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Cod and future climate change

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Summary

As part of the ICES/GLOBEC programme on Cod and Climate Change (CCC), a Workshop on Cod and Future Climate Change (WKCFC) was held between 17 and 20 June 2008 in Copenhagen (ICES, 2008a). The objective was to develop projections for the likely dynamics of Atlantic cod (*Gadus morhua*) over the next 20–50 years based on (i) regional climate scenarios that included anthropogenic climate change, and (ii) knowledge of the impact of climate on cod and other species gained during the CCC programme. The projections would consider not only the direct climate effects on cod, but also possible indirect climate effects resulting from changes in the prey (including zooplankton), predators, and competitors of cod.

The development of reliable regional climate scenarios by downscaling (statistical or coupled) from global circulation models (GCMs) depends on the overcoming of a number of problems. Most existing downscaled scenarios are based on GCMs that pre-date the recent IPCC model runs (IPCC, 2007a). One regional model for the North Sea was downscaled from a recent run; however, the IPCC GCM in question poorly reproduced the current climate for the region, which calls into question the credibility of regional downscaling. It was concluded that regional models should be downscaled from several GCMs, chosen by their ability to reproduce the current climate (not only temperature, but also wind and pressure fields, precipitation, etc.). Because many of the IPCC 2007 model results demonstrate large deviations from current regional climate observations, this limits the number of GCMs that can be used for downscaling. Furthermore, the two major modes of variability over the Atlantic Ocean during the past century, the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO), are reproduced poorly by the GCMs (Section 3.2). On an encouraging note, however, models that assimilate recent climate data (and include the decadal modes) demonstrate useful forecasting skill, at least over periods of a few years (Section 3.4).

Currently, the lack of reliable regional climate projections makes it unrewarding to implement coupled biological models of lower trophic level dynamics impacts on cod (*Gadus morhua*) populations for predictions over the next 20–50 years. Currently available global and regional climate models are probably only adequate for exploring impacts on the North Atlantic marine ecosystem in a preliminary way and not for quantitative projections. Considerable scientific effort will be required to design, initialize, run, and statistically test downscaled or fully coupled regional models that are consistent with observed climate modes and data at global and regional scales and that produce reliable output for the relevant variables affecting biological systems. Impact assessments can, for now, be based on “what if” scenarios, but the likelihood of these scenarios and the time-scale over which they may occur is not known.

In the absence of reliable regional climate projections, a range of scenarios was used to carry out an impact assessment in order to explore the interactions between climate and other pressures, particularly fishing, on fish stocks. Statistical (multivariate autoregressive) models were used to assess possible effects of different climate scenarios and fishery management strategies on Baltic Sea cod (Section 4.2). Results suggest that even a relatively small decrease in salinity (>3 psu) would impair recruitment of Baltic cod because of increased egg and larvae mortality. A large decrease in fishing mortality would reduce the risk of extinction of the Baltic cod stock, at least for a few more generations.

The results of a non-spatial model that includes temperature, zooplankton, prey, and predators indicate that a 1–4°C increase in temperature in the Barents Sea will cause increased cod growth, increased cod production, and decreased maturation rates. However, the positive effects on cod production are offset by cannibalism (Section 5.1).

Another study exploring the effect of temperature on all North Atlantic cod stocks found that a 3°C rise in temperature would lead to a 30% reduction in the carrying capacity of warm-water stocks (Section 4.1). Other likely impacts of warming include a general northward shift in distribution, increased growth and productivity in northern regions, and a decline in southern regions. Fishing pressure will play an important role in determining the rates of change of the cod populations. On the other hand, fishery management must consider climate effects and develop models that include the combined effects of climate and fishing.

Palaeological, archaeological and historical reconstructions, and recent data on the distribution of cod and other species were used to investigate the effects of past climate variability on distribution, stock separation, and changes in abundance. It is likely that the separation of the cod stocks between the eastern and western North Atlantic dates from before the last ice age (Section 2.2.1). During the Atlantic warm period (~6–9000 BP), cod persisted around Denmark (Section 2.2.2) at temperatures above those at which bioclimate models predict their disappearance, indicating that such predictions may be unreliable. A detailed analysis of changes in distribution of North Sea cod over the past century explored the effects of fishing, temperature, windfield, and other environmental variables, but was unable to explain observed patterns (Section 2.2.3). This also indicates that our ability to predict future patterns may not be very reliable, because of biological and environmental complexities not included in simple bioclimate envelope approaches. The Greenland cod stock is expected to increase with warming, but the rate at which this is happening is very slow and may depend on the state of adjacent stocks, particularly off Iceland (Section 2.2.4).

