

Dramatic changes in spawning stock age-structure of Barents Sea cod

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Abstract

Atlantic Cod (*Gadus morhua*) is one of the commercially most important fish species in the North Atlantic and plays a central role in several ecosystems. Fishing pressure has been heavy over a prolonged period and the recent decades have shown dramatic decline in abundance of many stocks. The Arcto-norwegian (northeast Arctic) cod stock in the Barents Sea is now the largest. We show that the age composition of the spawning stock has changed distinctly during the last 60 years, the average age of spawners has decreased from between 10 and 11 in the late 1940s to 7-8 now. Although less clear, there is also a tendency towards reduced age diversity in the spawning stock, fewer age classes now contributing. The trend towards a younger, less diverse spawning stock is worrying, in particular since earlier work by other authors has thoroughly documented that older Barents Sea cod produce disproportionately more and higher quality eggs than first-time spawners. There is evidence for fluctuations in climate, particularly sea temperature, being a main cause for the pronounced recruitment variability of this stock, higher temperatures being favourable for survival throughout the critical early life stages. We document, through studies of time series, that the climate-cod recruitment link has strengthened during the last decades. Our results suggest that this is a result of cod now being less resilient to adverse climate conditions due to the reduction in spawning stock age and age diversity.

INTRODUCTION

Background

Different age groups of a fish population may contribute unequally to reproduction, making the age composition of the spawning stock important for recruitment. In particular, older age groups often contribute disproportionately more to the number of successful recruits than younger (Scott *et al.*, 1999; Caddy and Agnew 2003). The recent overexploitation of marine fish populations typically results in the loss of the largest individuals. Depletion of this component of the stock may reduce the number of eggs produced, and in addition the reproductive output of the stock may decrease further if younger fish exhibit poorer gamete quality than older fish (Trippel *et al.*, 1997). Furthermore, older fish may have a key role in spawning migrations, maybe involving learned behaviour (Rose 1993; Caddy and Agnew 2003).

Spawning Stock Biomass (SSB) is an important characteristic of a fish stock. However, substantial evidence has been presented showing that SSB is a poor measure of reproductive potential for Atlantic cod. A general reason for this is that SSB is not a good representation of population fecundity (the total egg production for a given stock biomass), which may vary through changes in key reproductive parameters like age- or size-specific fecundity (Kjesbu *et al.*, 1991; Trippel *et al.*, 1997; Scott *et al.* 1999). Since egg production of cod goes up exponentially with fish size, SSB will underestimate the extra reproductive fitness of the population added by having a significant proportion of older fish present (Caddy and Agnew 2003). Furthermore, offspring viability has been shown to be influenced by maternal size affecting the size of eggs and larvae (Kjesbu *et al.*, 1996; Trippel *et al.*, 1997; Scott *et al.*, 1999; Cardinale and Arrhenius, 2000a; Vallin and Nissling, 2000).

For Arcto-norwegian cod, SSB based on VPA (virtual population analysis) is not proportional to total egg production (Marshall *et al.* 1998). Experimental work by Kjesbu *et al.* (1996) shows that larger and older Arcto-norwegian cod tend to have a longer spawning period than smaller and younger fish. Egg quality (e.g., survival, buoyancy, egg size, hatching success) also seems to vary according to maternal size (Kjesbu *et al.*, 1992; Kjesbu *et al.*, 1996; Marshall *et al.*, 1998). Further, offspring of larger and older cod tend to be large at the larval stage, and thus have higher survival rates than offspring from

younger parental fish (Kjesbu *et al.*, 1996). Repeat spawners also produce eggs which have a wider range of vertical distribution than recruit spawners, thus causing broader horizontal spreading (Kjesbu *et al.*, 1992). It follows that changes in the age structure may severely influence the reproductive capacity of Arcto-norwegian cod. Indeed, several earlier authors have voiced concern over juvenation of this stock (Borisov, 1978; Sætersdal and Loeng, 1987; Nilssen *et al.*, 1994) or reduction in the number of age classes contributing significantly (Ottersen *et al.*, 1994).

Sea temperature is an important regulatory factor for recruitment of Arcto-norwegian cod, at least in the sense that cold years never provide a strong year class (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989). The explanatory mechanisms involve inflow of warmer, prey-rich Atlantic water masses from the south-west (Ottersen and Stenseth, 2001).

