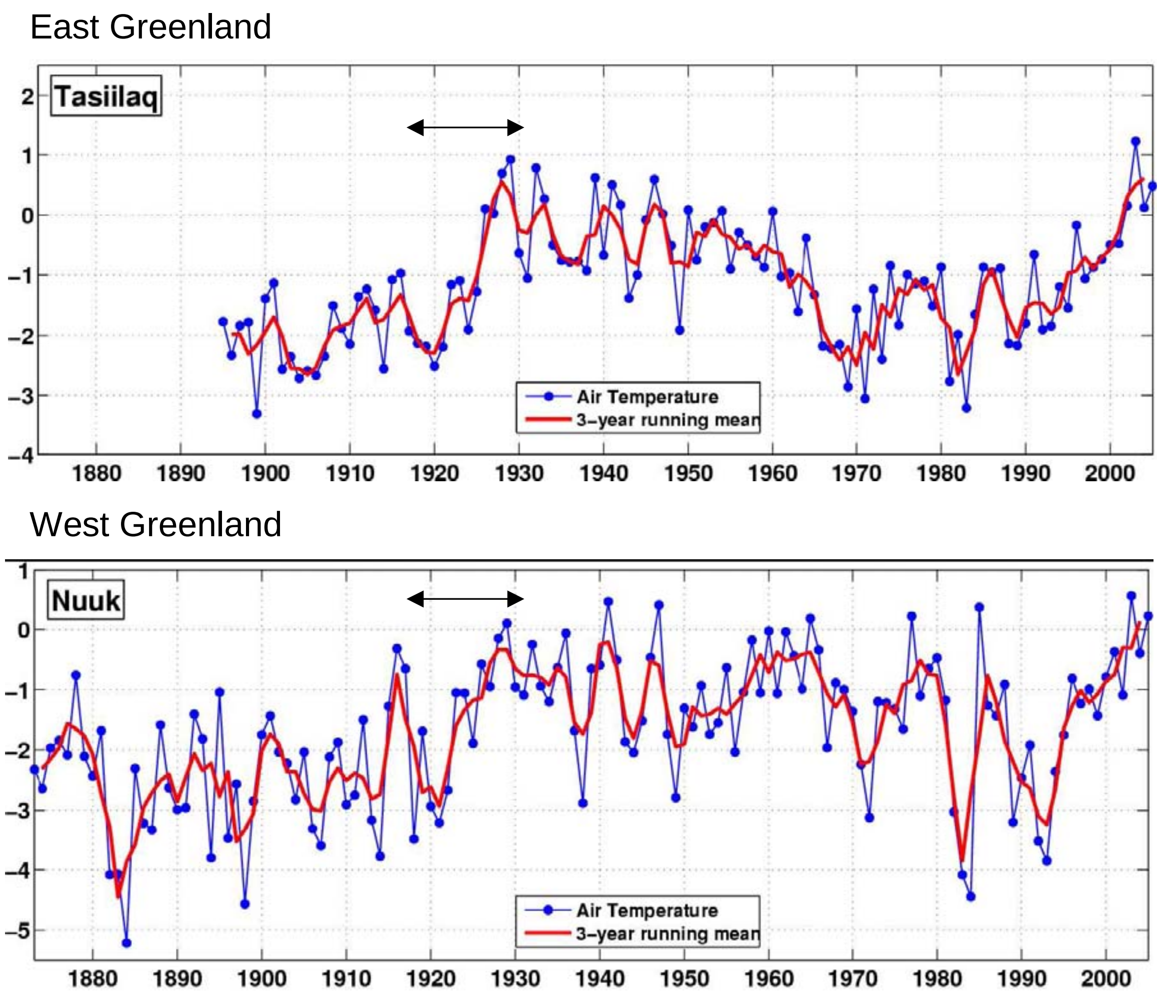
Period: **1999 - 2005** Survey data (Biomass, SSB, Recruitment)

	Biomass (kt)	SSB (kt)	Catch (kt)	E' (%)	Recruitment at age 3 (10^3)	Temperature (°C) Surface	Temperature (°C) Bottom
Range	4.2 - 135.0	1.7 - 33.3	0.0 - 0.8	0.4 - 8.9	0.5 - 19.1	1.7 - 3.8	3.9 - 5.5
Average	39.568	12.709	0.332	2.63	4.651	2.62	4.77
Average annual change	21.800	5.257	0.067	-1.39	3.093	0.20	-0.11

Significant factors for biomass change in multiple regression: n.a. (insufficient number of observations)

Both periods of recovery combined:

Significant factors for biomass change in multiple regression: Recruitment



East Greenland

West Greenland

Figure 1: Air temperatures at East and West Greenland (Ribergaard, 2006; arrows indicate period of cod invasion of East and West Greenland offshore waters).

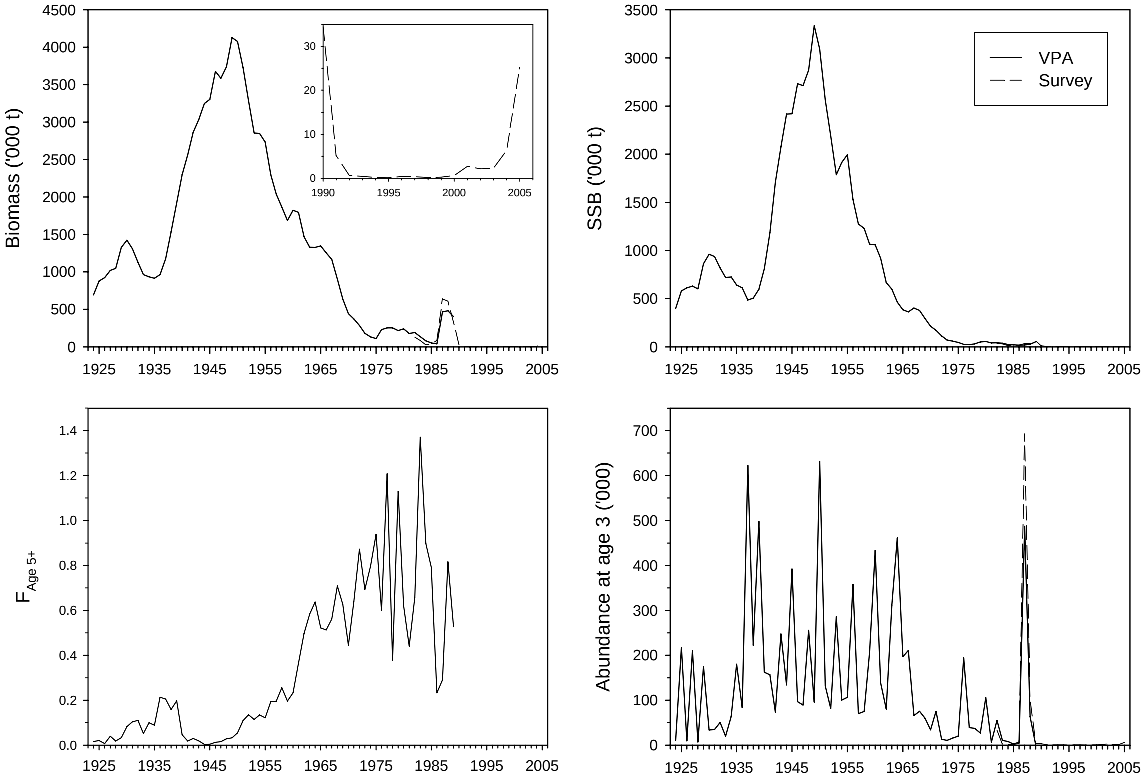


Figure 2. Total biomass (VPA: age 3+; survey: all ages), spawning stock biomass, average fishing mortality (age 5+) and recruitment at age 3 for Atlantic cod at West Greenland (VPA data: Buch *et al.*, 1994; survey data: Fock *et al.*, 2006).

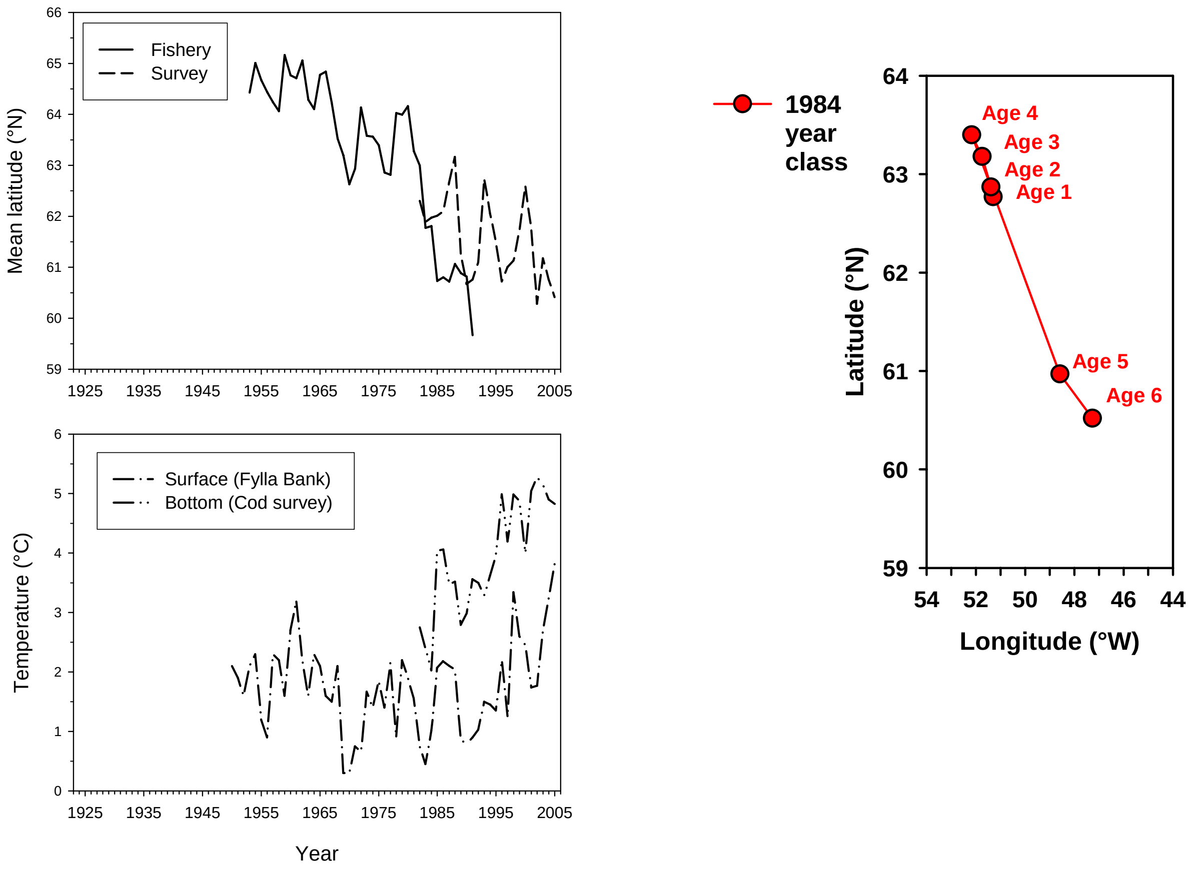


Figure 3. Changes of latitudinal distribution of Atlantic cod catches and survey biomass in comparison of time series of surface and bottom water temperature off West Greenland together with the change of center of mass with age for the 1984 year class (Catch data: Horsted, 2000; survey data incl. bottom temperature: Fock *et al.*, 2006, Surface temperature: Ribergaard, 2006).

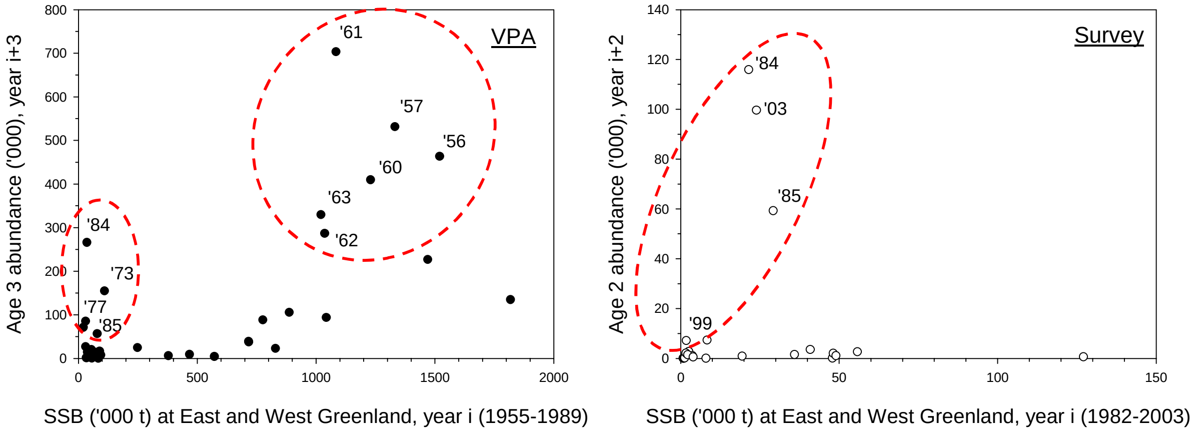


Figure 4. Stock-recruitment plots for Atlantic cod in East and West Greenland offshore waters combined (numbers at symbols indicate year classes; stippled circles enclose year classes with substantial contribution of recruits from Iceland; VPA data: ICES, 1996; survey data: Fock *et al.*, 2006).

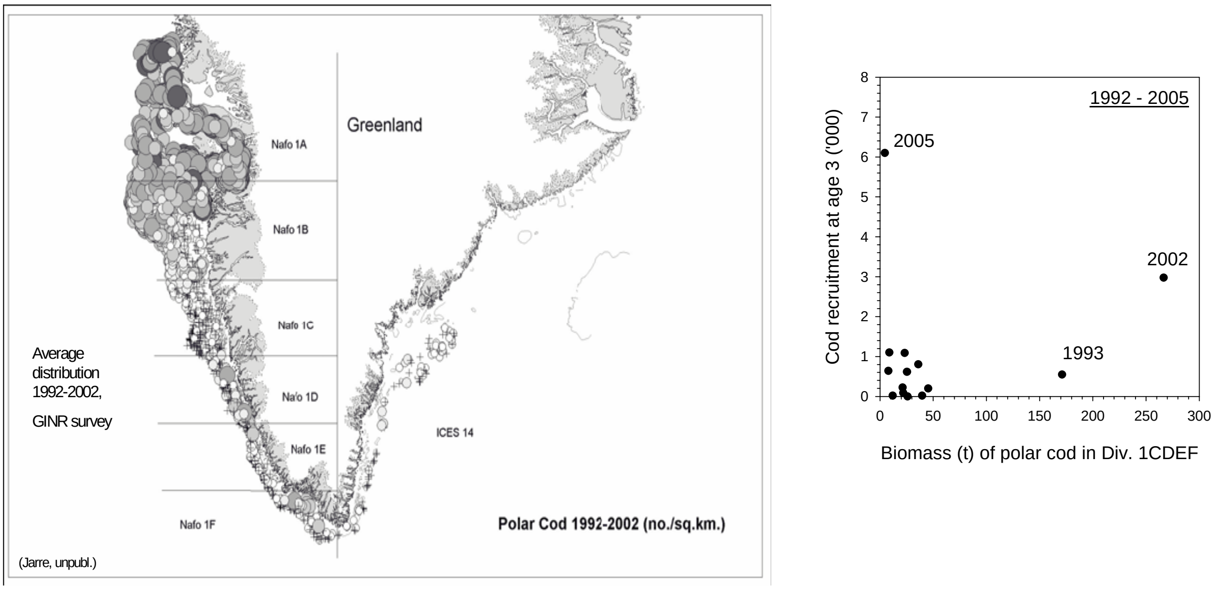


Figure 5. Average distribution of polar cod and comparison of biomass of polar cod off Southwest Greenland (NAFO Divisions 1C to 1F) with Atlantic cod recruitment at age 3 (numbers at symbols indicate years; GINR: Greenland Institute of Natural Resources).

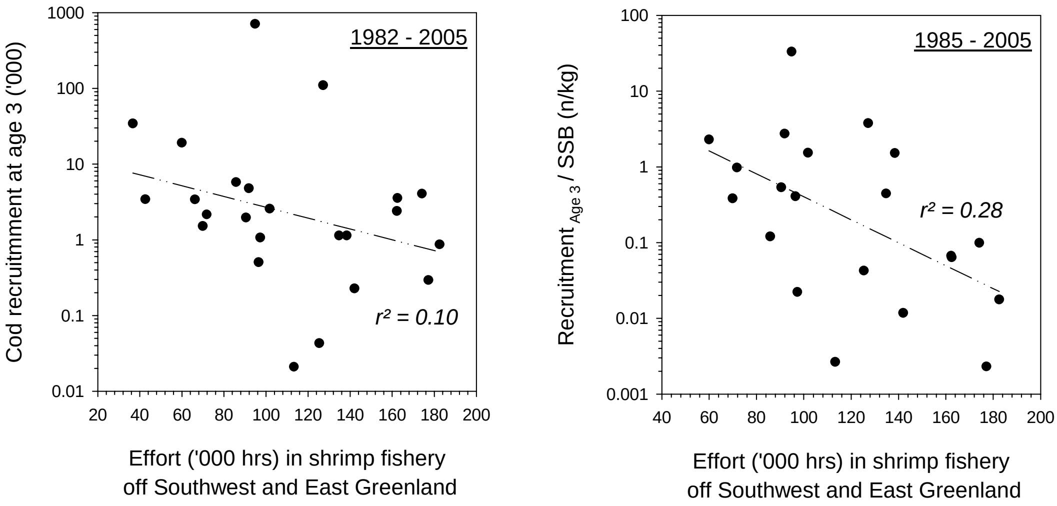


Figure 6. Comparison of Atlantic cod recruitment at age 3 (VPA data; ICES, 1996) and recruitment at age 3 per spawner biomass (survey data; Fock *et al.*, 2006) for East and West Greenland combined with effort in the fishery for northern shrimp off Southwest and East Greenland (NAFO divisions 1C to 1F and ICES area 14).