Examples of three classes of models that couple physics and biology were presented, and their utility for projecting future impacts was assessed.

- Mechanistic coupled biophysical models can provide information on processes and process interactions as well as identify patterns of ecosystem dynamics (Section 4.1). In contrast to statistical models that find correlations or linear relationships between variables (such as the multivariate autoregressive model for the Baltic), mechanistic models explicitly represent processes that directly or indirectly influence the abundance or biomass of marine organisms. They provide a deeper understanding of the functioning of ecosystems and can be developed into reliable models for future prediction of responses to climate.
- The representation of processes and interactions in statistical models is implicit, but they can also provide insight into the functional representation of ecosystem processes and into possible changes in functional relationships over time (Section 4.2).
- Mechanistic–stochastic models use meta-analysis to increase the observational basis for fitting functional relationships of known processes (e.g. growth, stock recruitment; Section 4.3).

The methodology for projecting future states of marine ecosystems and particular species, such as cod, is in its infancy. The present report has taken a fairly critical

view of existing physical and biological models and projections in order to identify present gaps in understanding and shortcomings in model structure. Studies that help to improve methods and evaluate the reliability and likelihood of physical and biological projections should be given priority. Interfaces between global and regional climate models and between climate and biological models require particular attention, and the report includes a number of specific recommendations for these. A general recommendation is that the kind of dialogue that took place during this workshop between climate scientists and scientists studying climate impacts should be further encouraged in order to ensure that each community is aware of the nature, needs, and limitations of the projections being attempted. More specific recommendations for future work on cod are:

- to develop more detailed and complete probabilistic climate projections that are designed to carry out “what if” studies for future cod scenarios;
- to convey the detailed needs of the fishery impact community to modellers working on improvements in the GCMs in order to provide a better climate basis for such impact studies;
- to develop regional models of future climate for areas inhabited by cod using statistical, dynamic, and blended downscaling of results from several GCMs that are able to reasonably represent local present climate conditions;
- to use coupled regional biophysical models to develop scenarios of phytoplankton and zooplankton under future climate;
- to apply the results of regional ocean–climate projections and lower trophic-level projections to explore the potential effects on cod; and
- to develop models that include the higher trophic levels, especially cod, and then use these to investigate the combined effects of climate and fishing in order to determine better management strategies under climate change.

1 Introduction

Many of the oceanic regions currently inhabited by Atlantic cod are predicted to undergo significant warming as a result of climate change. In recent years, much of the North Atlantic has experienced warming. Managers, politicians, and the general public have increasingly been asking what will be the impacts of future climate change. Such information for cod and the marine ecosystems they inhabit has been limited. Indeed, the few published studies have usually considered the response of individual species to increased warming without considering other components of the marine ecosystem, such as their prey or predators. However, climate change is expected to affect both the structure and function of marine ecosystems. Therefore, more plausible impact scenarios require us to consider species as part of the ecosystem. The Workshop on Cod and Future Climate Change (WKCFCC) in June 2008 built on the increased understanding gained through the ICES/GLOBEC Cod and Climate Change (CCC) programme, including past workshops, plus other research on the effects of climate variability on cod and its supporting ecosystem. The 16 participants from six countries (Denmark, Germany, Norway, Russia, UK, and USA), plus the ICES/GLOBEC Coordinator, are acknowledged as contributors to this report and are listed at the end of the report. In total, 13 presentations were given at the workshop and extended abstracts are provided in Appendix 1.

1.1 Terms of reference

Responses to future climate-change scenarios include:

- the adoption of 20–50-year probabilistic projections of future temperature, salinity, and nutrients as a basis for projections of fish population dynamics and distribution;
- the development of methodologies and the construction of projections of likely changes in phytoplankton and zooplankton production and distribution, especially those species eaten by cod and their predators or prey during their life histories;
- the development of methodologies and the construction of projections of likely changes in prey and predators of cod including the forage fish, such as capelin (*Mallotus villosus*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and mackerel (*Scomber scombrus*); and
- the development of methodologies and the construction of projections of likely changes in cod production (growth, reproduction, mortality, recruitment) and distribution.