To our knowledge, very few earlier authors have studied how changes in stock age structure may enhance the effects of climate fluctuations on recruitment. However, during the Theme Session on recovery plans at the ICES Annual Science conference 2003, the importance of having a good reserve of older, more fertile fish to kick-start recruitment when environmental conditions become better again after a period of unfavourable conditions was pointed to (reported by Neil Fletcher at <http://www.ices.dk/marineworld/recoveryplans.asp>).

Ottersen *et al.* (1994) suggested that the Arcto-norwegian cod stock had increased their sensibility to environmental fluctuations resulting in a greater difference in recruitment between warmer, more favourable, and colder periods than in the past. They argued that this was a result of changed properties of the stock structure. However, the proposition of stock age distribution influencing the climate-cod recruitment relation was not substantiated.

In this paper we document that the age composition of the spawning stock of Arcto-norwegian cod has changed dramatically. The age of the average spawner has decreased by more than 3 years from between 10 and 11 in the late 1940s to 7-8 now. There is also a tendency towards fewer year classes dominating the spawning stock. We further show that climate-cod recruitment link has become increasingly stronger during the last decades. Finally, based on time series of several climate variables, cod

recruitment and spawning stock biomass by age, we provide evidence supporting the hypothesis of Ottersen et al. (1994) that the observed changes in the spawning stock age structure has decreased the robustness of the recruitment of Arcto-norwegian cod to climate fluctuations.

The Barents Sea system

The Barents Sea is an open arcto-boreal shelf sea situated off the North Atlantic, north of Norway and north-western Russia between 70 and 80°N (Fig. 1). Interannual variation in sea temperatures is strongly influenced by the relatively warm Atlantic water masses flowing in from southwest (Loeng, 1991) as well as regional heat exchange with the atmosphere (Ådlandsvik and Loeng, 1991; Loeng *et al.*, 1992).

The impact of interannual and decadal shifts in regional climate, sea temperature in particular, on recruitment of cod in the Barents Sea has been well documented (see Sætersdal and Loeng (1987) and Ottersen and Sundby (1995) for references). A positive impact of above-normal sea temperatures on particularly the early stages of the fishes life is reasonable, given that “warm” years are good years production wise in the Barents Sea for three principal reasons: (1) a larger ice-free area allows for higher primary productivity; (2) warm years imply large influxes of zooplankton from the south into the Barents Sea, and (3) higher temperatures lead to higher biological activity at all trophic levels (Sakshaug, 1997).

The North Atlantic Oscillation (NAO), an alternation in the sea level air pressure difference between the Azores high and Icelandic low (Fig. 1), is an important source of seasonal to decadal-scale climatic variability in the North Atlantic sector (Hurrell, 1995; Stenseth *et al.*, 2003; Hurrell and Dickson, 2004). It quantifies atmospheric large-scale fluctuations between the subtropical and subpolar regions of the North Atlantic and is the dominant mode of atmospheric behaviour in the sector throughout the year, although it is most pronounced during winter. NAO variability has been related to a number of climatic factors throughout the North Atlantic region including speed and direction of the prevailing westerly winds and high atmospheric and sea temperatures in Western Europe (Hurrell *et al.*, 2003). Climate fluctuations in the Barents Sea are in part linked to NAO variability (Ottersen and Stenseth, 2001; Ingvaldsen et al., 2003).

MATERIAL AND METHODS

Year-class strength of Arcto-Norwegian cod was estimated by the number of recruits to the stock at age 3 (VPA₃) as estimated by virtual population analysis (VPA) based on commercial catch statistics. Because year-class strength for this stock is mainly determined during the first 6 months of life (Sundby *et al.*, 1989), VPA₃ is compared with the climatic conditions the winter the year class was spawned. VPA was also used for estimates of Spawning Stock Biomass (SSB) per age group from age 3 to 13+ (13 and older). Values for 1946-2002 (1943-1999 cod year classes) were taken from ICES (2003; Tables 3.25, SSB and 3.26, VPA₃).