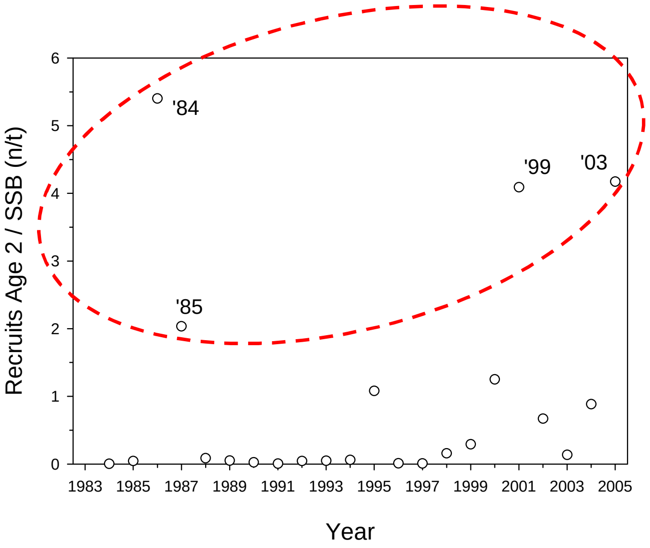


Figure 7. Time series of recruitment at age 2 per unit of spawner biomass for Atlantic cod off East and West Greenland combined (numbers at symbols indicate year classes; stippled circles enclose year classes with substantial contribution of recruits from Iceland; survey data: Fock *et al.*, 2006).

Extended abstract 8

Long-term (1913–2004) changes in the age-structure of Arcto-Norwegian cod strengthens climate-recruitment link

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The recent overexploitation of marine fish populations typically results in the loss of the largest individuals, decreasing the mean age as well as the age diversity of the spawning stock (Law, 1991, 2000; Caddy and Agnew, 2003). Ottersen *et al.* (2006) document such a development for the large, heavily-fished Arcto-Norwegian stock of cod (*Gadus morhua*) for the period 1943–2002. They further examine the consequences with regards to the impacts of environmental fluctuations on recruitment and describe mechanisms that may apply also to other stocks with a high fishing pressure.

In this presentation I, by means of VPA values made available by Hylen (2002), am able to expand the study period to 1913–2004. The age composition of the spawning stock has changed distinctly during this period (Figure 1). The age of the average spawner was between 10 and 12.5 during the period 1913–1950, but has since then decreased by more than 3 years to 7–8 (Figure 2a). This development is unfavourable due to the reproductive capacity of older, larger cod being disproportionably higher than that of younger, smaller individuals. The mechanisms involved are, however, many and complex.

Experimental work by Kjesbu *et al.* (1996) shows that larger and older females tend to have a longer spawning period than smaller and younger fish. Larger females tend to produce a relatively greater number of eggs, i.e. the number of eggs produced per gram body weight increases with increasing length (Marteinsdottir and Thorarinsson, 1998). Repeat spawners also produce eggs that have a wider range of vertical distribution than recruit spawners, thus causing broader horizontal dispersion (Kjesbu *et al.*, 1992).

The size of cod eggs and larvae generally increases with maternal size (Chambers and Waiwood, 1996; Kjesbu *et al.*, 1996; Trippel *et al.*, 1997; Vallin and Nissling, 2000), increasing also viability, as both field studies (Meekan and Fortier, 1996) and theory (Houde, 1987) suggest a tendency towards increased survival among faster growing larvae ("bigger is better"). Furthermore, experimental studies have more directly shown that larger egg size leads to increased survival of cod eggs (hatching success; Solemdal *et al.*, 1995) and yolk-sac larvae (Nissling *et al.*, 1998), although the latter study found no effect of egg size on viability up until hatching. In addition, older fish may have a key role in spawning migrations, perhaps involving learned behaviour (Rose, 1993). Collectively, these studies indicate that the proportion of older and larger fish present in a population may contribute significantly towards determining the number of successful recruits.

The development I find in the number of age classes contributing to the spawning stock of Arcto-Norwegian cod, as estimated by the Shannon diversity index, is characterized by pronounced short-term variability, but also of a decreasing trend since the early 1950s (Figure 2b). This is expected to be an unfavourable development in regard to the stock's reproductive capability. A diverse stock structure is likely to enhance a population's reproductive potential through size- or age-dependent differences in timing, duration or location of spawning, ensuring that a sufficient number of eggs and larvae encounter environmentally favourable conditions. There is extensive evidence in support of such mechanisms over a broad range of stocks including cod (O'Brien *et al.*, 2003) and haddock (*Melanogrammus aeglefinus*; Marshall *et al.*, 2003) on Georges Bank, Icelandic cod (Marteinsdottir and Thorarinsson, 1998), herring (*Clupea harengus*) on the east coast of Canada (Lambert, 1987,1990), and striped bass (*Morone saxatilis*) in Chesapeake Bay (Secor, 2000).

Recruitment to the Arcto-Norwegian cod stock has varied extensively. There is evidence for fluctuations in climate, particularly sea temperature, being a main cause for this variability, higher temperatures being favourable for survival throughout the critical early life stages (Ellertsen *et al*. 1989, Ottersen and Sundby 1995, Ottersen and Stenseth 2001). The present analysis presents compelling evidence for a strengthening of the climate-cod recruitment link during the last decades. The correlations between climate and cod recruitment increase throughout most of the study period (Figure 3a). I propose that this enhanced climate–recruitment link is influenced by the reduction of age and, to a lesser degree, age diversity in the spawning stock, leading to the cod population becoming less robust towards adverse climate conditions. There is statistical substantiation for the climate–recruitment link strengthening with reduced age of spawners, as suggested in Figure 3b.

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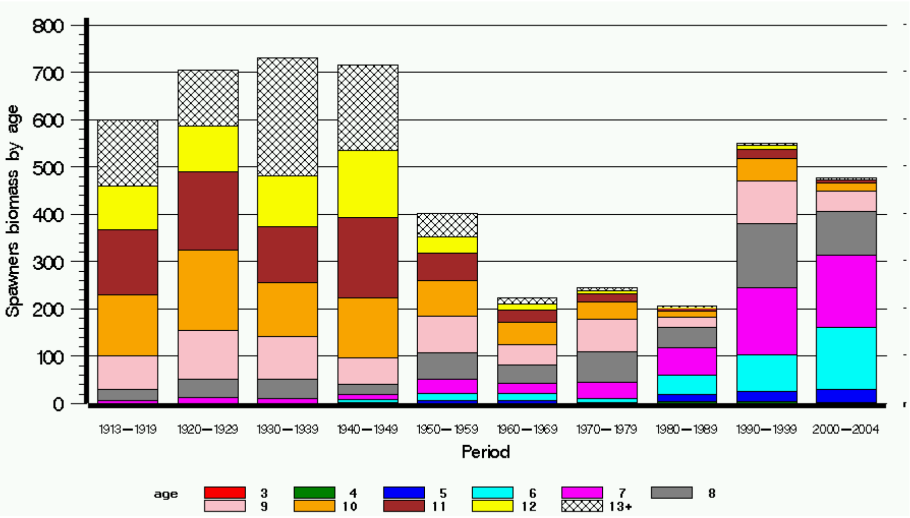
SPAWNING STOCK BIOMASS BY AGE (1000 tonnes)



PERCENT SPAWNING STOCK BIOMASS PER AGE

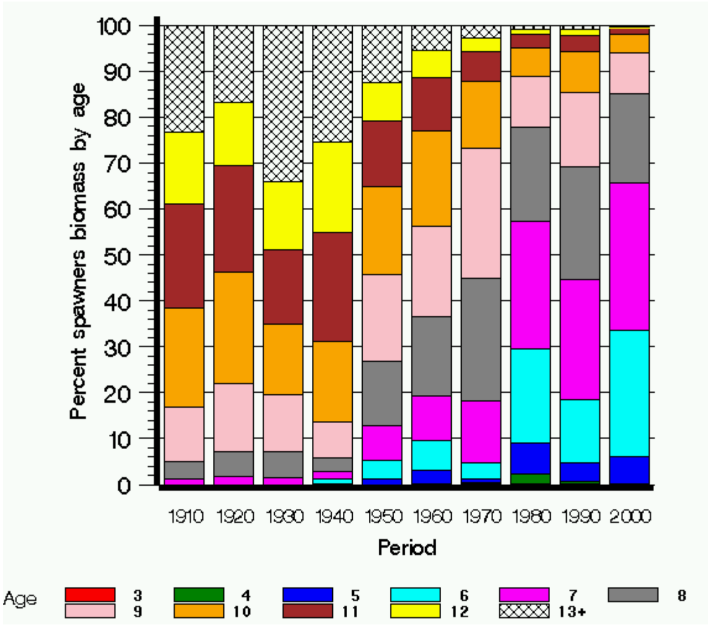


Figure 1. Decadal mean spawning stock biomass (SSB) in each age group (upper panel). Decadal mean percentage of SSB in each age group (lower panel).

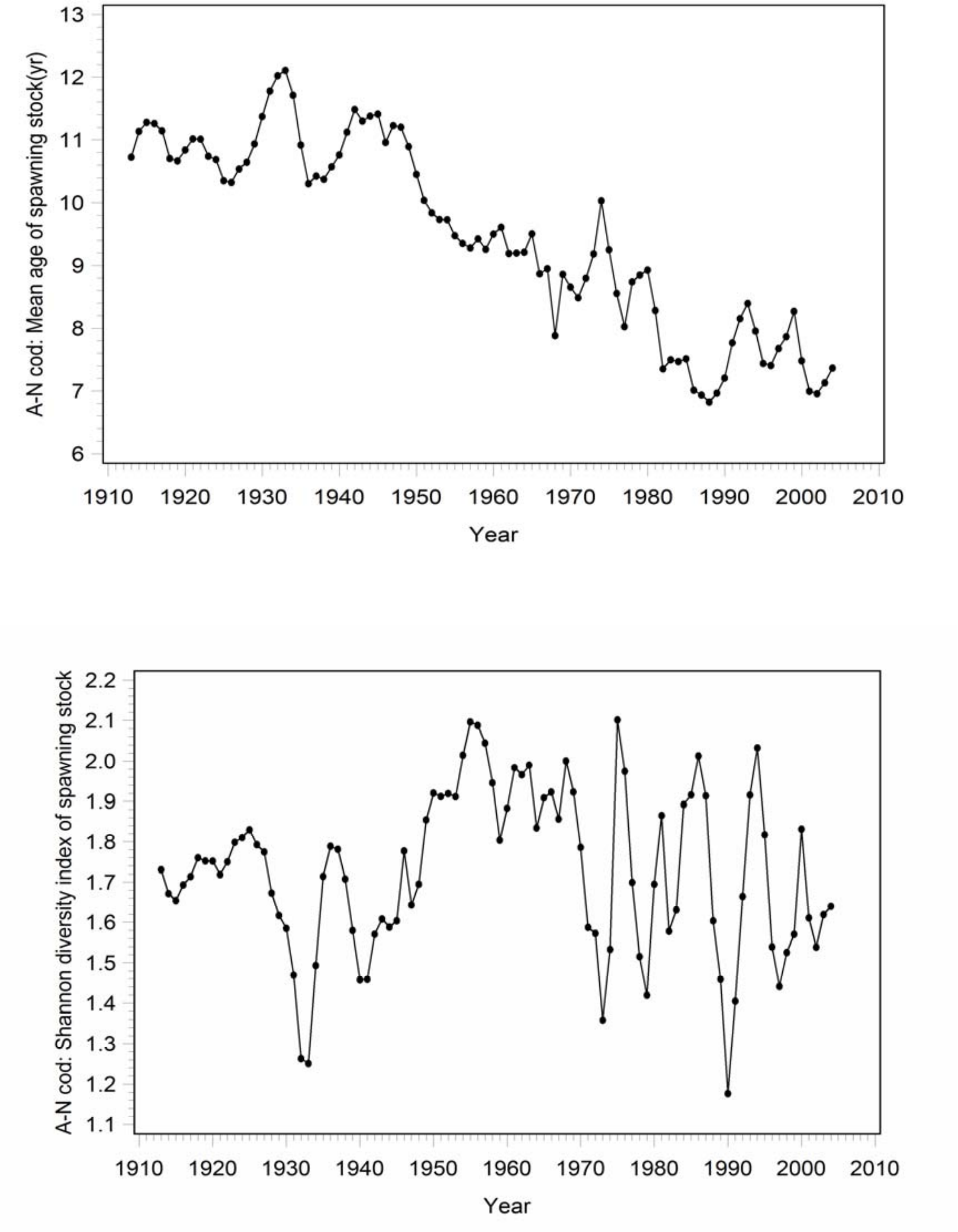


Figure 2. Biomass weighted mean age in the spawning stock (upper panel) and Shannon diversity index of spawning stock biomass by age (lower panel). For details on the calculation methods see Ottersen *et al.* (2006).

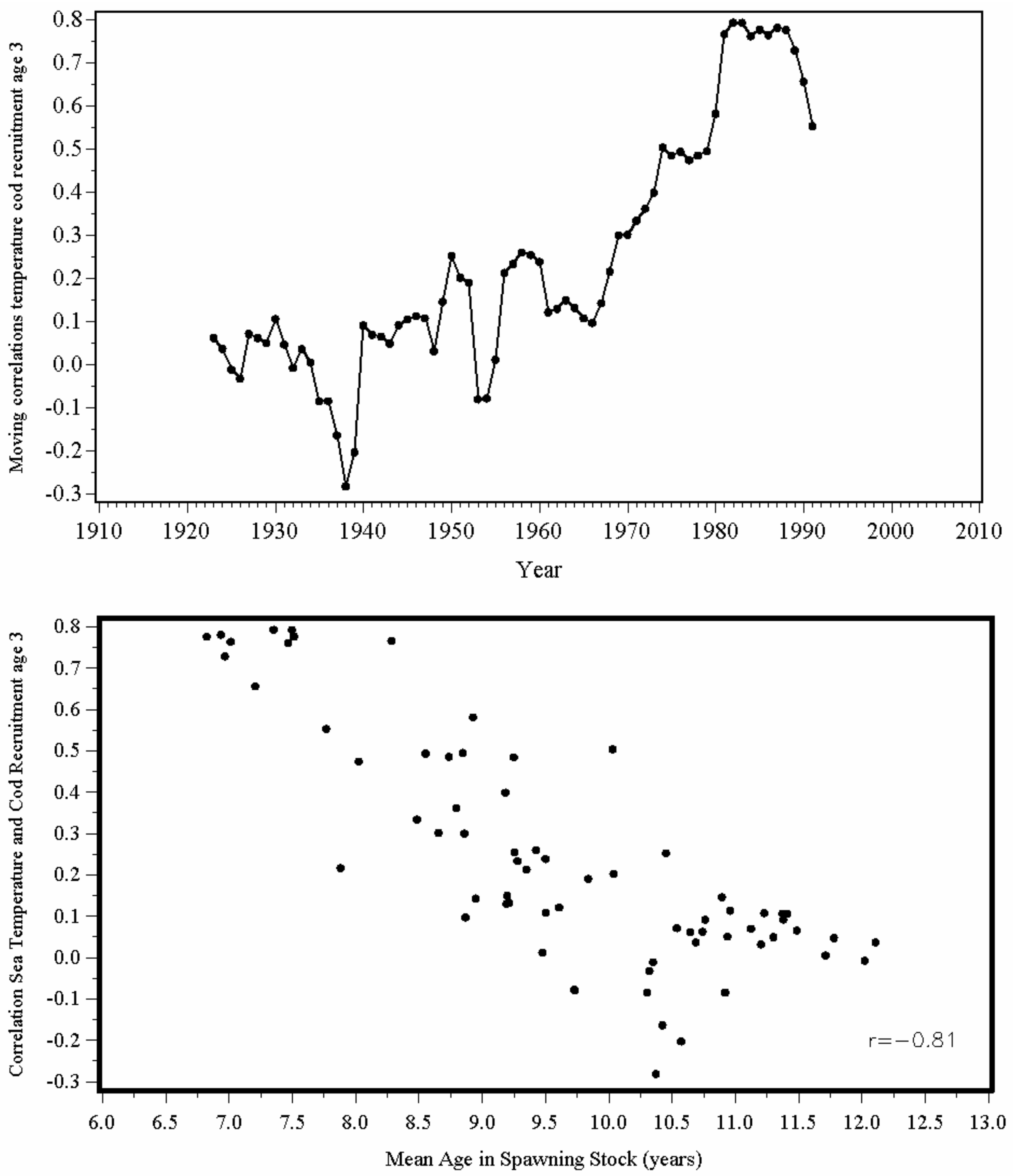


Figure 3. Upper panel: 21-year moving correlations between annual mean temperatures in the Kola-section and cod recruitment as estimated by VPA at age 3. Lower panel: Mean age in the spawning stock vs the correlations from the upper panel.

Extended abstract 9

Decline and recovery of cod (*Gadus morhua* L.) along the eastern Skagerrak coast in relation to population structure and offshore recruitment

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Introduction

The cod stocks in the Skagerrak and Kattegatt have declined in abundance, dispersal and size distribution since the 1970s (Degerman, 1985; Pihl and Ulmestrand, 1993; Svedäng, 2003; Svedäng and Bardon, 2003; Cardinale and Svedäng, 2004; ICES, 2005a,b). This decline is especially pronounced in inshore areas such as the eastern Skagerrak coast. Furthermore, when regular trawl surveys were resumed in 2000, very low abundance of cod >300 mm was observed in inshore areas along the Skagerrak coast, compared to historical records from the 1920s to 1970s (Svedäng, 2003). In contrast to low adult abundance, cod catches were dominated by immature fish that disappeared when they grew older. The persistently low abundance of adult cod thus coincides with high abundance of juvenile cod in some years (Pihl and Ulmestrand, 1993; Svedäng, 2003), suggests that the inshore demersal fish populations are presently regulated by recruitment from offshore sources, while historical information indicate that spawning aggregations were common in these areas.

It has been hypothesised that most juvenile cod at the eastern Skagerrak coast are recruited from offshore spawning areas mainly in the North sea (Svedäng, 2003; Cardinale and Svedäng, 2004), from which they are passively transported (Munk *et al.*, 1995; 1999). The following [unexpected] low abundance of adult of cod was suggested to be due to return migration of juvenile/ maturing fish at a certain size or age (c.f. Pihl and Ulmestrand, 1993). This theory was further supported by the fact that a relatively strong year class of cod in 2001 in the Skagerrak was genetically assigned to be originating from eastern North Sea cod populations, in contrast to the results in the year before when genetic analysis suggested local origin (Knutsen *et al*., 2003; 2004).

In similarity to 2001, cod recruitment in the Skagerrak was also high in 2003 (ICES, 2005b). It was therefore of interest to further elucidate the population dynamics of cod along the Swedish Skagerrak coast after a high, episodic recruitment event. It was thus assumed that also the year class in 2003, according to its strength and dispersal in the Skagerrak, originated from offshore spawning grounds.