This will be carried out using a combination of retrospective data analyses and a variety of modelling approaches.

1.2 Prediction and confidence

Keith M. Brander

In order to predict the distribution and productivity of cod under climate change, we need scenarios of future climate, information on the sensitivity of cod to changing climatic factors, and information on changes in other biotic factors that may indirectly affect cod. The credibility or confidence limits for such predictions depend on the reliability of each step in the causal chain and on the inclusion of all the processes

that may affect the outcome. Some general predictions can be made with reasonable confidence (e.g. distributions will follow shifts in thermal boundaries; growth, maturation, and recruitment, and will follow known temperature-response curves), and a number of studies are reported here. The level of confidence that can be ascribed to more specific, time-based, regional predictions is lower than the general predictions because they require

- regional climate forecasts, which include the necessary variables (temperature, salinity, oxygen, wind, vertical mixing, etc.);
- knowledge of local sensitivity to these variables (e.g. response of recruitment or growth to temperature depends on the location of the stock within the thermal range);
- the inclusion of all the relevant local processes and interactions (productivity, prey and predator abundance, effects on pathogens, and other biotic interactions).

Therefore, although it is possible to assemble models that incorporate many of these factors and predict future dynamics of cod, it is also necessary to make an estimate or judgement of the reliability of such models. This requires an assessment of the uncertainties that arise at each stage in the causal chain process, including the effects of process uncertainty, structural incompleteness, initialization errors, and model errors. The procedures for estimating error bounds and for quantifying levels of confidence are not dealt with formally in this report. However, the major sources of uncertainty are identified (i) to evaluate existing studies and provide some guidance on the associated degree of confidence, and (ii) to identify steps in the modelling chain that require improvement in order to reduce the uncertainty of the predictions.

Other options for predicting changes in cod and in marine ecosystems are (i) to use spatial or temporal analogues, and (ii) to carry out experiments. A number of examples of temporal analogues are provided in this report (e.g. distribution during the Atlantic warm period 9000–5900 BP, distribution and abundance changes during the warm period from 1920–1960). To date, very limited use has been made of experiments that study consequences of climate change for marine species, although this is changing very quickly, particularly for studying the effects of a decrease in pH. Extensive field experiments are the principal means of predicting future yields for terrestrial agriculture.

It is instructive to review our ability to identify the causes of observed changes in cod stocks, as has been done for North Sea cod (Section 2.2.2.3), because confidence in predictions of future changes can only be justified if the processes causing past changes have also been correctly identified.

1.3 Incorporating environmental information

Keith M. Brander

The Workshop on Integration of Environmental Information into Fisheries Management Strategies and Advice (WKEFA; ICES, 2007) provides a background for the present workshop. It supplied the principal term of reference for the present workshop (i.e. the development of 20–50-year probabilistic projections of climate) and also set out a framework of time-scales, population processes, and management issues. Although the present WKCFCC is concerned with future climate and long time-scales, many of the issues discussed are also relevant at shorter time-scales.

The time-scales identified by WKEFA were

- **extreme** events, which cause migration, mortality, or recruitment failure;
- **short-term** changes, which affect growth and maturation one or two years ahead and will affect total allowable catch (TAC);
- **medium-term** changes, which use stochastic projections and scenario testing (e.g. temperature, salinity, oxygen dependence of survival, species interactions, and food availability);
- **long-term** climate scenarios for sensitive areas such as the Baltic Sea.

The population processes were (i) entries and exits (recruitment, natural mortality, or M, migration); (ii) internal population processes (growth, reproduction); (iii) location and habitat (e.g. vertical and horizontal movement); and (iv) multispecies interactions.

The management issues were (i) to design management procedures that are either robust to or adapt to regime changes; (ii) to allow for changes in habitat which influence stock carrying capacity and measurement (e.g. interpreting surveys); (iii) to improve our ability to estimate changes in recruitment, growth, and maturation, which influence short- and medium-term management advice; and (iv) to include information on expected environmental change and its impact as part of each stock assessment.

The WKEFA report provided numerous case studies of management adaptation to environmental variability, inclusion of multispecies aspects, direct application of environmental information, and simulation of the management consequences of productivity shifts.