A linearised Ricker stock-recruitment model (Ricker, 1954) was fitted and the residuals compared with climate variables. The Ricker model may be expressed as

$$R = aSe^{-bS} \quad (1)$$

where R is recruitment, S spawning stock biomass, and a and b parameters. By taking the natural logarithms on both sides of the equation we get

$$\begin{aligned} \ln(R) &= \ln(a) + \ln(S) - bS \Leftrightarrow \\ \ln(R) &= a' + b'S + \ln(S) \end{aligned} \quad (2)$$

The sea temperature series from the Kola meridian transect (33°30'E, 70°30'N to 72° 30'N, Fig. 1), intersecting the Murman Current in the south central Barents Sea, is fairly representative of the whole Atlantic domain in the Barents Sea and particularly for the Atlantic Water continuing east towards Novaja Zemlya (Ingvaldsen *et al.*, 2003). Monthly values have been calculated by averaging along the transect and vertically from 0 to 200 m water depth. The historical data have been taken from Bochkov (1982) and Tereshchenko (1996), while the most recent values have been provided by PINRO, Murmansk. Winter (December-March) means are applied for 1943-2002 (year of January, February, March values).

NAO indices, slightly modified from the winter (December-March) index of Hurrell (1995), were obtained from Jim Hurrell's world wide web page at NCAR's Climate and Global Dynamics Division (<http://www.cgd.ucar.edu/~jhurrell>).

Monthly values of atmospherically driven water volume flux through the Fugløya-Bear Island section (Fig. 1), at the western entrance to the Barents Sea, was estimated by means of a numerical hydrodynamic model run for 1955-2001 (Ådlandsvik and Loeng, 1991; Loeng *et al.*, 1992). The model is a three-dimensional level model with linear shallow water equations and vertical eddy viscosity and is discretized by finite differences using the Arakawa-C grid. The implementation for the Barents Sea has a horizontal grid resolution of approximately 20 km (Ådlandsvik and Loeng, 1991). Density-driven (baroclinic) currents are not included in the model; hence the flux reflects only the variability in atmospheric forcing (barotropic component). Again, winter (December-March) means are applied.

Ordinary (Pearson product-moment) correlations were used to describe the degree of linear relation between two variables. Moving correlations were used to describe the temporal development of climate-cod links. We are interested in the long-term development and use a moving correlation window of 21 years. Note that at each end of the time series of correlated values 10 years are lost.

The “mean age” of the spawning population, calculated for each year separately, was estimated by calculating a mean value weighted on the SSB in each age group added over all age groups in the spawning stock (ages 3-13+).

$$AGE = \frac{\sum_{i=3}^{13+} (SSB_i \cdot AGE_i)}{\sum_{i=3}^{13+} SSB_i} \quad (3)$$

The coefficient of variation (CV= standard deviation/mean) of SSB between age groups for any given year was calculated. The CV was taken as a measure of to what degree one or a few age classes dominated the SSB. Large CV values describe cases with large differences between age groups regarding contribution to the total SSB, small CV values a more uniform distribution of SSB across ages.

The Shannon diversity index (H) (Shannon, 1948) is a well known descriptor of species richness described in a number of ecology text books, for example Magurran (1988). Following Marteinsdottir and Thorarinnsson (1998) we here apply H, not to species richness, but to estimate the diversity of the age structure of the spawning stock in each year. H was employed to obtain a single value, independent of stock size, which describes both the number of cohorts in the stock and the evenness of the distribution of

fish among cohorts (Marteinsdottir and Thorarinsson, 1998). Because we believe SSB to be a better measure of the state of the spawning stock and particularly reproduction potential than number of fish, we apply H to SSB numbers. In this case H may be defined as

$$H = -\sum_{i=1}^k (p_i \cdot (\log p_i)) \quad (4)$$

where log represents the natural logarithm, k is the number of age groups present and p_i the proportion in age group i of the total SSB. A large value of H thus denotes many year classes contributing equally to the SSB.