Recolonisation of areas depleted of cod stocks, such as along the Swedish Skagerrak coast (Svedäng, 2003), should be related to the general recruitment level and to dispersal rates (e.g. Stenseth *et al.*, 2005). However, one alternative hypothesis is that juvenile fish do not remain where they once have settled, unless they are in close vicinity to their parental spawning grounds. It was thus conjectured that the temporal development in distribution of cod in various size classes after a major recruitment event, should be a reflection of the migratory behaviour of its offshore origin. Accordingly, recolonisation in such a case will be a much slower process than otherwise anticipated. In this study, a temporal analysis of cod juvenile abundance in the eastern Skagerrak coast was made by using trawl survey data 2001–2005, comprising intense sampling both in inshore areas and off the coast.

In addition, as the temporal and spatial variation of the cod decline on the eastern Skagerrak coast is informative regarding the original population structure, a short summary on this subject was included.

Material and methods

Between 2000 and 2005, trawl surveys have been carried out by RV “Ancylus” along the Swedish Skagerrak coast. The stations were selected partly on previously fished stations as well as new information about suitable fishing grounds. Some areas were monitored already in 2000, whereas other areas and trawling stations were established 2001–2002.

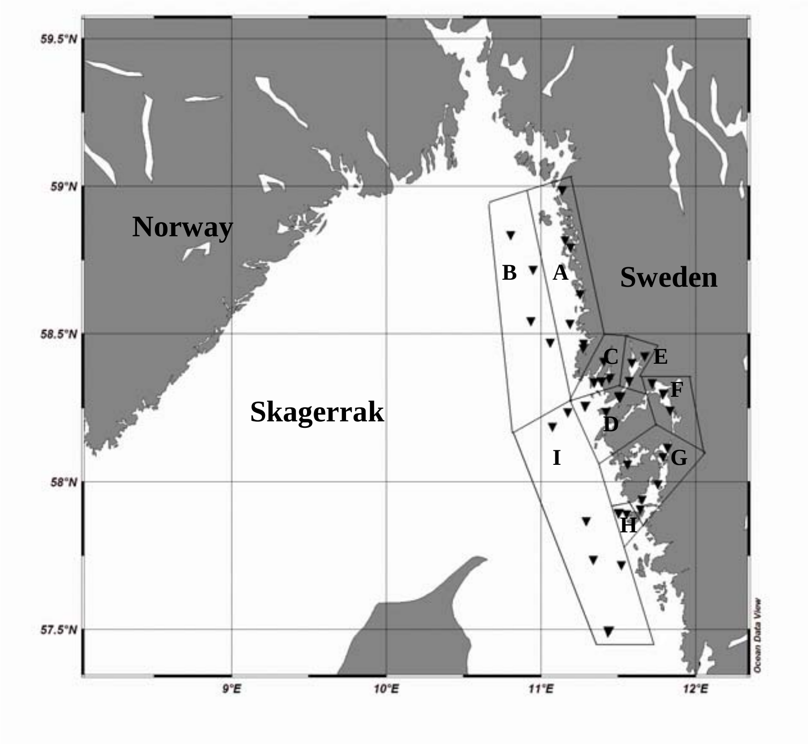

Figure 1. The study area along the eastern Skagerrak coast. Positions of trawling stations are indicated with inverted filled triangles. Delimitation of subareas are shown: A-Northern Skagerrak coast; B-Outer northern Skagerrak coast; C-Brofjord area, D-Outer part of the Gullmarsfjord; E-Inner part of the Gullmarsfjord; F-Havstensfjord; G-Hakefjord area; H-Marstrandfjord; I-Outer southern Skagerrak coast.

In this study, the trawling stations have been arbitrarily classified into different subareas according to hydrographical conditions, geographical dispersal, and similarity in catch development into nine (Figure 1)

Results

Decline part

Brofjord area

Survey cpue of cod (in weight) in the Brofjord area was drastically lower in 2000 and 2003 (unweighted mean for seven surveys: 1.5 kg h^{-1}) compared to values obtained during similar surveys in 1968–1980 (mean value 96 kg*h^{-1}; n=32; Figure 2).

It should also be observed that the catch rate in 1968-1980 showed a pronounced seasonal variation: cpue values were higher from January to March than in other parts of the year.

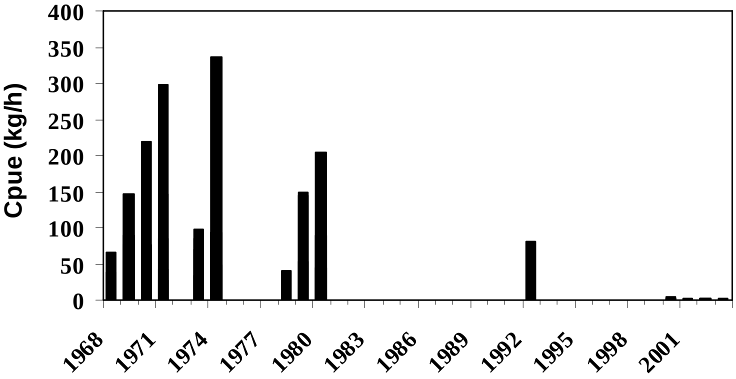

Figure 2. Mean cpue of cod by year: survey data from the Brofjord area, 1968–1980, and 2000–2003 (Modified from Svedäng, 2003).

This seasonal variation and the fact that sexual mature fish were observed in large amount indicates spawning activity in the Brofjord (Hallbäck *et al.*, 1974). In addition, tagging experiments conducted in the beginning of 1970s showed a high degree of stationarity and return migrations during the spawning season.

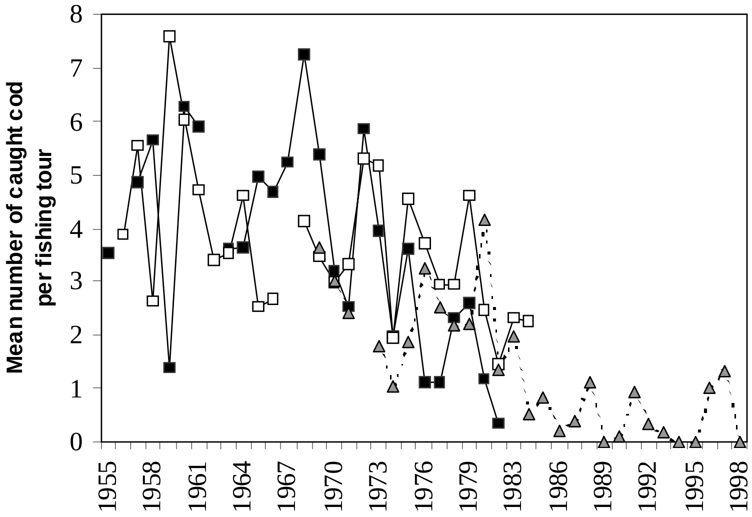

Figure 3. Leisure fishing index from the southern Skagerrak coast: Mean cpue of cod in number per fishing participant and fishing trip for three sport fishing club data sets (Svedäng, 2003).

The three time series obtained from sport fishing clubs varied regarding the period covered but all exhibit significant declines (Svedäng and Bardon, 2003; Figure 3). The declines do not completely coincide in time: in the more inshore area, the decline occurred at an earlier stage than in themore offshore area, at least for sfc A. The data from sfc B provide clear evidence that cod densities have remained extremely low throughout the 1980s. A comparison between the (normalized and smoothed) cpue in the offshore Nephrops trawl fishery in the Skagerrak and in the three sfc data sets suggests that the decline in inshore areas preceded the decline offshore by about 5–10 yr .

Recovery part

Temporal development in catch rates

Annual mean cpue of cod (in weight) was at very low levels in the beginning of 2000s along the entire eastern Skagerrak coast (Figure 5a).

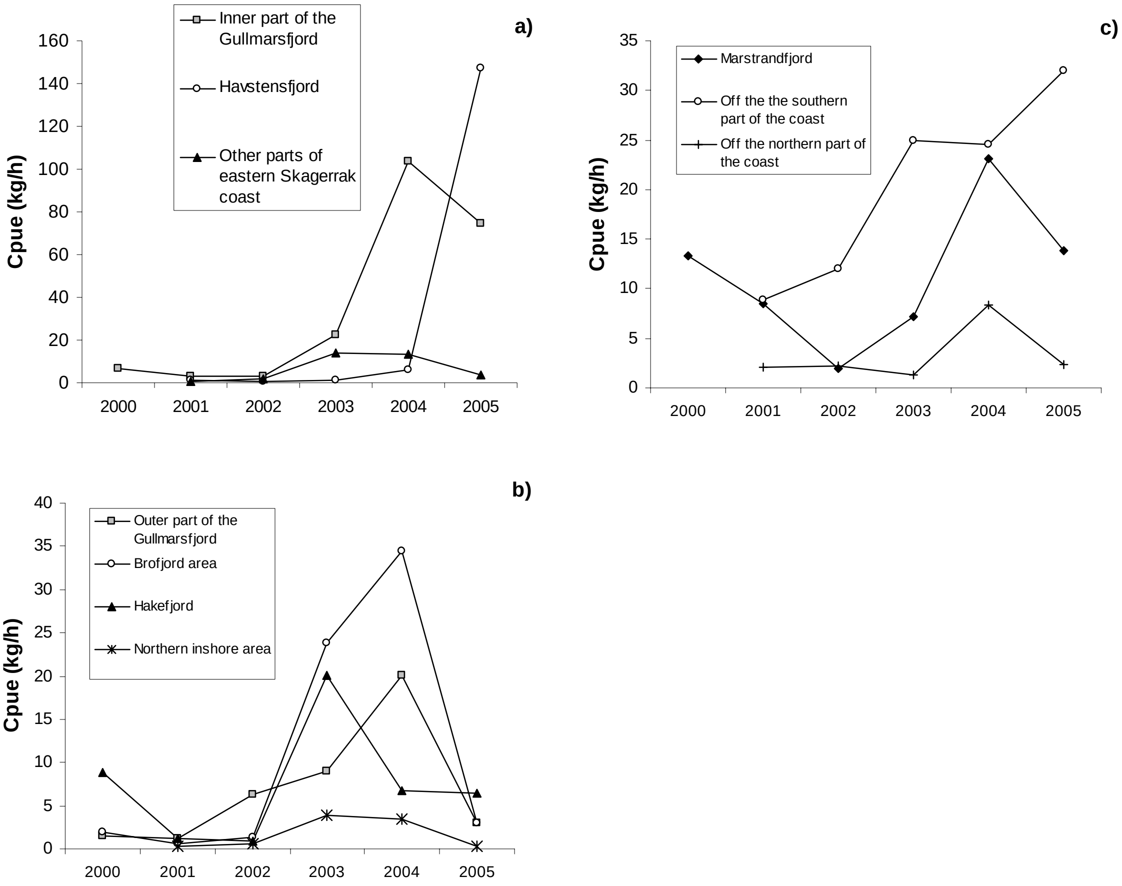

Figure 5. The annual mean cpue of cod (kg*h^{-1}) in the coastal survey between 2000 and 2005. a) Inner part of the Gullmarsfjord and Havstensfjord. A mean cpue for all other inshore subareas (i.e. the subareas shown in Figure 2b) is included for comparison; b) the northern Skagerrak coast, Brofjord area, Outer part of the Gullmarsfjord and the Hakefjord area; c) the outer northern Skagerrak coast, Marstrandfjord and the outer southern Skagerrak coast.

Cpue increased substantially along the whole coast in 2003 (Figure 5a–c). The increased catch rate in 2004 was stronger in the inner part of the Gullmarsfjord than elsewhere. In 2005, cpue decreased in all inshore areas but the Havstenfjord, where a marked increase in cpue could be observed. This marked decline was also discernible in the Gullmarsfjord, although cpue in this locality remained at a higher level. Off the southern part of the coast, cpue increased rather monotonically between 2001 and 2005 (Spearman's rho=0.90; $p<0.05$).

Discussion

In spite of a reduction in fishing pressure in recent years (e.g. removal of the trawling limit from 2 to 4 nautical miles from the base line), and high cod recruitment in the Skagerrak region in 2001 and 2003, no general recovery could be evidenced. The survey data clearly showed that low cod density areas were not recolonised, even though abundance of juvenile cod remained high for about a year after the recruitment episodes. Increased abundance of fish larger than 400 mm was only discernible at some scattered locations where other studies also have suggested local populations still to be present. The intermittent high recruitment has been linked to an inflow of egg and larvae from the North Sea, a theory which also has gained support from genetic studies. It was thus argued that the disappearance of the juvenile cod from the inshore is an effect of a migratory behaviour; the fish of offshore origin eventually leave the coast for the open Skagerrak or the North Sea.

The results of the trawl survey reported in this study revealed a very clear-cut pattern for all subareas where almost no cod longer than 400 mm were observed from 2001 to 2005: enhanced recruitment in 2001 in some localities, and along most of the Skagerrak coast in 2003, whereas recruitment in all other studied years was overall low. High abundance of cod, in size groups corresponding to one year old fish, was consistently observed in all localities in 2004, except in the Havstensfjord. Finally, abundance of cod declined in 2005 in all those areas. This development coincided with an increase in cod abundance off the coast 2002–2005.

One simple explanation to the observed temporal development in cod abundance would be that cod propagules from offshore spawning grounds have successfully settled in the coastal region in 2001, and, in particular, in 2003. Increased abundance of one year old cod in 2004 was consequently due to the better recruitment in 2003. The disappearance of this year class from the coastal region in 2005 was tentatively explained as an effect of migration off the coast. Increased abundance of two year old cod off the coast in 2005, was supporting for such a conclusion.

Observations of cod, in size groups corresponding to higher age classes, were made in two specific areas in the coastal zone: in the inner part of the Gullmarsfjord and the Havstensfjord. Genetic analysis on adult and juvenile cod from the Gullmarsfjord has suggested a local cod population, genetically divergent from the west Skagerrak/ eastern North Sea populations (Knutsen *et al.*, 2003, 2004). Sexual mature cod have also been observed (Svedäng *et al.*, 2004) during the spawning period in winter/ early spring (c.f. Vitale *et al.*, 2005). In the Havstensfjord, large catches of adult-sized cod were still made in the purse seine fishery during the winter 1997/1998, in contrast to most other areas along the Swedish Skagerrak coast (Arrhenius *et al.*, 1998). This observation could imply that a remnant local population in the Havstensfjord has survived, and has begun increasing in population size in recent years. It is also possible that the observation in Havstenfjord is an outlier, e.g. the migration from the coast to the open Skagerrak in this inshore area has been delayed for a shorter period of time.

The alternative explanation to the disappearance of two year old cod in 2005 along most of the Skagerrak coast would be an extremely high mortality rate for fish larger than 400 mm in total length. However, fishing intensity has decreased since 2004 as trawling limit has been removed from 3 to 4 nautical miles from the base line, including some areas inside the trawling limit where trawl fishery previously has been allowed. There has also been implemented a total ban on cod fishery in the first quarter of the year and the purse seine fishery has been restricted. Ironically, the environmental degradation is most prounouced in remote inshore areas such as the Havstensfjord (Anon. 2003), where a cod population evidently has shown some growth in size. All other possibilities, such as predation from seals and cormorants, parasites and deseases, cannot be completely ruled out, however, as our knowledge of all kinds of responses in the ecosystem is imperfect. Nevertheless, the likelihood for such massive kills, as it would inflict, has to be considered as low.

This study support the view that the present population dynamics of cod stocks in the eastern part of the Skagerrak depend on transport of recruits from offshore spawning areas (Munk *et al.*, 1995; 1999), and on return migration of juvenile and/or maturing fish when they reach a certain size or age (Pihl and Ulmestrand, 1993; Svedäng, 2003). This hypothesis has been supported by the observation of a general lack of correlation between recruitment (no trend during the past two decades) and abundance of cod >300 mm (significant decline) in the Skagerrak-Kattegat area (Cardinale and Svedäng, 2004).

In addition, a tagging study in the 1980s along the Swedish west coast, reported such a migratory behaviour in cod juveniles (Pihl and Ulmestrand, 1993). Already at this moment of time, most of the former coastal cod population structure was severely depleted (c.f. Svedäng, 2003), and the impact on recruitment from offshore resources was obvious. Similar results have been obtained in on-going tagging study in the Gullmarsfjord and off the Skagerrak coast (pers. obs.). These findings clearly suggest a strong behavioural component in the distribution pattern of cod in the eastern North Sea region.

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Extended abstract 10

The long-term decrease of cod recruitment in the North Sea – the mechanistic links to ocean climate, water mass characteristics, and the large-scale dynamics of *Calanus finmarchicus*

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The population of *Calanus finmarchicus* is a major food organism for many of the large fish stocks in the Northeast Atlantic region. Long-migrating pelagic species, such as the Norwegian spring spawning herring, the Atlantic blue whiting and Atlantic mackerel are summer feeding on the adult population of *C. finmarchicus* in its core production region in the Norwegian Sea. The larval and juvenile populations of the major fish species along the shelf regions surrounding the core production area in the Norwegian Sea are dependent on the early stages of *C. finmarchicus* for growth and survival. Since the distributions of the younger stages of fish at the surrounding shelves do not overlap with the distribution of the core production area, advective transport of *C. finmarchicus* onto the shelves is considered to be an important process in supplying food to the larval and juvenile fish populations. This mechanism has been described for advection of *C. finmarchicus* from the northeastern Norwegian Sea into the Barents Sea (Skjoldal and Rey, 1989; Helle and Pennington, 1999). Here, strong inflow of Atlantic water from the Norwegian Sea into the Barents Sea is associated with advection of warm and *Calanus*-rich water masses. For the North Sea similar process has been studied by Heath (1999).