The Working Group on Regional Ecosystem Description (WGRED; ICES, 2006) reviewed the reasons for including environmental information in management advice and why this is not easy to do. Their review has been cited or paraphrased in several places in the current report and is worth reading in the original. It includes commentaries on

- long-term climate change and global warming;
- regime shifts and implications for fishery management;
- recovery strategies and ecological-niche theory;
- inclusion of environmental information (in 2005);
- reasons why the inclusion of environmental information is so limited, and proposals for improving this.

1.4 What kinds of prediction are we aiming at?

Keith M. Brander

The title and terms of reference for the WKCFCC (to develop 20–50-year probabilistic projections of climate) make it clear that the main time-scale of interest is the long-term. However, there are interactions between the time-scales so that short-term events may affect much longer time-scales. For example, long-term trends in salinity in the Baltic depend on the frequency of the occurrence of short-term extreme events (i.e. Baltic inflows). Therefore, models of long-term changes in Baltic salinity need to have sufficient spatial and temporal resolution to resolve such short-term events and their frequency. Short-term events that have major effects on fish may cause changes

in populations which persist for long periods (e.g. mass mortalities caused by toxic blooms, triggered by unusual conditions of temperature, salinity, nutrients, and stratification).

The lead time over which climate forecasts are significant is difficult to estimate because it depends on the variable, region, initial state of the climate system, and availability of observations for the initialization. The results of Smith *et al.* (2007) and Keenlyside *et al.* (2008) have demonstrated that, for some variables and regions, predictability lies well beyond a decade. As scale interactions and regional predictability for ocean climate degrades back to the global pattern after a relatively short time, we interpreted our time-horizon to include all scales of climate forecasting. One- to five-year regional forecasts, for which skill estimates are available, will provide valuable additional information for fishery management and will complement existing general global scenarios.

Predictions of future distribution and productivity of a particular cod stock can be separated into a climate prediction (or scenario) and the expected biological impact. The current state of appropriate regional climate models, including their improving skill and limitations, are dealt with in Section 3. Depending on the type of climate information available, the biological impacts can be looked at under a range of “what if” scenarios, which has been done in several of the cases and studies that are reviewed. A common approach is to predict the consequences of a succession of increasingly higher mean temperatures (e.g. 1–4°C) for a given rate of warming; these increases may be associated with particular time-slices (e.g. 2020, 2050, 2080).

2 Review of climate impacts and lessons from the past

2.1 Previous work on climate impacts on cod

Ken F. Drinkwater

There have been several previous studies on the response of cod to future climate change, including two that have considered all of the major cod stocks in the North Atlantic. Drinkwater (2005) used “what if” scenarios of ocean climate change and considered changes to the cod stocks under increases of 1–4°C in ocean temperatures, which was within the range of changes suggested at the time (IPCC, 2001). His results were based on the relationship of recruitment to changes in temperature, found by Planque and Frédou (1999) and by Ottersen (1996), which demonstrated increasing recruitment with increasing temperatures for cold-water stocks and decreasing temperatures for warm-water stocks. This relationship was converted into a change in recruitment as a function of surface temperature change vs. mean annual bottom temperature of the stock (Sundby, 2000; Drinkwater, 2005). At bottom temperatures <5°C, recruitment tends to increase with increasing temperature, whereas at temperatures >8.5°C, recruitment decreases. At temperatures between these two values, there is little change in recruitment with temperature.

Drinkwater (2005) also used the present-day observation that no cod stocks are observed in waters with annual mean bottom temperatures above 12°C. If bottom temperatures warm beyond 12°C, he assumed that cod will disappear. Based on these criteria, cod stocks in the Celtic and Irish seas would be expected to disappear with only a 1–2°C increase, and stocks in the southern North Sea and Georges Bank would begin to decline because of decreases in recruitment. If temperatures increased by 4°C, these stocks would also probably disappear. Cod in northern regions, such as Labrador, Iceland, West Greenland, and the Barents Sea, would see increased recruitment and abundance. Coupled with an expected increase in growth throughout the North Atlantic, this would result in an increase in overall Atlantic cod production, despite potential losses in the southern regions. Drinkwater (2005) also predicted that cod would probably spread northwards along the coasts of Greenland and Labrador, occupy larger areas of the Barents Sea, and might even extend onto some of the continental shelves of the Arctic Ocean. For cod stocks that migrate, spring migrations would occur earlier than at present, and autumn returns would be later. He speculated on the distinct possibility that, where seasonal sea ice disappears altogether, such as in the Gulf of St Lawrence, cod may cease to migrate.