RESULTS

Reduction in spawning stock age and age diversity

The age-composition of the spawning stock has clearly changed from the first to the last decade studied (Figure 2). Particularly striking is the shift of the frequency distribution towards lower ages, but there also seems to be a tendency towards a larger part of the SSB being located in a few age classes. The change in age of the spawning stock is made further clear in Figure 3. Although there are interannual fluctuations, the downward trends in total biomass of fish of age 10 or older, percentage of the SSB in fish of age 10 or older, and the mean age of the spawners are all pronounced. The former displays a dramatic drop-off during the late 1940s, while the decline in the two latter is more gradual although just as strong. For instance, while more than 90 % of the SSB was in age 10+ fish in 1947, the most recent value, for 2002, was 2.5%. Age diversity in the spawning stock is represented by the Shannon index (H) and the coefficient of variation (CV). There is a decreasing trend in H and increasing in the CV (Figure 4). This indicates a development towards a SSB concentrated to fewer cohorts.

Temporal development of cod recruitment and environmental conditions

Abundance of cod at age three as well as the residuals from a stock-recruitment Ricker model have undergone pronounced fluctuations throughout the period studied, while the pattern dominating the SSB development is one of a sharp decline from the mid 1940s to the mid 1950s followed by less dramatic fluctuations and a peak in the early 1990s

(Figure 5). Similarities in the fluctuation patterns of sea temperature in the Kola-section, wind-driven inflow to the Barents Sea and the NAO, all for the winter season, should be noted, especially the generally increasing trend during the last decades (Figure 6; see Ottersen and Stenseth, 2001 for details).

Change in climate-cod relation

The 21 year moving correlations between cod recruitment and the three winter climate variables Kola section temperature, wind-driven inflow to the Barents Sea and the NAO increase with time (Figure 7). Similar results were found when replacing recruitment with residuals from a Ricker model. The systematic pattern of higher covariation between climate and cod recruitment for the latter decades is confirmed by calculating ordinary correlations separately for the years before and including 1970 and from 1971 and onwards (splitting the overlapping period between sea temperature [or the NAO] and cod recruitment in two equally long parts). For the first period the six correlations ranged from -0.33 to 0.19 (all $p > 0.10$). For the second period the three climate - cod recruitment correlations ranged from 0.54 to 0.59 (all $p < 0.05$), the three correlations with Ricker residuals from 0.33 ($p < 0.10$) to 0.59.

Change in climate-cod relation related to change in spawning stock composition

The correlations between climate and cod recruitment are linked to spawning stock characteristics (Figure 8). Large values of biomass of fish of age 10 or older, large percentage of the SSB in fish of age 10 or older, and high mean age of spawners all correspond to low correlations. The connection between the age diversity variables, H and CV, and climate-recruitment correlations is less clear. While small values of H and large values of CV denote low correlations between sea temperature and cod recruitment, no such link is found for inflow-cod recruitment or NAO-cod recruitment (Figure 8).

DISCUSSION

Younger spawning stocks with fewer age classes present has become a well known phenomenon for long-lived fish in many parts of the world as the results of high fishing pressure become evident (Law, 1991; Law, 2000). The age composition of most Atlantic

cod stocks is currently strongly biased towards young fish and reproduction is largely dependent on first-time spawners (Caddy and Agnew 2003). Possible detrimental consequences for recruitment to these stocks through reduced population fecundity and offspring viability are also well described; not least for Atlantic cod (see also Introduction). For instance, in the Baltic recent changes in the age-structure of the cod spawning stock has attracted substantial attention. This is recognized as one of the principal factors influencing recruitment of Baltic cod, eggs produced by older females having a substantial higher probability of survival (Cardinale and Arrhenius, 2000a; b; JarreTeichmann *et al.*, 2000; Vallin and Nissling, 2000). For cod in the northwest Atlantic, Hutchings and Myers (1993) describe a dramatic reduction in the fecundity contribution of older versus younger spawners. They observed a reduced duration of spawning time in younger fish and suggested that this would reduce the probability of cod larval emergence matching peak zooplankton abundance, increasing variability in cod recruitment. In addition to juvenation, a reduction in the number of age groups contributing to the spawning stock may adversely influence recruitment by reducing the spatial and temporal distribution of spawning (Hutchings and Myers, 1993; Marteinsdottir and Thorarinsson, 1998), the latter studying Icelandic cod.