North Atlantic cod stocks show adverse recruitment responses to changes in ambient temperature (Ottersen, 1996; Planque and Frédou, 1999). For cod stocks living at the lower temperature range (e.g. Barents Sea) years of above normal temperatures are generally associated with higher probability of strong recruitment, while for cod stocks living at the higher temperature range (e.g. North Sea and Irish Sea) years of above normal temperatures are generally associated with higher probability of poor recruitment. For cod stocks living in the middle of the temperature range recruitment show lower sensitivity to temperature changes (e.g. Icelandic cod). Sundby (2000) proposed a unifying mechanism for this particular relationship between temperature and recruitment in Atlantic cod where the key issue is that temperature is a proxy for the advection of *Calanus*-rich water masses from the core production region of *C. finmarchicus* onto the surrounding shelves. The mechanism is conceptually described in Figure 1. The general features are that the cod stocks at the European shelves are distributed at the fringe around the core production area of *C. finmarchicus* in the Norwegian Sea proper. An increase in the advection of *Calanus*-rich water masses in the Norwegian Sea proper onto the surrounding shelves will be associated with a corresponding temperature change. For advection onto the Barents Sea this will result in a temperature increase because the *Calanus*-rich water masses in the Norwegian Sea has higher temperature than in the Barents Sea (Panel A in Figure 1). For advection into the North Sea this will result in a temperature decrease because the *Calanus*-rich water masses in the Norwegian Sea to the north of the North Sea has lower temperatures than the water in the North Sea (Panel C in Figure 1). For stocks like the Icelandic cod which have ambient temperatures similar to the temperature in the core production area of *C. finmarchicus* and increase in the advection of the *Calanus*-rich water masses do not result in significant changes in the temperature (Panel B in Figure 1).

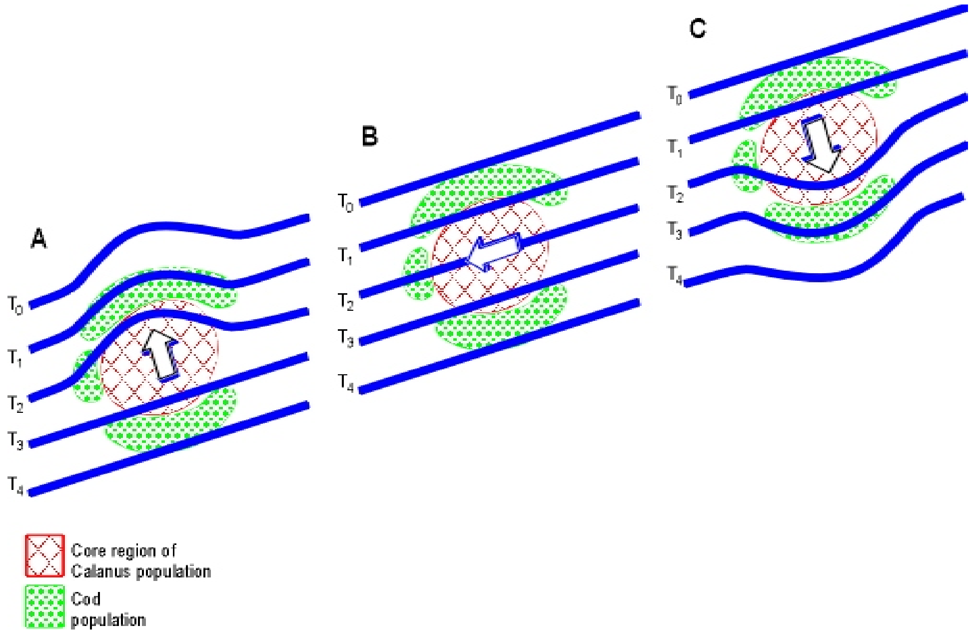

Figure 1. Conceptual model for the link between changes in advection, temperature, abundance of *Calanus finmarchicus* and recruitment in Atlantic cod stocks (Sundby, 2000).

In the northeastern Norwegian Sea the Atlantic water masses are the Calanus-rich water masses. Hence, increased influx of Atlantic water masses increases the advection of *C. finmarchicus* into the Barents Sea. Russian time series of zooplankton in the northeastern Norwegian Sea shows increasing abundances during the second half of the 20th century. During the same period the time series from the Sir Alistair Hardy Foundation for the ocean area to the north of the British Isles shows the opposite trend for the abundance of *C. finmarchicus* (Figure 2). This trend is also caused by the increased inflow of Atlantic water since the downstream abundance of *C. finmarchicus* is lower southeast of the Nordic Seas.

In the North Sea proper a similar decrease in the abundance of *C. finmarchicus* has occurred (Reid *et al*., 2003). It will be here shown that this decrease is linked to the general change in the ocean climate and to the advection pattern of water masses into the North Sea. Differently from the advection into the Barents Sea, where the Atlantic water is the conveyer for *C. finmarchicus*, it appears in the North Sea that the cool Norwegian Sea Intermediate Water (NSIW) is the conveyer for *C. finmarchicus*. The conclusion here is that the upper distribution of overwintering *C. finmarchicus* from the Norwegian Sea is carried with NSIW through the Norwegian Trench into the North Sea and fuels the subsequent spring and summer population of *C. finmarchicus* in the North Sea.

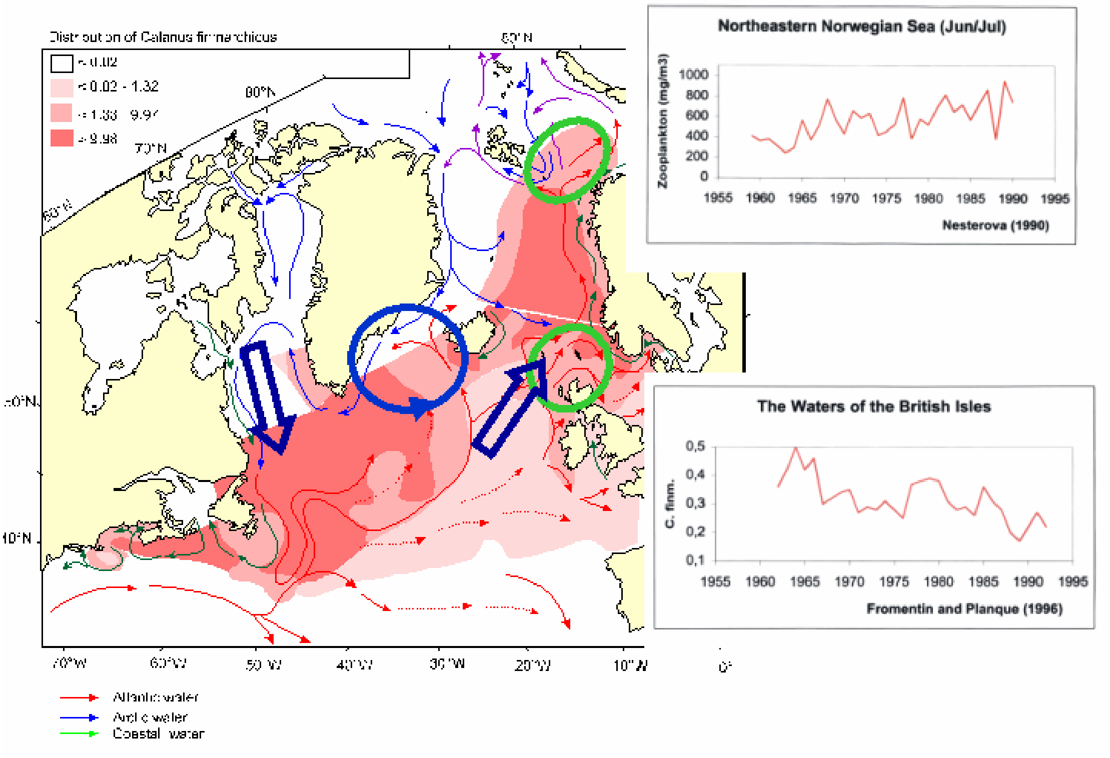

Figure 2. General distribution pattern of *Calanus finmarchicus* in the North Atlantic in relation to the currents (Sundby, 2000) and the long-term change of *C. finmarchicus* in two sub regions of the Northeastern Atlantic (Fromentin and Planque, 1996; Nesterova, 1990).

We have used: 1) hydrographical time series for the spring of the east-west section Feie-Shetland across the northern North Sea to show how the fraction of NSIW at the bottom of the Norwegian Trench varies between years, 2) results from the NORWECOM circulation model for the North Sea and adjacent waters to show that the inflow of Atlantic water (AW) to the North Sea and the inflow of NSIW are inversely correlated, and that the hydrographical observations of the fraction of NSIW from the Feie-Shetland section is positively correlated with the modelled inflow of NSIW, 3) results from the Atlantic basin-scale ROMS circulation model to show that the two branches of the Atlantic Current, northward into the Norwegian Sea along the Norwegian coast and southward into the North Sea, is positively correlated. Finally, 4) we have used the time series from the SAHFOS grids in the northern North Sea (C1, C2 and B2) to show that the spring/summer abundance of *C. finmarchicus* is positively correlated with the modelled inflow of NSIW during winter and inversely correlated with the modelled inflow of AW, and that the temperature observations at the bottom of the Norwegian Trench is inversely correlated with the subsequent abundance of *C. finmarchicus* during spring/summer.

These results lead to the conclusion that *C. finmarchicus* in the North Sea is supplied from the overwintering population of *C. finmarchicus* in the Norwegian Sea and that the Norwegian Trench is the gateway for *C. finmarchicus*. A warmer North Atlantic ocean climate with increased inflow of Atlantic water to the Nordic Sea has, therefore adverse effects on cod recruitment in the Barents Sea and the North Sea. Figure 3 shows conceptually how the recruitment is the two seas is influenced by the ocean climate.

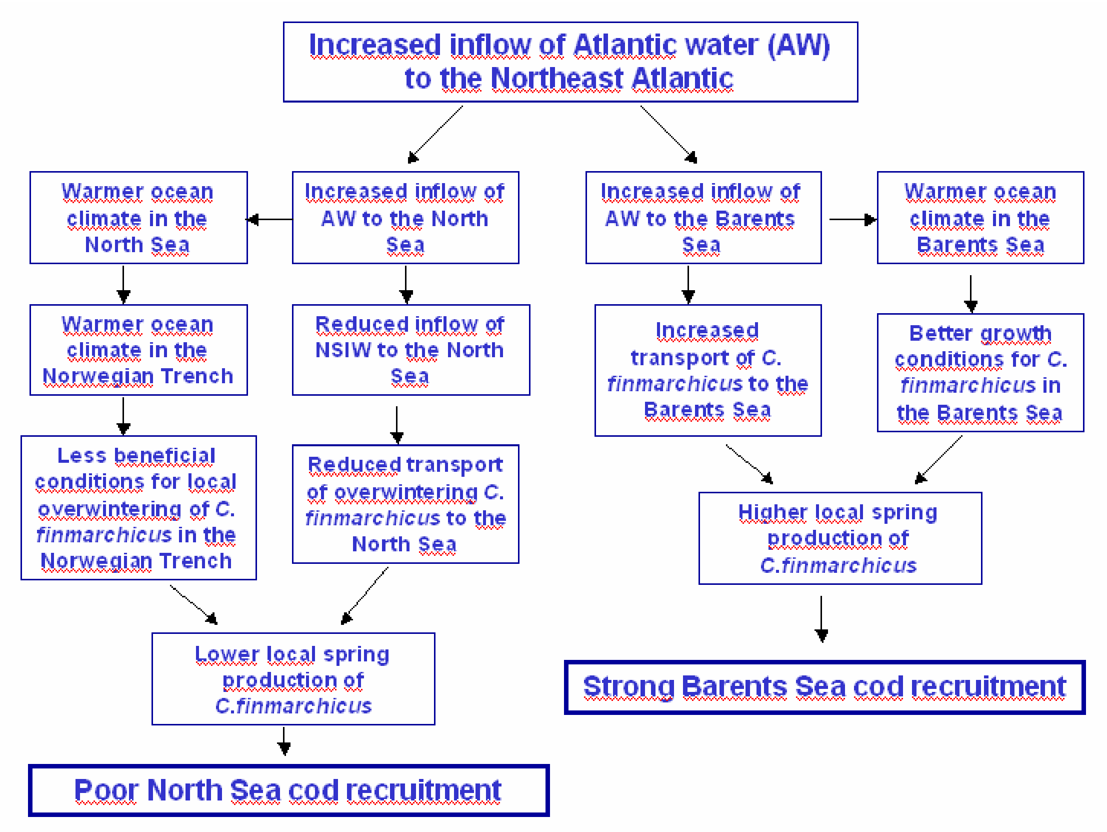

Figure 3. The concept of how increased inflow of warm Atlantic water to the Nordic Seas influence recruitment of cod from the Barents Sea and North Sea.

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Extended abstract 11

Eastern Baltic cod recovery: the importance of species interactions

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The Eastern Baltic cod stock declined from historic high during the early 1980’s to lowest levels on record in the beginning of the 1990’s, showing basically no sign of recovery afterwards (Figure 1). The Baltic sprat stock size increased to historic high level concurrently, whereas Central Baltic herring abundance remained relatively stable, while biomass declined due to a substantial decrease in weight at age. The decline of the cod stock was caused by a recruitment failure, which was mainly driven by: i) anoxic conditions in deep water layers of spawning sites causing high egg mortalities, ii) high egg predation by clupeid predators, iii) reduced larval survival due to the decrease in abundance of the main food item *Pseudocalanus acuspes*, and iv) high juvenile cannibalism at high stock size (Köster *et al*., 2005). The intensity and significance of all these processes are in one way or the other steered by the hydrographic conditions, which were in the 1990´s characterized by low salinity due to lacking inflow of highly saline water from the North Sea and increased run off, but as well by warmer thermal conditions. An increasing fishing pressure accelerated the decline of the cod stock, with current exploitation levels being still on a very high level. The decline of the cod stock released sprat from predation pressure, which in combination with high reproductive success, due to in general favourable temperature conditions enhancing egg and larval survival, resulted in exceptionally high sprat stock sizes in the 1990s (Köster *et al*., 2003). The present contribution investigates the importance of predation on early and juvenile life stages of cod for stock recovery. Indications for compensatory processes in growth, maturation and individual egg production exist as well, however, appear to be of limited impact on the cod stock dynamics.

Predation by herring and sprat has a significant impact on cod egg survival although being variable in time and space (Köster and Möllmann, 2000). In spring and early summer sprat predation on cod is important due to the spatio-temporal overlap in sprat spawning time with cod. In summer, herring is the principal predator of cod after returning from their coastal spawning areas to their deep water feeding grounds, while sprat have mainly left the area. Because the population of herring is presently substantially lower than that of sprat, predation pressure is higher in spring than in summer. Egg predation was found to be considerably lower in the Gdańsk Deep and Gotland than in the Bornholm Basin (CORE, 1998). Thus, only cod egg predation in the Bornholm Basin is considered in the present study.

Predation intensity in the Bornholm Basin depends on the vertical overlap between predator and prey. Köster *et al*. (2005) modelled the daily consumption of cod eggs by individual clupeids in spring and early summer as linearly related to cod egg abundance considering the vertical predator/prey overlap. The model is based on the observation that oxygen concentration in the bottom water limits the clupeid vertical distribution during the daylight-feeding period, while the density regime determines the vertical distribution of cod eggs. This results in clupeids dwelling below cod eggs in inflow situations whereas clupeids co-occur in high egg density water layers during stagnation years (Köster and Möllmann, 2000). Based on these observations, the average capture depth of clupeids and the average depth where highest cod egg concentrations occurred were combined into an index of vertical predator/prey overlap. Predation pressure by clupeids on cod eggs was determined over 1976-1992 using daily egg consumption rates by individual predators, predator population sizes from area disaggregated MSVPA and hydroacoustic survey results as well as standing stocks of cod eggs.

Comparing daily cod egg consumption rates by sprat and herring populations in the Bornholm Basin during cod spawning periods with daily production rates and standing stocks of cod eggs confirmed high predation by sprat during the early 1990s, when the cod spawning season was still in spring and early summer (Figure 2a). Predation was estimated to be above daily production and standing stocks in 1990–1992 and above the production in 1993. After the shift of cod spawning to summer, the importance of predation by herring increased, consuming 50 to >100% of the daily production and up to 50% of the standing stock. Assuming these consumption estimates were unrealistically high, and expressing the predation pressure in relative terms, i.e. as the ratio of daily consumption to production scaled to the maximum value determined for sprat in spring 1992 (Figure 2b), revealed a minimum of egg predation in 1993–1995. This can be explained by a combination of limited vertical overlap between predator and prey after the 1993 major inflow and the shift of cod spawning time to summer.

The effect of the shift in spawning time can be inferred from a seasonal comparison of the relative predation pressure during May/June and July/August 1994–1997 respectively. The predation pressure by sprat was approximately 2.5 times higher in spring/early summer than in summer, while the predation pressure by herring was approximately 8 times higher in summer than in spring (Figure 2b). The effect of the vertical predator–prey overlap can be deduced from a comparison between May/June 1990–1992 and 1993–1996. Sprat and herring predation decreased by a factor of 6.0 and 3.5, respectively (Figure 2b).

Comparing average daily rations of cod eggs by individual sprat and herring with egg abundance (Figure 2c), confirms that the individual egg predation by sprat follows closely the predator-prey overlap (Figure 2d), while the relationship is less obvious for herring. Comparing the oxygen related egg mortality during stomach sampling cruises (Köster *et al.* 2005) revealed a similar trend in hydrography induced egg mortality and predator - prey overlap and hence predation pressure (Figure 2d). This can be explained by the same hydrographic parameters affecting the vertical predator/prey overlap and oxygen related egg mortality, i.e. salinity and oxygen concentration. This is also obvious from a comparison of modelled relative predation pressure and oxygen related egg survival for the period 1966 until mid 1990s (Figure 3). Deviations in most recent years are caused by the shift of cod spawning time from spring to summer.

Decadal changes in cod cannibalism have been described by Uzars and Plikshs (2000). During 1963–1979 the distributions of young and adult cod were widespread, but separated in time and space, resulting in an overall low cannibalism. When the biomass of clupeids decreased in the late 1970s, competition for food and concurrently cannibalism increased. In the late 1980s, unfavourable oxygen conditions in the bottom water affected the benthic community negatively, and cod shifted from a benthic to a more benthopelagic mode of life utilising mysids and sprat as food resource. This distribution pattern is believed to have reduced cannibalism pressure substantially (BECAUSE, 2005).

A pronounced time trend in cod cannibalism is as well apparent from Multispecies Virtual Population Analyses (MSVPA) applying the 4M model (Vinther, 2001). On average 50% and 30% of the 0-group and 1-group cod were removed from the stock by cannibalism during the 1970’s and early 1980’s respectively. During the 1990’s the corresponding values were below 20 and 10% respectively. Age-specific differences in predation mortality are obvious, with cannibalism rates on 0-group being considerably higher than on 1-group cod (ICES, 2003).

Predation on 2-group cod was in general low, i.e. less than 50% of the applied residual mortality of 0.2.