Another study examining the response of cod throughout the North Atlantic was conducted by Cheung *et al.* (2008), using a bioclimate envelope model. Bioclimate envelopes are a set of physical and biological conditions that are suitable for a given species and are generally identified from present-day or past associations. Cheung *et al.* (2008) included sea temperatures, bathymetry, habitat, and distance from sea ice as their set of variables, and determined the responses to climate change from 1–30 years using a uniform hypothetical temperature increase. They predicted a general northward shift in the distribution of cod, similar to Drinkwater (2005), with declines in the southern stocks (i.e. Georges Bank, Gulf of Maine, and Scotian Shelf in the Northwest Atlantic; and in the North, Irish, Celtic, and Norwegian seas in the Northeast Atlantic). On the other hand, the relative abundance of the Icelandic, Faroe Islands, and Barents Sea cod stocks would increase.

Several other more regional studies have been carried out. Stenevik and Sundby (2007), in a paper on the effects of climate change in Norwegian waters, commented on the effects on cod. They examined a global-warming scenario in which there was a high NAO and high Atlantic inflow to the Barents Sea. Under this scenario, cod in the North Sea were predicted to decline as a result of the reduction in *Calanus finmarchicus* and warm temperatures. northeast Arctic cod, which spawn along the Norwegian coast off the Norwegian Sea, drift into the Barents Sea as larvae or small juveniles and spend their adult life there. This stock was predicted to increase in abundance because of higher recruitment and, coupled with improved growth rates, to have a higher biomass. Cod would also move farther north and eastwards, with a greater percentage of the total population moving out of Norwegian waters and into the Russian Economic Zone. However, because of the overall increase in production, the total number of fish in the Norwegian Economic Zone would not decrease, although their percentage of the population would decrease. Cod is also expected to spawn farther north (Sundby and Nakken, 2008), and new spawning sites will probably be established.

Vikebø *et al.* (2007a) examined the potential impact of a reduction in the thermohaline circulation (THC) in the North Atlantic, caused by climate change, on the larval drift of northeast Arctic cod. This circulation pattern brings warm water north, and this cools, sinks, and returns as a deep-water current. Using a regional ocean modelling system (ROMS), they imposed a threefold increase in river discharge to the Nordic seas and the Arctic Ocean, which reduced the strength of the THC by 35%. This is near the projected reduction of ca. 25% in the THC predicted by the end of the 21st century in the IPCC report (IPCC, 2007a). This reduction results in a southward and westward drift of cod year classes from the Barents Sea onto the Norwegian and Spitsbergen shelves, a reduction in the number of pelagic juveniles that survive, and an increase in the proportion of larvae and juveniles advected along West Spitsbergen, and possibly into the Arctic Ocean through the Fram Strait (Vikebø *et al.*, 2007a). However, cod that make it into the Arctic Basin are not expected to survive.

The projected increase in cod abundance, recruitment, and biomass, as well as the distributional shift farther eastwards and northwards, will depend to a large degree on future fishing intensity. Indeed, in his examination of the effect of different management regimes on Norwegian cod fisheries in conjunction with climate change, Eide (2008) concluded that these management schemes would play a more significant role than climate change in the economic performance of the fishing industry in the Barents Sea.

Clark *et al.* (2003) examined the role of temperature on cod in the North Sea. They found that temperature affects the survival of cod through influences on recruitment. Given the expected rise in temperature under future climate change, they suggested that North Sea cod could disappear unless fishing mortality rates are drastically reduced.