With size-selective overfishing becoming more and more frequent, there is a need to address the dire consequences more thoroughly, not least within the context of global climate change. There is no reason to doubt that the combination of a development towards a more unknown climate, with increased variability and number of extreme events, and less robust and resilient stocks, will seriously influence many of the world's fish resources. In the words of Marteinsdottir and Thorarinsson (1998) "Fisheries can increase the vulnerability of target populations to climatic change by altering their age structure, increasing predatory fish populations, and reducing populations of food fish". While we're struggling to halt or even reduce climate change, fisheries managers may have better chances at preventing stock collapses by taking age structure into consideration. Within the idea of the precautionary approach it is particularly important that management take environmental conditions into consideration for depleted stocks with high sensibility to climate fluctuations.

The clear results shown here concerning reduction in the age of the spawning stock (Figures 2 and 3) confirms a development observed already 40 years ago by Sætersdal and Hysten (1964) and later recognized by several authors. Sætersdal and Hysten (1964), cited by Nakken (1994), were concerned about the catch of old and large Arcto-norwegian cod being reduced relatively to that of the younger and smaller fish. Furthermore, they noted that the mean age of the spawners had decreased, and blamed this on increased exploitation. Borisov (1978) expressed concern about the juvenation of the spawning population and Nilssen *et al.* (1994) described the abundance of cod older than 10 years at the time to be at less than 1% of that in the late 1940s. In light of the extensive degree of change in the age structure of the stock revealed here (Figure 3), the reduction in percentage of fish age 10 and above and mean age at the time of Sætersdal and Hysten (1964) seems quite moderate, while the actual SSB of 10+ fish already then was drastically reduced compared to the late 1940s, when the stock structure partly reflected the reduced fishing during the second World War.

The trend towards a closer connection between climate variables and cod recruitment seems convincing (Figure 7). However, one might expect the suggested mechanism to lead to increasing amplitudes in recruitment variability with time, something that does not appear to be the case (Figure 5a). On the other hand, variability at the 0-group stage (5 months old) seems to have increased. The available 0-group time series, from 1966 (Anon. 2002), is a lot shorter than that for recruitment at age 3. However, by simply splitting it in two and calculating the standard deviation for each half we obtain an indication of the development. The standard deviation for 1966-1983 is 0.62; from 1984-2002 it is 0.96. The overall long-term trends of increasing climate – recruitment links are in any case present. Moreover, the consistent negative correlation between the different moving climate-recruitment correlations and the three variables representing spawning stock age strengthens our argumentation. A younger spawning stock leads to recruitment being more dependent on environmental conditions (Figure 8).

There is a tendency towards fewer year classes dominating the spawning stock (Figure 2, Figure 4). This is far less clear than the juvenation trend, though. Thus, it is not surprising that our data give a somewhat unclear picture of to what degree this tendency towards concentration of the spawning biomass to fewer year classes affects the climate-

cod recruitment relation. Only the temperature-cod recruitment link seems to be stronger when the age diversity is low (Figure 8; large CV, small H), neither the inflow nor the NAO influence on recruitment seems to be affected.

Working on Icelandic cod, Marteinsdottir and Thorarinsson (1998) suggest that a less diverse age structure in the spawning stock may result in a narrower spatial and temporal distribution of spawning, related to size- or age-dependent timing, duration, or location. A wider ‘spread’ of mature year classes in the population is likely to prolong the spawning season, and help ensure that temporarily unfavourable conditions do not completely compromise spawning success (Caddy and Agnew 2003).

Hutchings and Myers (1993) argue that decline in both spawner age and the number of spawning age classes may shorten the duration of the spawning season, reducing the likelihood that larvae begin feeding during the peak of zooplankton production, and increasing interannual cod recruitment variability. Following this, our spawning stock age structure links to climate-recruitment relations may be mediated through food availability and the match-mismatch hypothesis of Cushing (1990).

CONCLUSIONS

The juvenation of the spawning stock of Arcto-norwegian cod over the last 60 years or so has been pronounced, whether measured as biomass of fish of age 10 or older, percentage of SSB in this age category or mean age of the fish constituting the SSB. Also the age diversity of the SSB has been reduced. Simultaneously, the link between climate and recruitment to Arcto-norwegian cod has become stronger with time. We suggest that the enhanced climate-recruitment link is an effect of the reduction of age and age diversity in the spawning stock, leading to the cod population becoming less resilient towards adverse climate conditions.