Area-disaggregated MSVPA-runs conducted for ICES Subdivisions 25, 26 and 28 (ICES, 2001) confirmed the trends in population abundance and spawning biomass as derived in the different areas by research surveys. Results showed highest cannibalism on 0-group cod in Subdivision 25, i.e. the larger area of the Bornholm Basin, while predation on 1-group cod was historically highest in eastern areas, i.e. Subdivision 26 and 28, but reduced substantially in Subdivision 28 since late 1980's. The spatial/temporal trend of predation mortalities for age 1 confirm results from previous area-disaggregated MSVPA runs (Köster *et al.*, 2001), while 0-group mortalities showed a different spatial pattern. The rather high predation mortalities in the 1970's and 1980's as well as the inconsistent spatial pattern raised the question on the reliability of the estimates.

According to Neuenfeldt and Köster (2000), recruitment estimates from MSVPA runs are substantially affected by the choice of the suitability submodel and whether a suitability model is used at all. Deviations in recruitment estimates from MSVPA runs using different suitability models are obvious for the beginning of the time series. A MSVPA run without a suitability model (i.e. based on observed stomach content only) suggested highest recruitment for year-classes 1976 and 1977, while otherwise highest year-classes were determined for 1979 and 1980. The former result fits better to the larval abundance, indicating that the 1977 year-class may be under- and the 1980 year-class overestimated by the present MSVPA runs. However, independent of how prey selection is modelled in the MSVPA, cannibalism is confirmed to be a significant source of juvenile mortality at high cod stock size.

Alternative MSVPA runs using different stomach content data were applied to test for the effect on suitabilities. The 1. scenario comprised stomach content data from 1977 to 1983. These data contain most of the cod cannibalism observation over the whole time series. The 2. scenario comprised stomach content data from 1984 to 1993. Mainly the 0-group cod was subject to changing suitability in the different runs (Figure 4). Up to predator age 4 there was no major difference, but from age 6 onwards the usage of the 1977–1983 stomach data set generated clearly higher suitabilities of 0-group cod as prey.

To test for the effect of utilising these different suitabilities in medium-term multispecies projections the following forecast scenarios were setup:

1) Key-run: Food suitabilities as estimated by using stomach content data for the entire time period and recruitment estimated from a stochastic Ricker SSB-recruitment relationship.

2) Fpa: Similar to the Key-run, but prediction Fs were scaled to Fpa.

3) High cod stock: suitabilities based on MSPA runs with stomach data from 1977 to 1983 and recruitment estimated from a log-normal distribution fitted to data for the period 1974–1983.

4) Low cod stock: suitabilities based on MSPA runs with stomach data from 1984 to and recruitment estimated from a log-normal distribution fitted to the period 1984–1999.

Applied prediction weight at age in the sea and in the catch, maturity ogives and residual natural mortalities as well as food rations were averages of the period 1996–2000, and kept constant in all prediction. Status quo fishing mortalities were copied from the year 2000 values. All forecast were made for the period 2001–2031, with stochastic recruitment, repeated 100 times. The key-run prediction result suggests that at status quo fishing mortality, the SSB and yield of cod will remain at present levels. The prediction using Fpa shows in contrast a steep increase in SSB in the first 7-8 years, however in the longer run the average SSB is lower than Bpa (Figure 5).

The high cod cannibalism and recruitment scenario shows a remarkable fast increase in SSB (Figure 6). The highest SSB is achieved in the beginning of the prediction period with very few older cod and thereby a limited cannibalism. The effect of cod cannibalism causes considerable oscillations of stock size and yield, but the stock remains well above Bpa, even though status quo F is used. The low cannibalism and low recruitment prediction revealed that SSB increases slightly, but staying around Blim (Figure 6).

The main message from these simulations is that recruitment success drives stock recovery and that cannibalism is of second order importance. Cod egg predation by clupeids is most intense during periods of unfavourable hydrographic conditions for egg survival, i.e. low oxygen concentrations in the bottom water. Additionally, periods of prolonged stagnation are characterised by low availability of *Pseusocalanus* nauplii as food for early cod larvae. Thus, enhanced hydrographic conditions, i.e. major inflow situations, are a prerequisite for stock recovery. The rate of recovery will depend on fishing mortality and cannibalism, the latter in dependence of the availability of other prey and spatial overlap between juveniles and adults.

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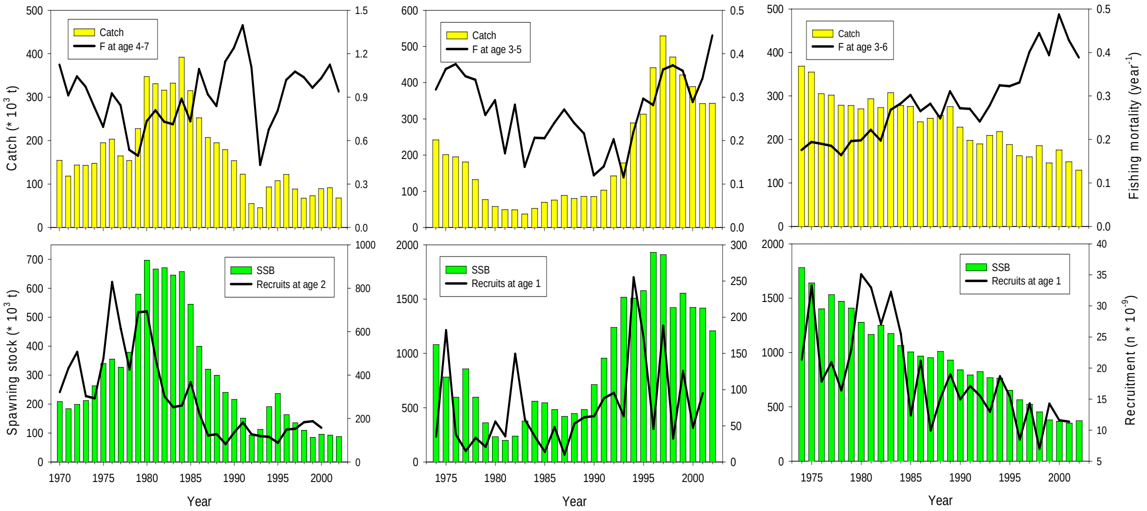

Figure 1. Catch, fishing mortality, spawning stock biomass (SSB) and recruitment of cod (a), sprat (b) and herring (c) in the Central Baltic.

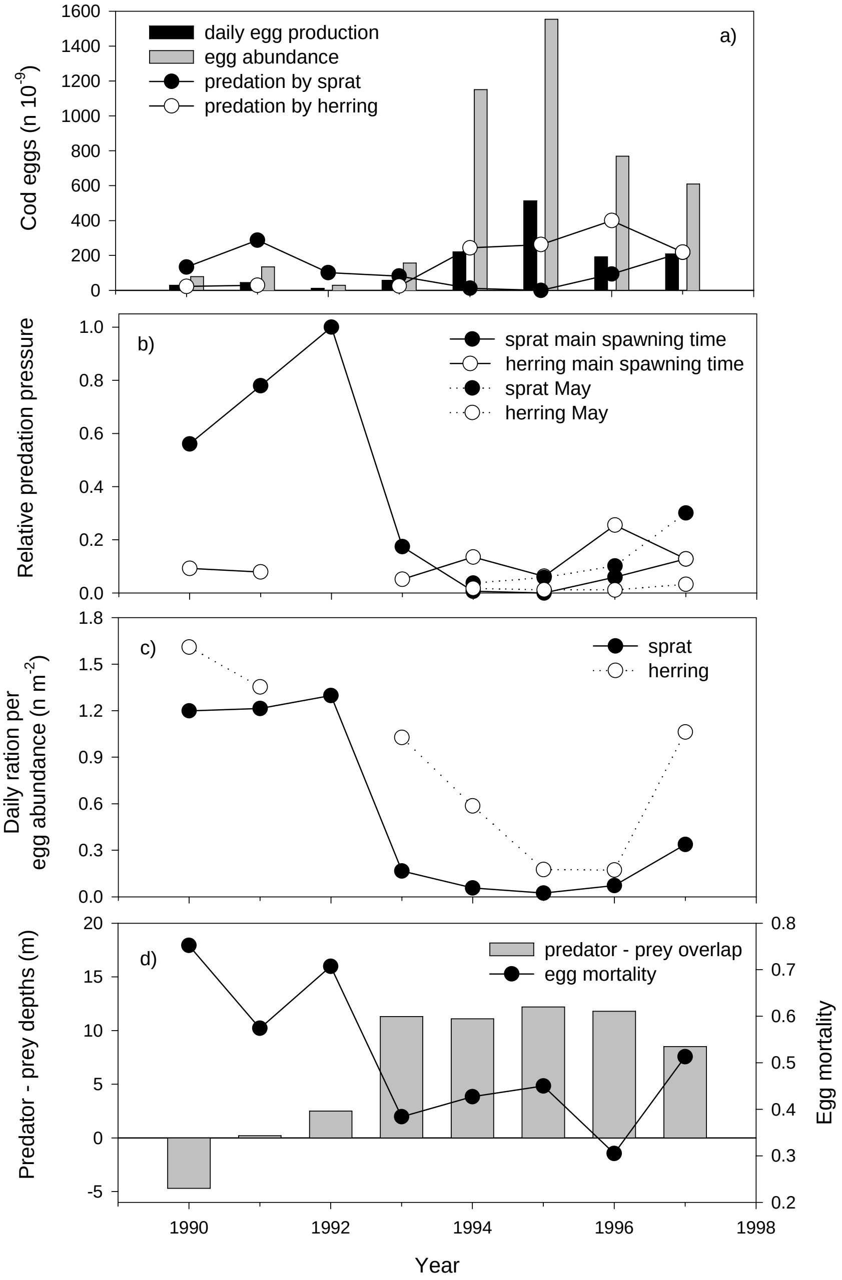

Figure 2. Daily cod egg consumption by clupeids in the Bornholm Basin during main spawning periods in comparison to daily production rates and standing stocks of eggs (a); corresponding relative predation pressure (b); daily ration by individual sprat and herring per egg abundance (c); spatial overlap between predator and prey and daily cod egg mortality based on vertical resolving ichthyoplankton and hydrography sampling during stomach sampling cruises (d).

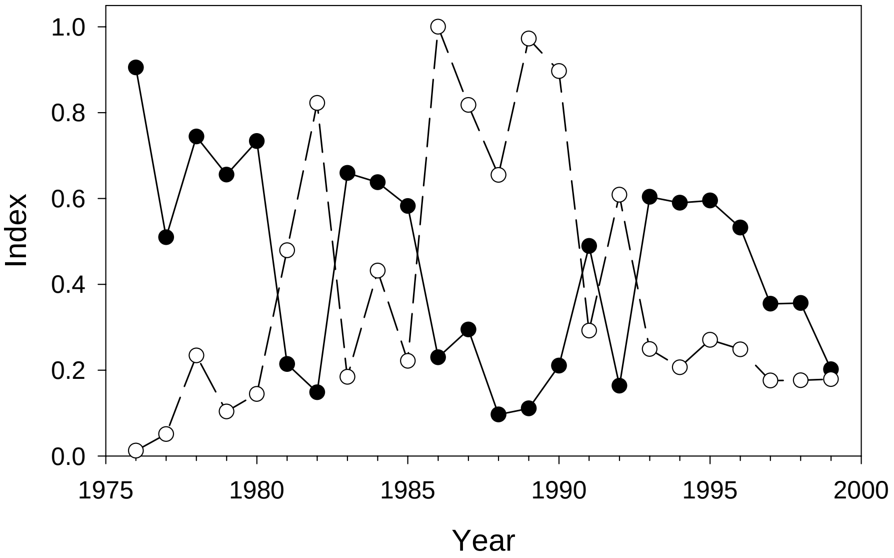

Figure 3. Time series of relative predation pressure on cod eggs by clupeids (open circles and dashed line) and oxygen related egg survival (filled circles and solid line) in Subdivision 25.

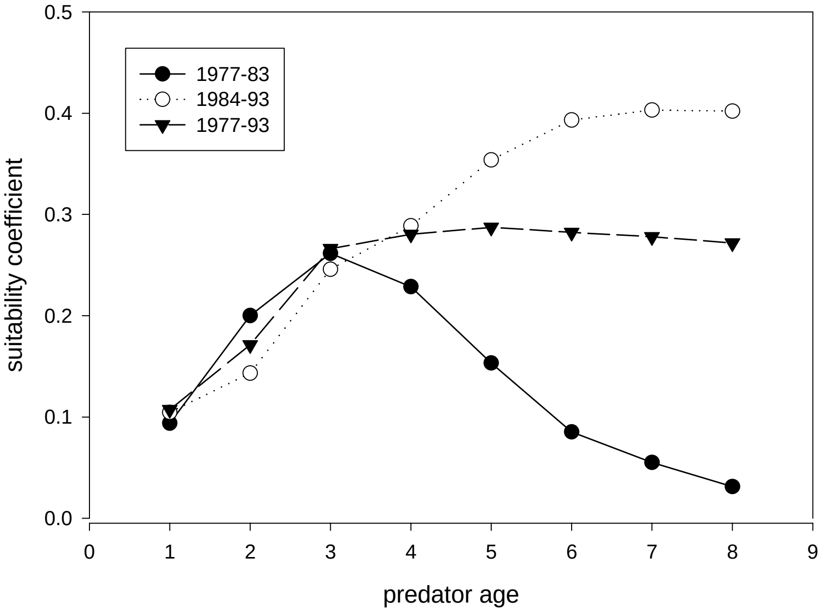

Figure 4. Suitabilities of 0-group cod as prey for cod age-groups 1–8 from MSVPA, based on stomach contents from different periods.

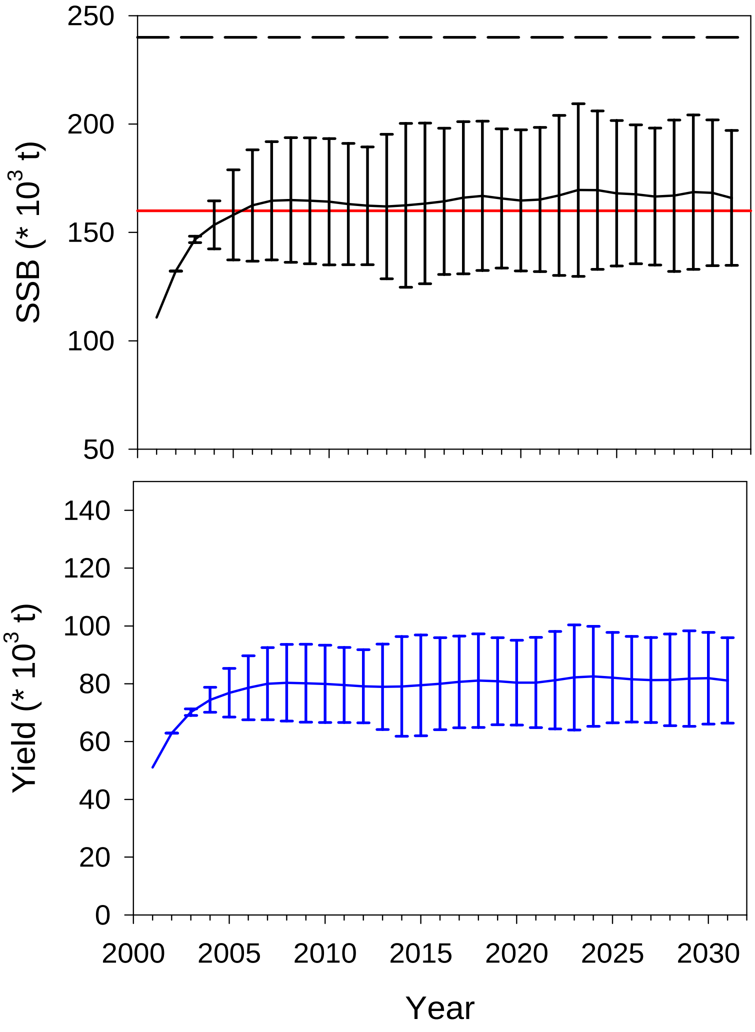

Figure 5. Medium-term projection of cod stock and catch development applying Fstatus-quo, results from MSVPA key run, i.e. using all stomach content data available and recruitment based on a stochastic ricker stock recruitment relationship utilising the entire time series for fitting. Presented is the mean and 95% CV's. The solid horizontal line in the upper figure represents Blim, the dashed line Bpa.

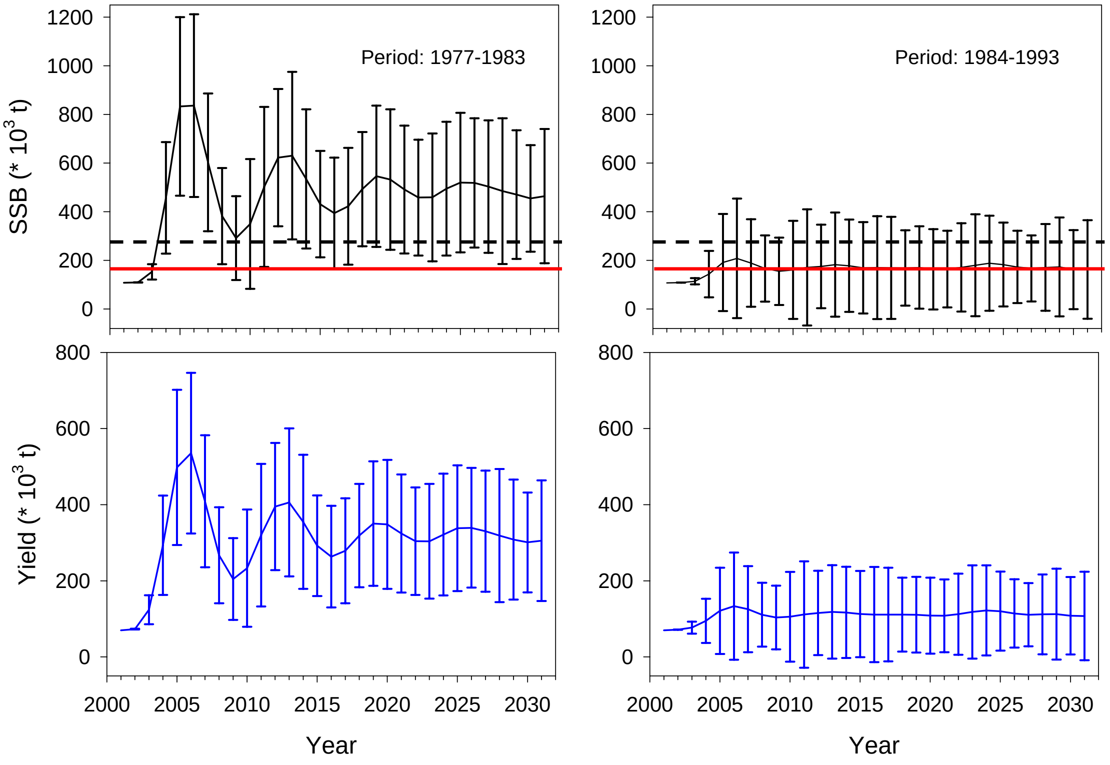

Figure 6. Medium-term projection of cod stock and catch development applying Fpa, results from MSVPA high and low cannibalism and recruitment scenario, i.e. using stomach content and recruitment data for periods 1977–1983 and 1984–1993 respectively. Presented is the mean and 95% CV's. The solid horizontal lines in the upper figures represents Blim, the dashed lines Bpa.