MacKenzie *et al.* (2007) examined the possible responses to climate change of fish, including Atlantic cod, in the Baltic Sea. Mean annual temperatures are expected to rise by 2–3°C in surface waters, with greater increases during the spring–summer period, especially in the central Baltic. Precipitation will increase, leading to higher run-off and a 7–47% reduction in surface salinities, depending on location. Stable or lower salinity would be detrimental to cod through reduced reproductive success and possibly reduced larval survival resulting from changes in the zooplankton community. It is also predicted that there will be less frequent major Baltic inflows,

which will result in less oxygenated waters in the deep basins. In the western Baltic, reduced surface salinities and lower oxygen levels in deep waters will reduce the cod spawning habitat. Climate change may also affect the predators of cod eggs, such as herring and sprat, with major consequences for cod dynamics. MacKenzie *et al.* (2007) speculated that cod stocks in the eastern Baltic could collapse completely under the warmer and fresher conditions. Changes in the ecological basis for production of cod would have consequences for its management and exploitation, as well as for the overall management of the Baltic Sea foodweb. For example, fishery management thresholds that trigger reductions in fishing quotas or fishery closures in order to conserve local, genetically (Nielsen *et al.*, 2001, 2003), and physiologically (Nissling *et al.*, 1994; Nissling and Westin, 1997) distinct populations of cod will have to be re-assessed if these thresholds become more variable or are altered by climate.

On the other side of the Atlantic, on the Scotian Shelf, Frank *et al.* (1990) speculated that climate change may result in increased stratification through surface heating and increased precipitation, which would tend to favour pelagic over demersal fish, such as cod, and hence cause a decline in cod abundance.

Fogarty *et al.* (2007) examined the potential impacts of climate change on the distribution and production of Atlantic cod on the northeastern USA continental shelf. Their analysis of future changes in water temperature, based on three coupled atmosphere–ocean general circulation models under high and low CO₂ emissions, predicted an increase of <1.5°C in spring and autumn by 2100 under the low-emission scenario. Under a high-emission scenario, temperature increases range from ~2°C in the north to >3.5°C in the Mid-Atlantic Bight. Under these conditions, cod appear to be vulnerable to a loss of thermal habitat on Georges Bank and possibly a substantial loss farther south. Cod survival during the early life stages would decline with increasing water temperatures, offsetting any potential increases in growth under warmer temperatures. This results in a predicted loss in yield and increased vulnerability to high fishing mortality rates under climate-change scenarios.

2.2 Lessons from natural climate variability of the past

Understanding the factors that limit present and past distributions of species is critical for predicting how the ranges of species may change as a result of climate change. Terrestrial ecologists have developed models of extant ranges (ecological-niche models, bioclimate-envelope models) by correlating information on species occurrence with annual rainfall, temperature, and other environmental factors. Palaeoclimatic records can be used to reconstruct the contraction and expansion of terrestrial and marine species' ranges during past climatic cycles (Hugall *et al.*, 2002). The study of climatically driven range changes for marine species is greatly complicated by the dynamic, three-dimensional nature of their environment. Conditions of temperature and other variables can vary greatly over a few metres in water depth, and different life-cycle stages may occupy different habitats.

2.2.1 Ice age

Geir Ottersen

Bigg *et al.* (2008) addressed the challenges of palaeoclimate reconstruction when they examined the persistence of Atlantic cod populations during the last ice age (last glacial maximum (LGM), ca. 21 000 BP) using two ecological-niche models (ENMs) and the first broad synthesis of multilocus gene sequence data for this species. One ENM uses a maximum-entropy approach (MAXENT); the other is a new ENM for

Atlantic cod that uses ecophysiological parameters based on observed spawning locations rather than adult distribution. Envelopes defining suitable habitat are set for several factors, including water depth where spawning occurs (0–400 m), seasonality of spawning, and ambient temperatures for spawning (0–9°C; Figure 2.1).