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FIGURE CAPTIONS

Figure 1. a) The North Atlantic with the location of the Barents Sea indicated. b) The Barents Sea and northern part of Norway showing important spawning areas (grey areas along the Norwegian coast) and nursery/feeding areas (large grey area in the Barents Sea) of Arcto-norwegian cod. Double line arrows indicate spawning migration, single line arrows seasonal migration of young fish. The stippled line indicates the Fugløya - Bear Island section (FB), the dotted line the Kola section. The region belongs to ICES areas I, IIa, and IIb delimited by the thick lines. Panel b) is adapted from Aure *et al.* (2000), graphics work by Karen Gjertsen, IMR.

Figure 2. Age-composition of the spawning stock in percent per age group for a) The first decade studied 1946-1955 and b) The last decade studied 1993-2002.

Figure 3. Temporal development 1946-2002 of a) Biomass of spawners age 10 and older, b) Percentage of spawning stock biomass of fish of age 10 and older, c) Mean age in the spawning stock biomass (see text for calculation method).

Figure 4. Temporal development 1946-2002 of measures of age diversity of spawning stock biomass. a) Coefficient of variation and b) Shannon diversity index.

Figure 5. Temporal development of a) Cod abundance at age 3, 1943-1999 year class (number of 3 year old fish in 1946-2002), b) Spawning Stock Biomass, 1946-2002, and c) Residuals from a Ricker stock-recruitment model (1946-1999).

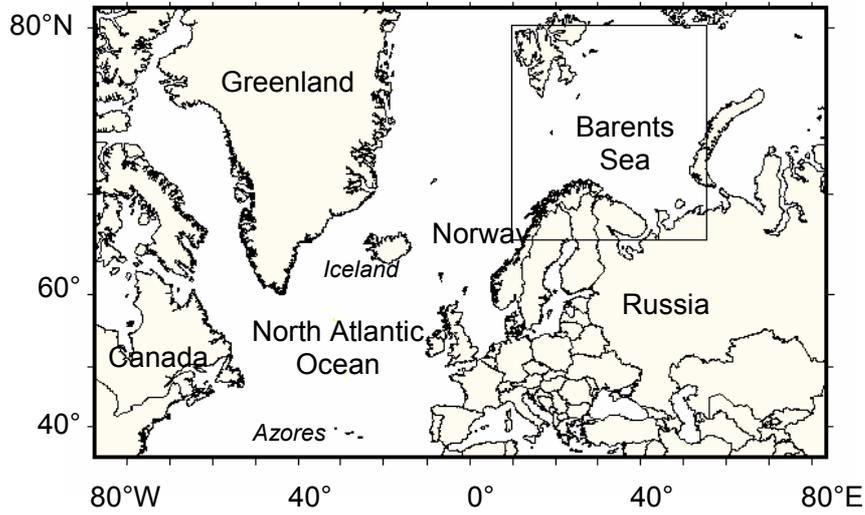
Figure 6. Temporal development of winter (December-March) means of a) Sea temperature along the Kola meridian in the south-central Barents Sea 1940-2002, b) Modelled, atmospherically driven inflow to the Barents Sea from the southwest 1955-2001, and c) The NAO index of Hurrell (1995) 1943-2003.

Figure 7. Moving, 21 year time window, correlations between a) Cod year-class strength at age 3 (VPA_3) and Kola section sea temperature 0-200 m depth (T_{Kola} ; data 1943-1999),

b) Cod year-class strength at age 3 and the NAO (data 1943-1999), c) Cod year-class strength at age 3 and inflow to the Barents Sea (data 1955-1999), d) Residuals from a Ricker spawning stock biomass-recruitment model (Res_{Ricker}) and Kola section sea temperature (data 1946-1999), e) Ricker residuals and the NAO (data 1946-1999), and f) Ricker residuals and inflow to the Barents Sea (data 1955-1999). All climate data for winter (December-March). A 21-year correlation outside the stippled bands is statistically significantly different from 0 ($P < 0.05$, two-sided test).

Figure 8. Scatter plots of variables characterising spawning stock biomass age structure versus moving, 21 year time window, correlations between temperature and cod recruitment. a) Biomass of spawners age 10 and older, b) Percentage of spawning stock biomass of fish of age 10 and older, c) Mean age in the spawning stock biomass, d) Coefficient of variation of spawning stock biomass by age, and e) Shannon diversity index of spawning stock biomass by age.

a)



b)