Extended abstract 12

The collapse of the Atlantic cod (*Gadus morhua*) stock on Flemish Cap

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Even Flemish Cap was first described in 1750, a significant cod fishery probably did not start until the 20th century, when trawling was available. The activity in the bank might increase in parallel to the decrease yields in the Newfoundland Grand Banks. The fishing pressure was the highest after 1977, when the EEZ zones were established. Soon after the stock showed depletion signals and a fishing moratoria was agree from 1988 to 1990, however the estimated annual catch in those years remained high, in the level of 40 000 tons. Last abundant year-classes were those of 1990 and 1991, which were deeply caught from 1992 to 1994. The fishery remained at high CPUE levels until near its end, in 1995, due to cod congregated in dense aggregations when it had a low abundance. The stock is under moratoria since 1999.

The SSB decreased after 1991, but it remained higher than the current accepted Blim for the next four years: 1992–1995 (Figure 1). Some abundant year-class could have been produced in those years, but it did not happen. Variability in recruitment had been described many times: strong recruitment had been irregular. The continuation of an intense fishing after recruitment failure resulted in a depletion of the SSB. Unfavourable environmental conditions could impede any strong recruitment in the 1992–1995 time period, but the depletion of the SSB completed the conditions for the stock collapse. Finally, SSB decreased too much, bellow the accepted Blim level, and no abundant year-class appeared since then. The SSB in 1991 was formed by few year-classes, as it corresponds to a deep exploited stock, so it could not support four years with very poor recruitments.

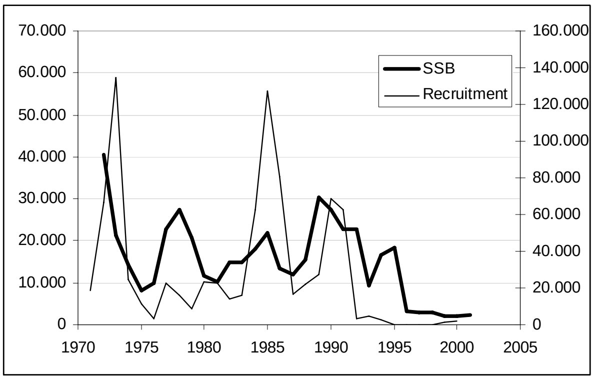

Figure 1. SSB and recruitment from XSA (Vázquez and Cerviño. 2005. A review of the status of the cod stock in NAFO Division 3M. NAFO SCR Doc. 05/38)

The last strong year-class appeared in 1991, but it had been before the neighbouring cod stocks also collapsed: last reasonable strong year-class for 3NO cod appeared in 1990 and it was even early for the 2J3KL stock. If a decisive unfavourable oceanographic condition had been the main factor in the collapse, it might have affected the three stocks at the same time.

Age at first maturity was observed at age 5 in the past; current observations indicate age 3–4, quite close to the assumed biological limit of the species. The growth also increased in parallel to the decline in total biomass (Figure 2), and it seems to indicate plenty availability of food or, most precisely, that the current food, being available at the same level for a more reduced stock, resulted in a higher ratio for the remaining individuals. Cod is a wide diversity feeder, as well as Greenland halibut and American plaice, and main available preys are redfish, which roughly maintained the same biomass level, and shrimp, which increased biomass.

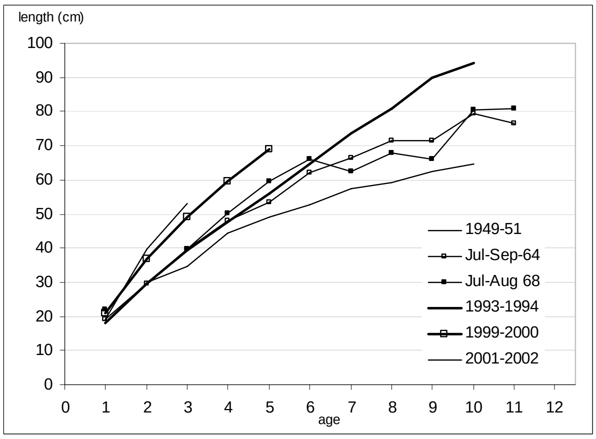

Figure 2. Growth in size of cod at different years and cohorts (Vázquez and Cerviño. 2005. A review of the status of the cod stock in NAFO Division 3M. NAFO SCR Doc. 05/38)

Cod collapse was followed by the collapse of American plaice. Last abundant year-classes were: 1991 for cod and 1992 for plaice. Once the total biomass of these two species had been reduced, some other species invaded the Cap: Greenland halibut, which had been restricted to the deepest strata of the Cap, got a wider distribution, and shrimp, which had been a common species but with small biomass, increased so much as to allow a fishery producing 40–50 thousand tons annual catch. Other changes were not documented, but these ones described are enough to indicate some change in the ecosystem on the Cap.

Extended abstract 13

Fisheries-induced evolutionary change and recovery potential of cod stocks

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Fisheries-induced changes

Fishing subjects fish stock to substantially high mortality, and this mortality is often also strongly selective targeting fish of for example a certain size. Such selection may cause changes in for example life history, behavioural, morphological, and physiological traits. Of the life history traits, size and age at maturation have both been found to decline as a result of intensive fisheries. Decline in age and size at maturity also declines the reproductive potential and consequently the yields of harvested stocks because fecundity is, especially in fish, strongly correlated with individual size (Roff, 1992, Stearns, 1992) and age (Trippel, 1998, 1999)

Changes in maturity schedule may arise through three different mechanisms: 1) direct demographic response, which means that as the total mortality increases, the stock becomes dominated by younger individuals and as result the average age at maturation decreases only because there are no older individuals in the population, 2) phenotypic plasticity, where the decrease in population abundance releases the competition between individuals and with the extra resources they are able to grow faster and mature earlier, or 3) genetic response, when the harvesting has removed all the late and at big size maturing individuals and only the early and in smaller size maturing individuals have been able to reproduce and this has caused a change in the genetic structure of the stock. Unlike generally assumed, such changes may occur within just a few generations (Conover and Much, 2002).

Probabilistic maturation reaction norms

It is impossible to judge which of the abovementioned responses is behind the observed decline in age and size at maturation in several cod stocks by just observing the maturity ogives or trends in age and size at maturation. However, these fisheries-induced genetic changes in maturation schedule can be studied by estimating the probabilistic maturation reaction norms (PMRN), which describe the different phenotypic life history parameters produced by a one genotype and rule out the influence of growth and mortality from the maturation process. Traditional reaction norms describe the deterministic maturation schedule, but in reality there is a substantial stochastic component on the probability of individual maturing, as it is dependent on many other factors than just age and size, such as resource availability and the condition of an individual (Bernando, 1993).

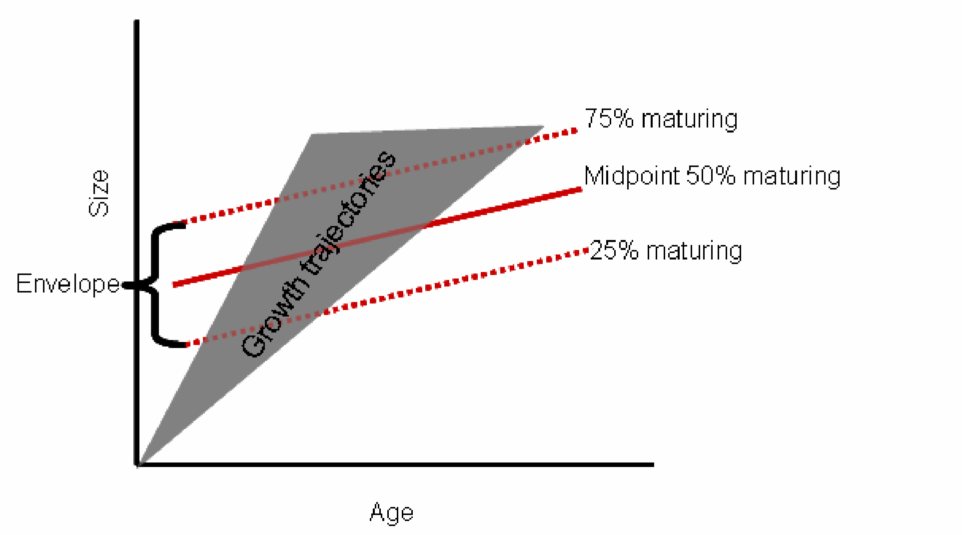

Figure 1. A schematic presentation of probabilistic maturation reaction norm. Within the growth trajectories the slowly growing individuals will grow on the right edge and fast growing individuals on the left.

For calculation of PMRN a sampling of a cohort at regular intervals is needed. The individuals should be classified as i) immatures, ii) maturing (or newly matured) or iii) mature individuals (Heino *et al.* 2002). From this data the size distribution of immature and maturing individuals as well as the proportions of immature and maturing individuals in the sample can then be calculated. However, if data on maturing individuals is missing, it is still possible to calculate the PMRN based on the information on immature and mature individuals but at least 100 individuals (mature and immature) per cohort need to be included in the analysis (Barot *et al.* 2004). For more detailed methodology, see Heino *et al.* 2002 and Barot *et al.* 2004.

The probabilistic maturation reaction norms of the cod stock around the Atlantic

The probabilistic maturation reactions norms have been calculated already for several cod stocks (see Table 1), and work on the remaining stocks (at least on West Atlantic) is soon going to be initiated by some of the workshop participants.

Modelling fisheries-induced change

In my talk I presented also the individual based eco-genetic modelling framework (developed at IIASA by Erin Dunlop in collaboration with Ulf Dieckmann and Mikko Heino) which I will use to study the recovery processes of exploited fish stocks. This model allows the evolution of multiple life history traits, and at the moment the traits included in the model are the PMRN parameters (slope, intercept and the envelope width), somatic growth rate and reproductive output (gonadosomatic index GSI). With the help of this model it is possible to study the evolution of life history parameters caused by fisheries and also the possible recovery when the harvesting pressure is released.

Table 1. The cod stock for which the PMRN has already been calculated.

Cod stock	Reference	Trend towards earlier maturation
Northern	Olsen *et al*. 2004, 2005	Yes
Southern Grand Bank	Olsen *et al*. 2005	Yes
South Newfoundland/St Pierre Bank	Olsen *et al*. 2005	Yes
Southern Gulf of St Lawrence	Swain unpublished	Yes
Georges Bank	Barot *et al*. 2004	Yes
Gulf of Maine	Barot *et al*. 2004	Yes
Arcto-Norwegian/Northeast Arctic	Heino *et al* 2002	Yes
Baltic	Vainikka unpublished	Yes

Conclusions

Based on the research done on several cod stock it seems evident that changes in the maturation schedule have occurred due to harvesting and that these changes are also likely to be genetic. These changes may be difficult to reverse especially if the genetic variance of the stock has been dimished.

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Extended abstract 14

Do evolutionary responses to fishing play a role in the non-recovery of the collapsed cod stock in the southern Gulf of St. Lawrence?

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Age and size at maturity

Age and size at maturity of cod in the southern Gulf of St. Lawrence decreased in the 1960s and 1970s, as the stock declined due to overfishing. These changes are in the direction expected for evolutionary responses to fishing. They reflect substantial changes in maturation reaction norms (Figure 1), also consistent with a genetic response to fishing.

Earlier maturation is expected to result in decreased adult size. Size-at-age of adults decreased sharply in the late 1970s and early 1980s in this stock. However, the declines in age at maturity preceded the declines in adult size-at-age by several years, suggesting that earlier maturation was not a cause of the sharp decrease in adult size-at-age in this stock (Figure 2). Maturation at smaller sizes has been suggested to result in increased mortality costs to reproduction, providing a possible explanation for increased natural mortality of adults in this stock. However, the decline in size at maturity preceded the increase in adult natural mortality by several years, again inconsistent with a causal connection. Thus, early maturation at a small size may contribute to the current slow growth and high adult natural mortality in this stock, but other factors must also be involved because rapid growth and low mortality have also been observed in this stock at the same early age and small size at maturity.

These changes in age at maturity require a substantial revision to estimates of spawning stock biomass (SSB) in the 1950s and 1960s (which had been based on maturity ogives from the 1990s). SSB was lower and recruitment rate higher in the 1950s and 1960s than had been thought (Figure 3). However, the main signal in the recruitment rate time series remains the unusually high rates from the mid 1970s to the early 1980s, and estimated recruitment rates in the mid 1990s remain greater than those in the 1950s and 1960s. Thus, conclusions about the factors that appear to be most closely linked to variation in the recruitment rate of southern Gulf cod remain unchanged.

Following the declines in the 1960s and early 1970s, age at maturity of southern Gulf cod has changed little over a 25-yr period (1980–2005), despite the rapid recovery of the stock in the early 1980s and 12 yr with little fishing since the stock’s second collapse in the early 1990s. This suggests that a) little additive genetic variation for age at maturity remains in the stock following strong selection in the 1960s, b) selection for age at maturity has not been strongly directional since the 1970s, or c) high natural mortality has replaced high fishing mortality as an agent of selection on age at maturity.

Genetic response to size-selective mortality

Genetic changes in growth rate have also been predicted as a direct response to size-selective fishing. Size-at-age of southern Gulf cod remained small in the 1990s and early 2000s despite good conditions for growth and little size-selective fishing. This continued slow growth may reflect a genetic response to size-selective fishing in the 1980s and early 1990s. Using otolith backcalculation data, I calculated selection differentials for length at age 4 yr for the spawning stocks that produced the 1977–2001 year-classes. Selection differentials were strongly positive for year-classes produced in the late 1970s, switching to strongly negative for those produced in the early to mid 1980s. Selection differentials remained negative for subsequent year-classes, though they have tended to be weaker for recent year-classes and approached zero for the 2001 year-class.

I tested for a genetic response to this size selection using the following model:

$$\Delta L_{4,4} = \Delta G + \Delta E$$

where $\Delta L_{4,4}$ is the change between offspring and their parents in mean back-calculated length at age 4 yr in fish observed in their fourth year, ΔG is the genetic change between offspring and their parents (i.e., the response to selection), and ΔE is the difference in environmental conditions experienced by parents and offspring.

$$\Delta G = h^2 S$$

where h^2 is the heritability and S the selection differential for $L_{4,4}$. ΔE consisted of differences in density experienced by parents and offspring (Δd) and/or differences in temperature conditions during the first four years of life (Δt). The temperature index was a measure of the ambient temperature of cod during the feeding season, based on the age-specific temperature distributions of cod catches in the annual September survey of the southern Gulf. A temperature index based on general environmental conditions (average bottom temperature in the annual survey, not weighted by cod catch) was also examined but had lower explanatory power than the index of cod ambient temperature.

The genetic response to selection was highly significant in all models. Δd and Δt were strongly confounded, making it difficult to estimate the independent effects of these two variables. The most parsimonious model included a term for the genetic response to selection and a term for the differences in density between parents and offspring, and explained 61% of the variation in $\Delta L_{4,4}$. The density-dependent effect was highly significant ($P<0.0001$) and in the expected negative direction. The genetic response to selection, also highly significant ($P=0.001$), indicated high heritability for $L_{4,4}$.

These preliminary analyses suggest that there has been a strong genetic response to size-selective mortality in this stock, providing an explanation for the continued slow growth in this stock despite good conditions for growth.

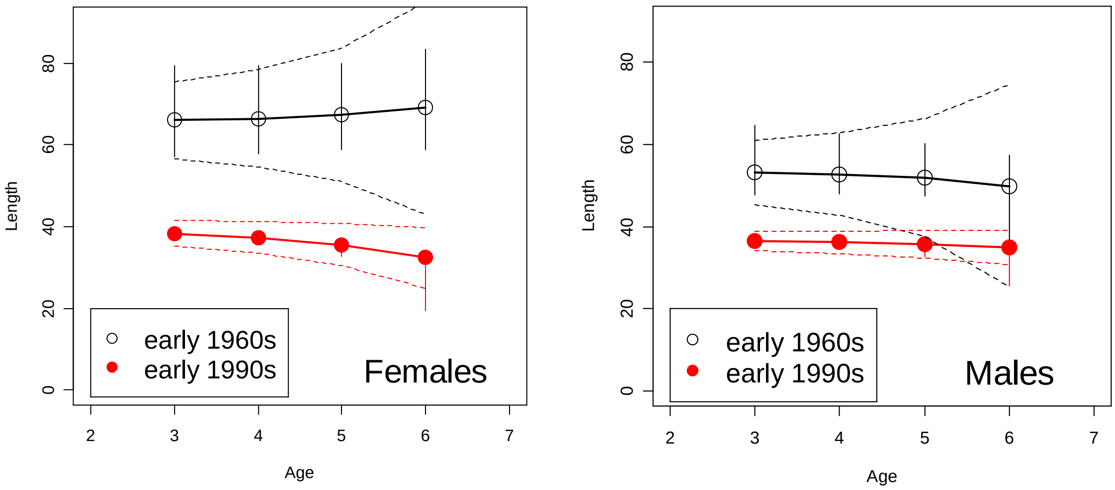

Figure 1. Maturation reaction norms for southern Gulf of St. Lawrence cod in early 1960s and the early 1990s. Circles indicate the length-at-age where the probability of maturing is 50% and vertical lines are the 95% confidence intervals around this length, based on bootstrapping. Dashed lines are the lengths where the probability of maturing is 25 or 75%.