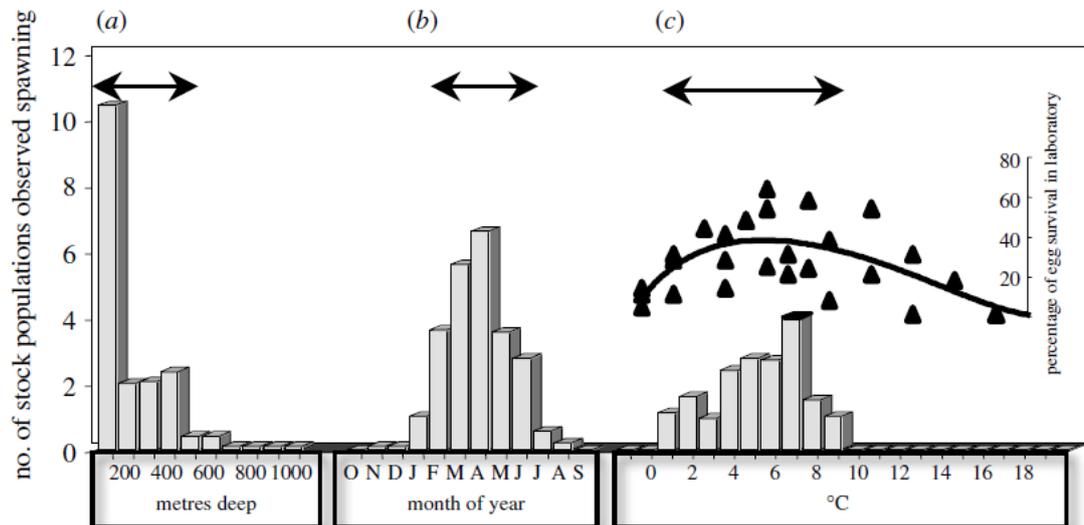


Figure 2.1. Environmental factors defining suitable habitat for cod, based on present-day distributions (Brander, 1994, 2005). (a) Water depth in which spawning occurs (data for 18 stocks). (b) Seasonality of spawning ($n = 23$). (c) Ambient temperature for spawning and eggs ($n = 18$). For each histogram, the arrowed range shows boundaries used for modelling. Multistock laboratory egg survival data (Pepin *et al.*, 1997) is also given in upper part of (c), as a function of temperature. The curve is fitted with a third-order polynomial. (Figure from Bigg *et al.*, 2008.)

Both ENMs were tested for present-day conditions and then used to hindcast ranges, employing climate-model data (Figure 2.2). Although the LGM range of Atlantic cod was much smaller and more fragmented than at present, both ENMs agreed that populations should have been able to persist in suitable habitat on both sides of the Atlantic. The genetic results demonstrated a degree of transatlantic divergence consistent with genealogically continuous populations on both sides of the North Atlantic since long before the LGM, confirming the ENM results. In contrast, both ENMs and the genetic data suggest that the Greenland cod population post-dates the LGM (Figure 2.2; Bigg *et al.*, 2008).

The ability of cod populations to maintain genealogical continuity over extreme natural climate variability, as demonstrated by Bigg *et al.* (2008), suggests considerable inherent resilience. Yet the effects of future climatic conditions need to be considered in relation to demographic structures (Andrews *et al.*, 2006), as well as to the major population changes resulting from human exploitation (Frank *et al.*, 2005).

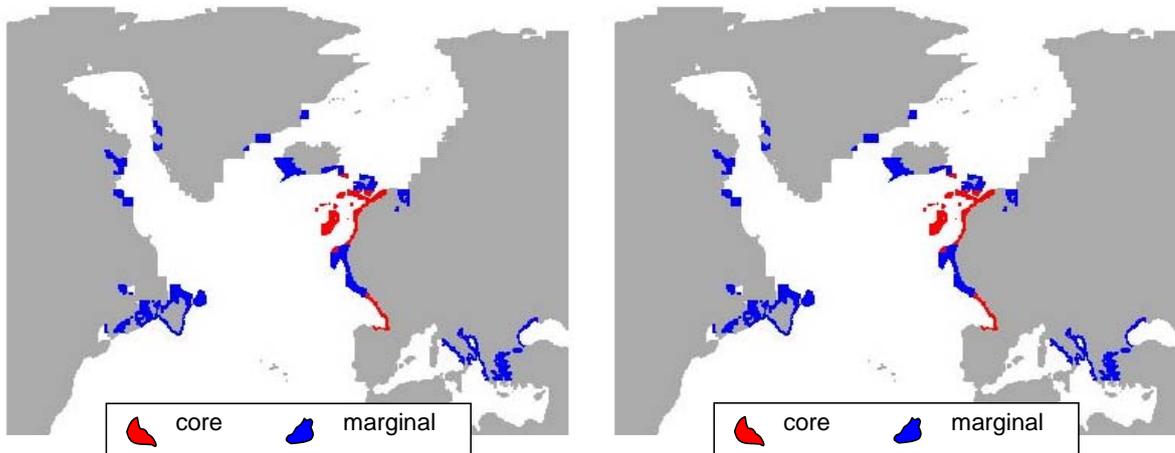


Figure 2.2. Result of model run for 21 000 BP applying ecophysiological parameters, indicating habitat suitable for cod spawning at the last glacial maximum. Red areas indicate the core regions of suitable habitat; blue areas indicate marginal habitat.