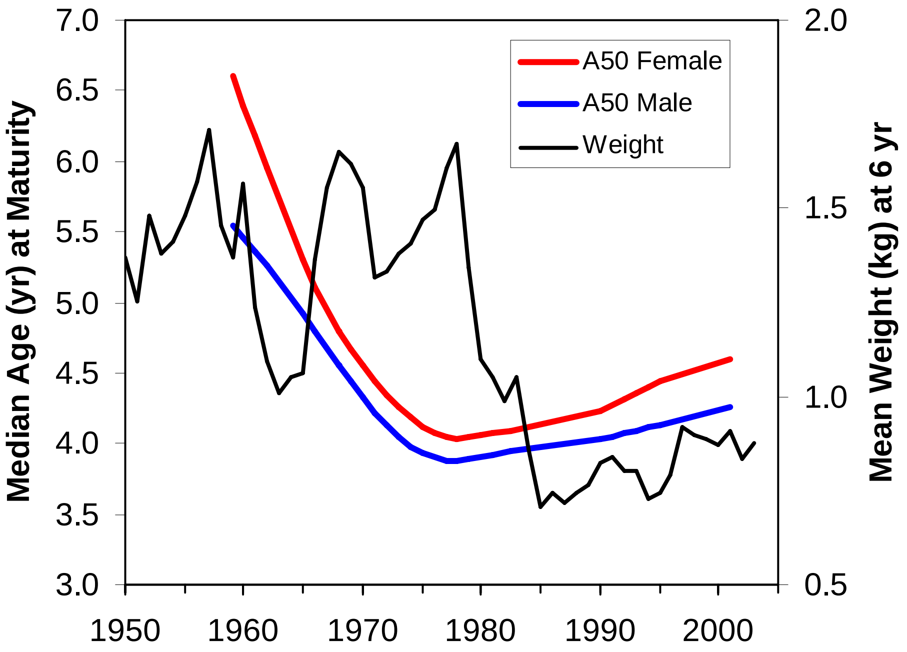

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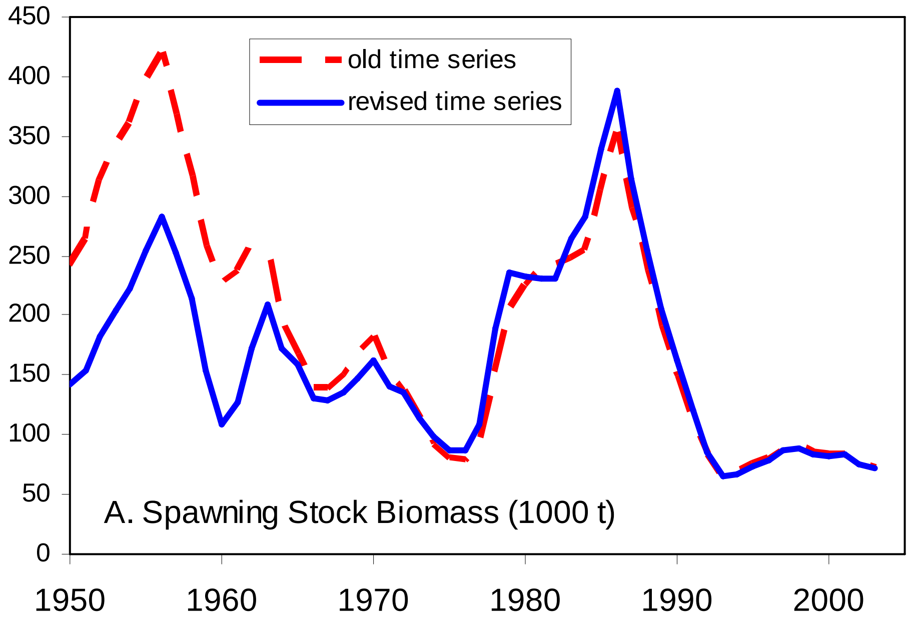
Figure 2. Trends in age at 50% maturity (A50) and mean weight at six years of age for cod in the southern Gulf of St. Lawrence.



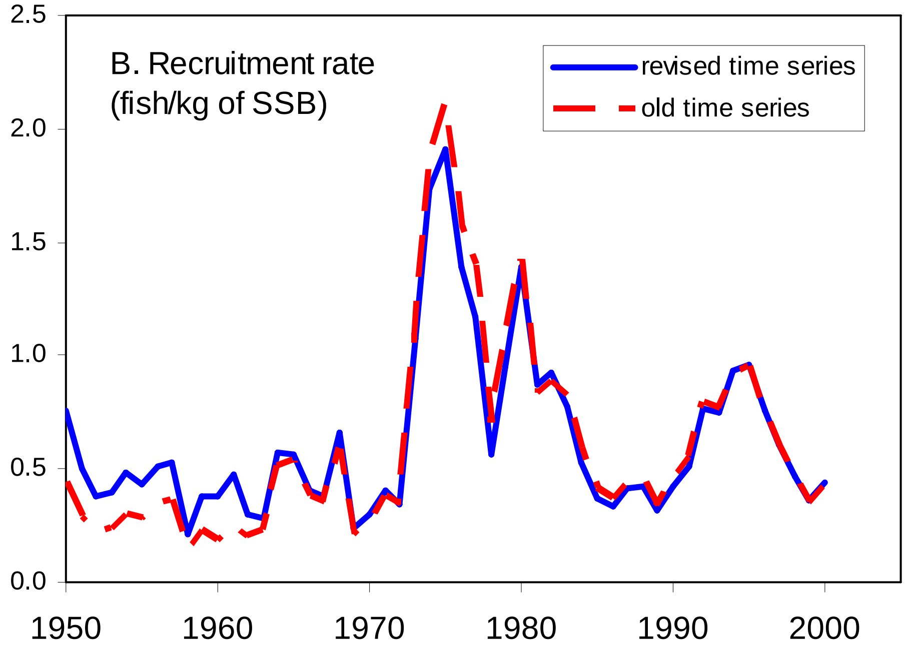


Figure 3. Revision to time series of spawning stock biomass (SSB) and recruitment rate (abundance at age 3 yr/SSB) for cod in the southern Gulf of St. Lawrence, incorporating changes in age at maturity. (The old time series was based on a maturity ogive from the 1990s.)

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The Role of Cod in the Ecosystem

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The purpose of this abstract is to draw attention to draft text (Link *et al.*, in prep) regarding the role of cod in various ecosystems across the North Atlantic. The paper reviews the extent to which cod dynamics can be influenced by interactions with predators, prey and competitors, and explores the extent to which changes in cod stock size can affect other species in the ecosystem. The interactions are reviewed for each of six ecosystems: three are cod-capelin systems toward the northern limit of cod distribution (Barents Sea, Iceland, and Labrador-Newfoundland), two are more diverse systems toward the southern end of cod distribution on either side of the Atlantic (North Sea and Georges Bank – Gulf of Maine), and one is a species-poor system with an unusual physical and biotic environment (Baltic Sea). A synthesis of the role of cod is attempted based on information from these and other ecosystems.

Reference

Link, J.S., Bogstad, B., Sparholt, H., and Lilly, G.R. In prep. The role of cod in the ecosystem. Draft text for a chapter in the book on cod being written by the ICES/GLOBEC Working Group on Cod and Climate Change. A draft of the chapter was available on the ICES/GLOBEC website at the time of the Workshop.

Extended abstract 16

Interactions between Harp seals and Atlantic cod off west Greenland.

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Harp seals prey on Atlantic cod and on species like capelin, sand eel and krill, which also are important prey for cod. Changes in number of harp seals in the northwest Atlantic (presently around 5.9 mill) or in their migratory pattern can therefore potentially be important for development of the cod stock in both Canada and Greenland.

The number of harp seals caught in the subsistence hunt along the west Greenland coast gives a good indication of the abundance of harp seal here. A time-series on skin purchase- and catch statistics indicates that harp seal abundance in Greenland waters declined strongly after a high and unsustainable harvest on the breeding grounds in the first half of the nineteenth century. The catches in southwest Greenland has stayed low up until the recent recovery of the harp seal stock (the 1990s). Since then a high number of harp seals started to arrive in the fjords in Southwest Greenland (Figure1) in late May and early June to feed on pre spawning capelin. This pattern did also exist prior to the decline in the1860s, but to judge from the catch statistics only few seals came this way during the period with a small harp seal stock (1860s–1990s).

The concentration of foraging seals off Labrador is exceptional high in the first weeks after the moult in late April. It is therefore likely that a certain threshold exists, when the area no longer can sustain the large number of seals. This would trigger changed behavior among the harp seals (like an earlier start of migration). Similar, the large number of seals is likely to have strong influence on the abundance and behavior of prey species in the area (could explain why large schools of capelin has disappeared from the area) and this would enhance the need to change the timing or pattern of migration. If such a threshold exist, than a reduction of the seal stock only have little impact on the harp seal consumption along the Labrador coast (consumption will not be a linear function of population size).

Only few harp seals were caught in southwest Greenland both prior, during and right after the years with many cod. More harp seals were, however, caught along the northwest coast of Greenland during fall, when the capelin distribution moved northward with the warmer water around 1930 (Figure1). The harp seal migratory pattern and the degree of interaction between seals and cods in southwest Greenland therefore seems to be linked the status of the harp seal stock as well as to the distribution of the shared cod and seal prey.

Do harp seals benefit from a large cod stock?

The timing of increase and decline of the Atlantic cod in southwest Greenland, Labrador and Newfoundland were quite similar. Harp seals therefore competed with and predated on cod in a large fraction of their distribution. Both cods and seals were heavily exploited during the entire period and both stocks were therefore strongly influenced by fishing and hunting mortality. Stock size of both species and the reproduction rate of 4-year-old harp seals during 1960–2005 are shown in Figure 2.

Harp seals in the Northwest Atlantic normally mature when they are around 4-6 years old. Age of maturity is likely to be linked with food availability, so the fraction of females that are pregnant when they reach 4 years of age is therefore linked to food availability in the preceding 4 years. Data shows that the fraction of 4-year-old pregnant harp seals in 1978–79 was significantly higher than during 1965–1970 and during 1991–1995 (Fisher's exact test $p < 0.0001$), whereas there were no significant difference between 1965–1970 and 1991–1995.

This means that harp seals matured earlier in the late 1970s when the cod had disappeared than in the mid 1960s when the cod was still abundant (the harp seal stock was roughly same size in the two periods). The harp seal stock now increased strongly, due to high productivity and strict hunting regulations and with the increased population followed a later maturation, which would be expected as a consequence of intraspecific competition (density dependence).

The fact that maturity occurred at the same age during the late 1960s and the mid 1990s despite an almost threefold increase in the population, indicate that the harp seal carrying capacity had increased. The disappearance of the cod stock seems to be an obvious cause, as this should release more prey for harp seals. Other more complex interactions in the system might also have been involved, but the data strongly indicate that seals and cod compete and that the seals are better off without the cods.

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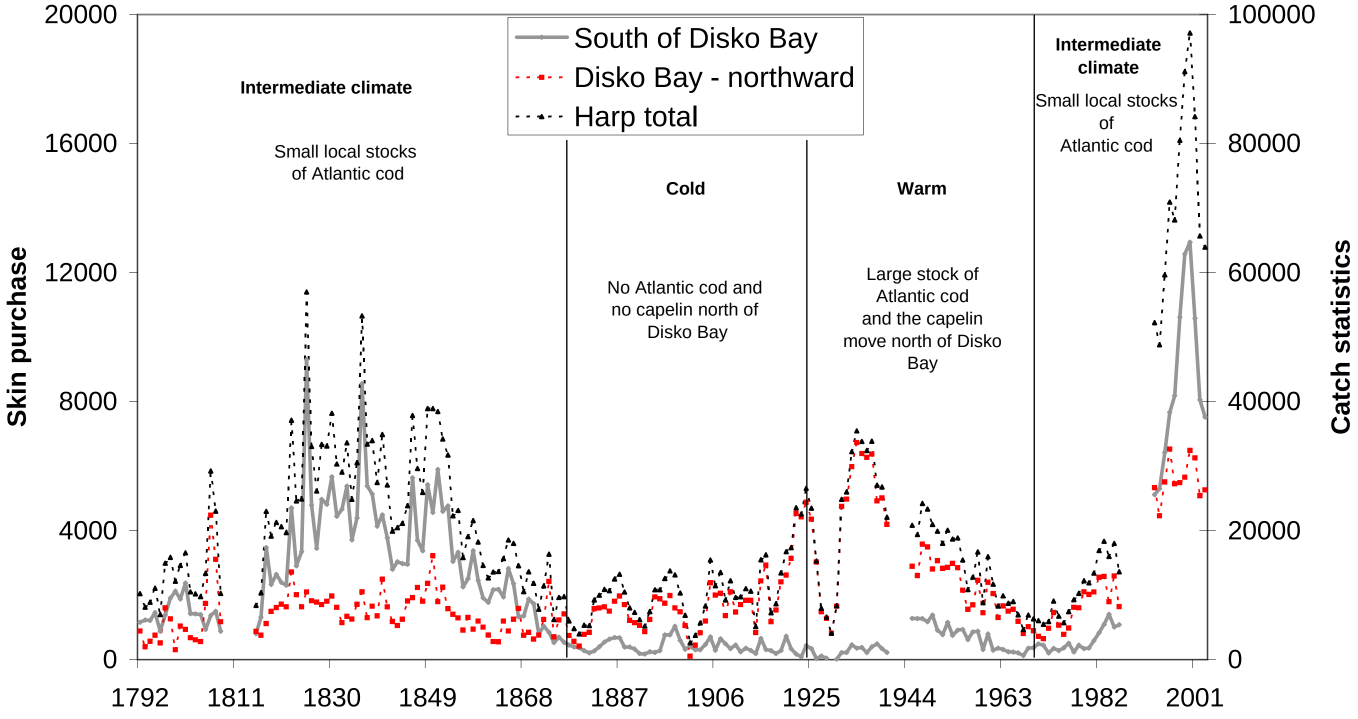

Figure 1. Catch data on harp seals in west Greenland. Data from 1792-1940 are skin purchase data (Vibe, 1967). Data from 1945 to 2003 are estimates based on catch statistics (Vibe, 1967; Anon., 1954–1983, 1993–2003).

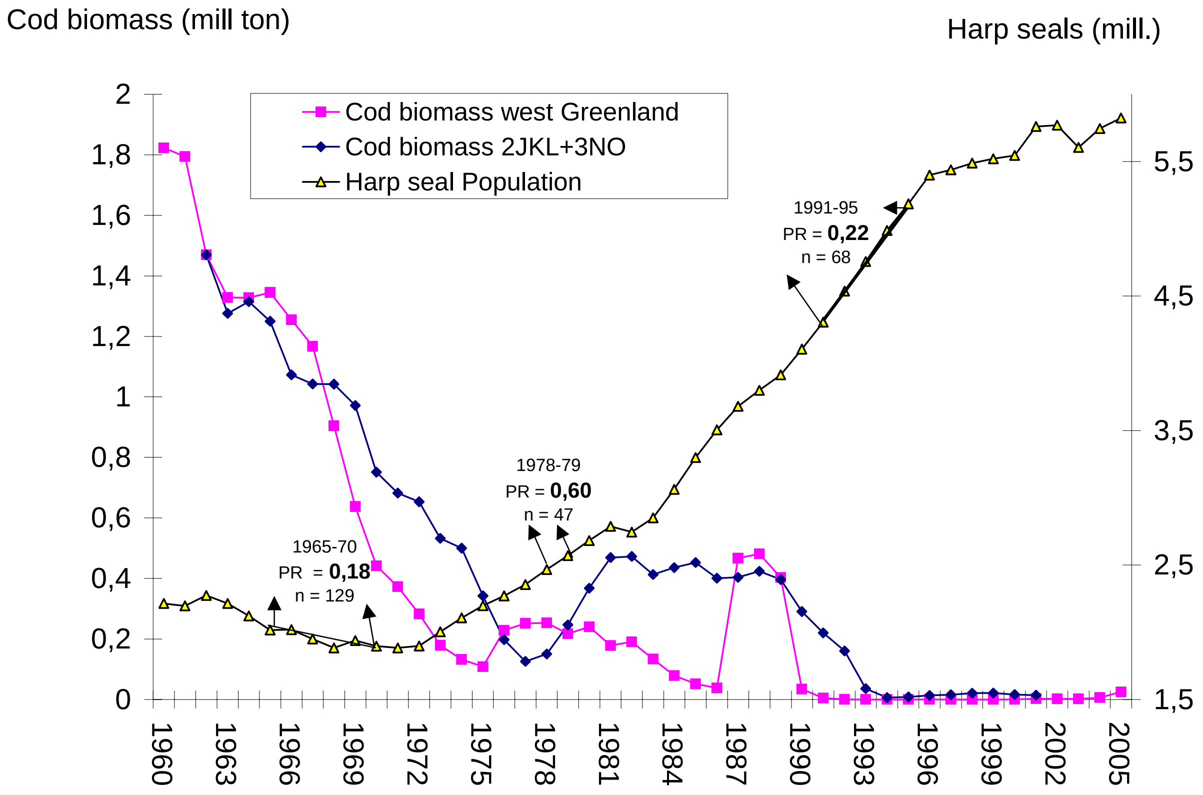

Figure 2. Cod biomass Greenland (1960–89: VPA: age 3+; 1990–2005: Survey: all ages) (Buch *at al.,* 1994; Fock *et al.*, 2006). Cod spawning biomass 2JKL+3NO (Lilly *et al.*, 2003; Smedbol *et al.*, 2002) (all data divided by 1.1 to give the same starting point as the data from Greenland). Harp seal population numbers (Hammill and Stenson, 2005). Pregnancy rates (PR) of 4-year-old harp seals (Sjare *et al.,* 2004).

Extended abstract 17

Harp seal predation on Northern Gulf cod: fitting historical data and projecting cod recovery under various seal hunt scenarios

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The marked decline, and lack of recovery in the northern Gulf of St. Lawrence (Gulf) cod stock has coincided with a marked increase in the Northwest Atlantic harp seal population. This has lead to concerns that seals are an important factor in limiting recovery and that reducing the harp seal population might favour cod recovery. Evaluating the role that seals may play in this conflict is complicated by trophic relationships, which involve both direct and indirect (cascade) effects. However, managers often have difficulties in understanding these complex interactions between different components in the ecosystem. The object of this presentation is to examine the potential impact of harp seals on the recovery of cod, assuming that the removal of seals translates directly into improvements in recovery, without any increased mortality from other components within the ecosystem

A simple age-based Leslie matrix model was developed for the Northern Gulf cod population (3Pn4RS), using all the standard assessment input data such as weight at age, maturity ogive, catch at age. The model also requires assumptions for M at age like any fish population cohort model. In this case however, we broke natural mortality into two components: that caused by harp seal predation and a residual value. These were termed M2 and M1, respectively, in keeping with the usage established in multispecies virtual population analysis (MSVPA). Recruitment was modelled as numbers of 0-group fish and results from a hockey-stick model with recruits per spawner defining the slope and a set maximum recruitment. Estimates of harp seal numbers at age, a seal consumption rate and a functional response describing the proportion of cod in seal stomachs as a function of cod abundance were used to model seal predation. We included fishing mortality in the model and assumed that using this model structure we could reconstruct the historical trend in cod abundance (1974–2005) and fit parameters for recruits per spawner, M1 at age, seal functional response parameters and therefore M2 at age.

The historical trend in cod spawning stock biomass from the assessment was modeled quite well from 1974 to 1989, but after 1989, the fit of the model to the biomass data was poor and no single set of parameters would fit the entire time series with any degree of certainty (Figure 1). This poor fit is thought to be linked to a period of extremely poor recruitment, which might reflect natural declines in recruitment, or mis-reporting and dumping of small cod at that time. In the first period, the proportion of cod in seal stomachs varied between about 2% and 12%, consisting of cod less than five years of age, based on the length frequency distribution of cod in seal stomach contents (Figure 2). However, in the later period (1990–2005) no reliable parameter set could be obtained, though all optimizations suggest that that the proportion of cod in the diets of seals was much lower than in the earlier period. Though no definitive fit could be found, it does make sense that seals would eat less cod in the period of low cod abundance and especially during a period of low recruitment.

A series of projections for cod recovery, assuming that a SSB of 80 000 t constitutes recovery, were made based on current fishing levels experienced by this stock, the fitting parameters obtained from the fits of the model to the different periods in the history of this stock and by varying seal population size. Using the whole projection period of 1974–2000 and 1974 to 1989, 4RS cod recovered to minimum biomass conservation point (Blim) by 2012, and had the potential to fully recover within 25 years. During the recent period of 1990–2006, the stock increased to Blim by 2016, but never reached a fully recovered level. Using fitting conditions from 1990–2006, SSB increased to Blim by 2014, when the seal population was reduced by 20%, and by 2012, when the seal population was reduced by 50%. Under both scenarios, cod had the potential to recover fully. During the low productivity period (1986–96), the cod stock was extirpated in spite of a 20% reduction in the harp seal population. If harp seals were completely eliminated, the cod stock still failed to recover.

This analysis assumed that fishing will continue throughout the future at rates similar to those currently in place on the 4RS cod stock. We focused on evaluating the impacts of seal predation, since this was the focus of the meeting and how changes in seal predation might affect recovery. Under current conditions, almost all projections show a decrease in SSB given current levels of fishing. Changes in seal predation could improve the potential rate of recovery of this stock, but reductions of 20–50% in the herd, would only improve the rate of recovery by 2–4 years.

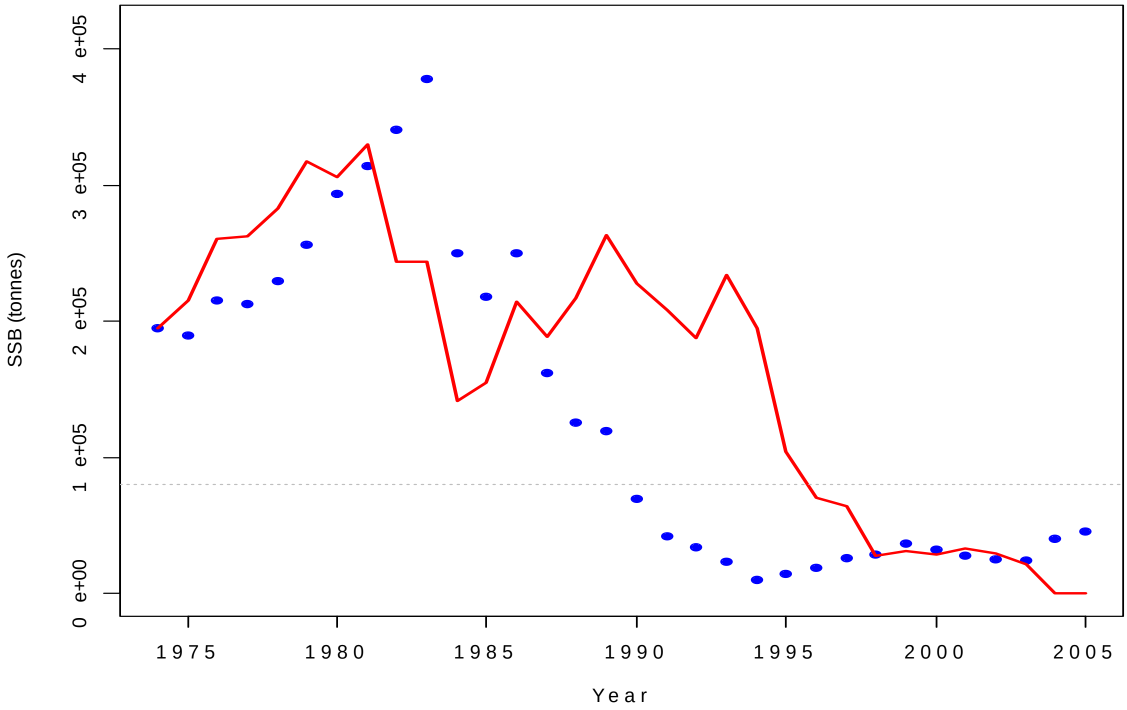

Figure 1. Plot of changes in Atlantic spawning stock biomass (SSB) (dotted line) in NAFO zone 4RS between 1975–2005. Solid line represents the model fit to the SSB data.

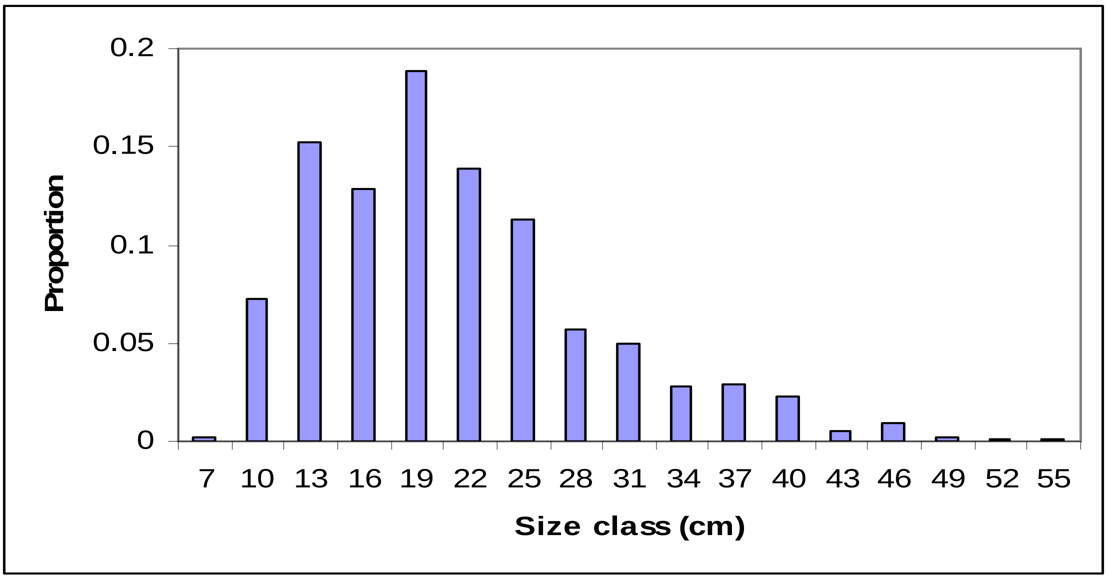

Figure 2. Length frequency distribution of cod in the diet of harp seals (Stenson, unpublished data)

Extended abstract 18

Predator-prey interaction between harp seals and Atlantic cod: An exploration of sources of variation

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The Northwest Atlantic ecosystem has undergone dramatic changes in its structure during the last 30 years. Among these changes, the collapse of Atlantic cod is certainly one of the most important. Atlantic cod was the dominant demersal fish in the Newfoundland shelf marine community and now it is reduced to a relict of what it was, and without any clear sign of recovery. The reasons for the lack of recovery are still a matter of debate, but the potential role of harp seals is often put forward as a possible explanation.

Harp seals have increased its population size from less than 2 millions in the early 1970s to around 5.5 million individuals in the early 1990s, remaining fairly constant since then. This population increase has fueled hypotheses that an increased consumption of Atlantic cod by harp seals may be limiting the recovery. However, harp seals are generalist predators and a proper assessment of their role as Atlantic cod predators needs to consider the variability in the diet.

It is a fair assumption that harp seal's diet can vary over time, age, and geographical region. Time variability can be considered as a surrogate for changes in prey availability over time. These changes can be seasonal or long-term (prey population dynamics). Age variability is associated with ontogenetic changes in the diet (e.g. behaviour, changes in energetic requirements, learning). Geographical variability is associated with foraging habitat and the spatial structure of prey assemblages. This variability can involve both latitudinal changes (e.g. north-south clines) and depth-related changes (e.g. inshore and offshore areas).

Current estimates of trophic consumption by harp seals take into account several of these sources of variation, but a formal assessment of them was still lacking. In this context, the objectives of this work are a) examine the effect of sources of variation on the overall diet of harp seals, and b) look at the effect of these sources of variation on Atlantic cod predation.

In order to examine the effect of time, age, and geographical region on the diet of harp seals we implemented a multicategory logit model. The response variable in this model is the number of harp seals that had a given prey species as main prey in terms of biomass in the stomach. The explanatory variables (sources of variation) are year, age group (pups, juveniles, adults), zone (2J3K, 3LMNO), area (inshore, offshore) and season (summer, winter).

All these sources of variation had significant effects on the probabilities of being a main prey (by weight) in a harp seal stomach (p-values <0.0001). From the 12 prey groups considered, Atlantic cod ranked 10th; and can be considered a minor prey. However, an interesting finding is that the probability of Atlantic cod to be a main prey increased in the period 1986–2001, while capelin has shown a slight increase and Arctic cod has declined.

In order to look at the effect of these sources of variation specifically on Atlantic cod predation we fitted a binomial logit model. In this case , the response variable was the number of harp seals that did or did not have Atlantic cod as prey, regardless if cod was the main prey in the stomach or not. We found that year and season did not have a significant effect on the probability of consuming cod (i.e. the probability of eating Atlantic cod did not change over time), while the factors associated with geographical (zone and area) and ontogenetic (age groups) features were highly significant (p-values <0.0001). The examination of the odds-ratios indicated that the probability of eating Atlantic cod increased with age (p-values <0.001), and was an order of magnitude higher in the inshore than in the offshore (p-value <0.0001).

We further explored the data by repeating the previous analysis excluding the sample from the offshore, eliminating the non-significant sources of variation (year and season) and increasing the resolution of the zone factor by disaggregating the NAFO divisions. In this inshore analysis, we considered the NAFO divisions 2J, 3K and 3L as levels within zone. The results from the analysis of the inshore data confirmed the observed pattern with age, and indicated a significant latitudinal trend in the probability of consuming Atlantic cod from North (2J) to South (3L) (p-values <0.01).

By putting all these analyses together, one interesting observation can be made: the probability of Atlantic cod being a main prey in a harp seal's stomach increased over time, but the probability of consuming it (i.e. the proportion of seals that actually consume cod) remained constant over time. This means that for those seals which actually ate Atlantic cod, this prey has become more important over time. Considering the inshore data from NAFO divisions 2J3KL, we examine two hypotheses that can account for this observation. For those seals that ate Atlantic cod: 1) the average number of Atlantic cod in a stomach has increased over time (i.e. each seal ate more fishes), and 2) the average weight of the individual Atlantic cod consumed has increased over time (i.e. each seal ate larger fishes). The correlation between the average number of Atlantic cod in the stomachs and year was not significant ($r_{Spearman}$=0.415 p-value=0.110), but the correlation between the average weight of a cod in the stomachs and year was highly significant ($r_{Spearman}$=0.776 p-value=0.0006). These results suggest that the increase in importance of Atlantic cod over time is related to an increase in the consumption of larger fish in the inshore area, and supports previously observed data indicating that the age of cod consumed by harp seals in the area has increased.

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Estimating Consumption of Atlantic Cod (*Gadus morhua*) by Harp Seals (*Pagophilus groenlandicus*)

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Because of their large size and abundance marine mammals are thought to have an important influence on the structure and function of some marine ecosystems. This has lead to the view that seals can have a negative impact on commercial fish stocks, including Atlantic cod. Over the last decade several Atlantic groundfish stocks have collapsed while many marine mammal populations, particularly seals, have shown marked increases leading to suggestions that seals were involved in the failure of the fishery. Although it is now considered that seals played no, or only a minor role, in the collapse of Canadian groundfish stocks in the early 1990's, they may play a more important role in slowing the recovery of certain Atlantic cod stocks. In a recent review, McLaren *et al.* (2001) concluded that cod consumption by seals in NAFO zone 4RS3Pn and 2J3KL was large compared to biomass estimates suggesting that seal predation was a substantial component of the high mortality experienced by these stocks. Similar concerns have been made concerning the impact of predation by seals and whales on commercial fish stocks in the northeast Atlantic and Barents Sea.

The current discussion about the impact of marine mammal predation is based upon estimates of consumption obtained from a bioenergetics model. The modelling approach is similar for most species. The model assumes that the energy requirements of a population can be estimated and that the marine mammal obtains the energy required. Estimating prey consumption requires information on population size, energetic requirements, diet composition, and distribution of feeding effort, as well as size classes and energy density of the prey.

Here, we model fish consumption by harp seals, taking into account seasonal changes in feeding and variability in seal abundance, distribution, and diet composition. In addition, we incorporate all possible sources of uncertainty in these estimates and examine the impact of these assumptions on our estimates of total consumption. The model is developed using harp seals in the Gulf of St. Lawrence. Our overall objective is to examine the general approach to estimating consumption and how uncertainty might be incorporated into the model.

Prey consumption by harp seals in northern Gulf of St. Lawrence (NAFO Divisions 3Pn and 4RS) from 1985–2005 is estimated by:

$$C_{jt} = \sum_{s=1}^{s=S} \sum_{a=1}^{a=A} \sum_{i=1}^{i=I} N_{it} E_i D_{ias} P_{jas}$$

Where:

C_{jt} = Consumption of prey species j in year t.

N_{it} = No. of seals in age class i in year t.

E_i = Annual gross energy required by a seal aged i.

D_{ias} = Prop.of the total annual energy obtained by a seal aged i in area a during season s.

P_{jas} = Prop. of prey species j in the diet of seals in area a during season s.

I = Total no. of age classes, currently 13 (ages 0 - 11 and 12+).

A = Total no. of areas.

S = Total no. of seasons, currently 2 (Winter and Summer)

A similar model is used to estimate prey consumption by marine mammals in a number of areas.

For northwest Atlantic harp seals, changes in population size over time are monitored by fitting the model to independent estimates of pup production. Uncertainty (mean and standard deviation in the numbers in each age group (0 through 11 and12+) for each year was estimated from the population trajectories.

Energy requirements were assumed to be constant throughout the year and to also vary by month. Age-specific energy requirements were calculated using a simple allometric equation based on body mass:

$$GEI_i = GP_i * (AF*293 *BM_i^{0.75}) /ME$$

where:

GEI_i = Daily gross energy intake (kjoules/day) at age i,

GP, = Growth premium (i.e. the additional energy required by young seals < age 6).

AF = Daily activity factor

BM_i = Body mass (in kg) at age i

ME = metabolizable energy

Harp seals are highly migratory and our knowledge of their seasonal distribution is primarily based on historical catch data, tag returns and anecdotal reports. Recent studies of harp seal movements using satellite telemetry have improved our understanding of seasonal distributions significantly. Northwest Atlantic harp seals summer in the Canadian Arctic and/or West Greenland. During the fall and early winter, seals move southward along the Labrador coast. One component of this population remains off the east coast of Newfoundland/southern Labrador (i.e. 2J3KL) while the other moves into the Gulf of St. Lawrence in December. In the late spring, the animals return to the Arctic. Annual changes in ice conditions or food availability likely affect the seasonal movements of the population. The proportion of energy obtained from various areas was assumed to be equal to the seasonal residency in that area.

The diet of harp seals was estimated using reconstructed wet weights of stomach contents from animals collected in various areas between 1986 and 2002. Prey lengths and weights were estimated from hard parts using part length – total length and part length – and/or length – weight regression equations. Reconstructed wet weights were converted to energy densities using published energy values for each prey species.

Consumption of Atlantic cod in 2003 was estimated to be in the order of 27 000 (SD = 6800) tonnes. Sensitivity analysis indicated that the model was most sensitive to changes in population size, the parameters required to estimate energy requirements (ME, AF, body mass), the proportion of seals that enter the Gulf and the length of winter residency. Assumptions about the proportion of animals that remain throughout the year in the Arctic or southern waters had little impact on the estimates of cod consumption.

Estimates of consumption by predators often exceed estimates of prey abundance. One difficulty is that seals often prey on the younger age classes, which are poorly estimated from research surveys. An additional challenge occurs because of a lack of understanding of the functional relationship between prey abundance and its importance in the diet. Estimates of consumption are only one component in the analysis of the impact of seal predation on the recovery of cod stocks. In order to understand the role that seals may play, it is necessary to partition mortality into its different components and to analyse mortality within the context of mortality due to other sources including seal predation.

Reference

McLaren, I., Brault, S., Harwood, J., and Vardy, D. 2001. Report of the eminent panel on seal management. Department of Fisheries and Oceans. Ottawa, Canada.

Annex 4: Recommendations

RECOMMENDATION	ACTION
1. Fisheries management must be sensitive to possible changes in stock productivity and must either respond quickly, to prevent increased mortality and further stock decline, or regulate fishing in a precautionary way, which is robust to uncertainties about stock productivity.	The Action Plan for the ICES/GLOBEC office should include proposals for developing (i) indicators of change in stock productivity, (ii) models for evaluating the causes and consequences of changes in stock productivity and (iii) management procedures which are responsive to changes in stock productivity or are robust to such changes.
2. The effect of size-selective mortality on size-at-age should be further investigated including more stocks.	Further work by the ICES Community and others
3. The examination how the age structure and geographical substructure of the spawning stock affects resilience to climate change should be extended to other stocks.	Further work by the ICES Community and others