2.2.2 Lessons from the Baltic

Brian MacKenzie

The Baltic Sea is a large, brackish, semi-enclosed sea whose species-poor fish community supports important commercial and recreational fisheries. The strong horizontal salinity gradient between the Baltic and North seas has led to genetic differentiation in several marine fish species in the area, including cod (Nielsen *et al.*, 2001, 2003). Reproduction in this species is also adapted physiologically to lower salinity, especially of the eastern Baltic Sea (Nissling *et al.*, 1994; Nissling and Westin, 1997). Trophic interactions in the Baltic foodweb are strongly affected by both climate processes (see references below) and fishing (Casini *et al.*, 2008; Möllmann *et al.*, 2008).

The most important climatic–hydrographic influences on cod dynamics are related to variations in salinity and oxygen concentration. Cod eggs can be fertilized and hatch successfully at salinities greater than ca. 11 psu (Vallin *et al.*, 1999). This physiological effect of salinity restricts successful cod reproduction to depths and areas in the Baltic Sea that have relatively high salinity (i.e. deep basins). However, oxygen conditions in waters that have sufficient salinity can be too low for successful egg development (Plikshs *et al.*, 1993; Wieland *et al.*, 1994). As a consequence, cod reproduction, recruitment, and population dynamics are significantly influenced by salinity and/or oxygen conditions in spawning areas (Plikshs *et al.*, 1993; Jarre-Teichmann *et al.*, 2000; Köster *et al.*, 2005). Salinity and oxygen concentrations themselves depend on climate-induced major inflows of saltwater from the Kattegat and North Sea (Matthäus and Schinke, 1994). The frequency of these inflows between 1897 and 1979 was ca. 1 year⁻¹, but since then has decreased to ca. 1 decade⁻¹ (Schinke and Matthäus, 1998). During this time, fishing pressure was high and stock productivity decreased; as a result, biomass declined sharply to record low levels and has not recovered to the long-term average level, despite reductions in fishing mortality (ICES, 2008b).

Long-term measurements of temperature in the Baltic at the surface (MacKenzie and Schiedek, 2007a, 2007b) and in deeper layers (MacKenzie and Köster, 2004; Alheit *et al.*, 2005) demonstrate an increase in the past 10–15 years. Direct effects of temperature on cod biology and dynamics are relatively poorly documented, but effects via the foodweb are likely. For example, the concentration of copepod nauplii

(potential prey for larvae and 0-group juveniles) in spring is usually higher in warm years (MacKenzie *et al.*, 1996; Möllmann *et al.*, 2003; Alheit *et al.*, 2005), but higher temperatures also stimulate consumption rates of oxygen in cod-spawning areas and reduce solubility of oxygen. These latter mechanisms reduce oxygen concentrations at depths where cod eggs are neutrally buoyant, thereby increasing the possibility of oxygen-related egg mortality. Warm temperatures also promote higher growth (Baumann *et al.*, 2005) and survival of predators (sprat, herring; Köster and Möllmann, 2000) and of cod eggs and larvae (Axenrot and Hansson, 2003; MacKenzie and Köster, 2004; Baumann *et al.*, 2006).

There is archaeological evidence (cod bones recovered at human settlements) that cod was present near Bornholm, as well as at other sites in Denmark (e.g. North Sea–Skagerrak–Kattegat coastal areas) during the Atlantic Warm Period, ca. 7000–3900 BC (Enghoff *et al.*, 2007). At that time, temperatures in northern Europe were ca. 2–3°C higher than during the late 20th century and, therefore, similar to sea temperatures that could be reached in the Baltic Sea by 2100 under future climate change (Döscher and Meier, 2004; BACC, 2007). These observations suggest that cod populations could persist in these waters even if temperatures rise by these amounts. However, during the Atlantic Warm Period, Baltic salinities have been estimated to be ca. 4 psu higher than at present (Sohlenius *et al.*, 2001). The higher salinity would have had a strong positive effect on cod reproduction in the Baltic Sea, as a result of improved fertilization and hatch success of cod eggs at salinities >11 psu. In addition, cod populations in the Baltic and other areas near Denmark during the Atlantic Warm Period would have experienced much lower fishing mortality than during the late 20th century, which may have partly offset potential detrimental effects of higher temperatures on overall cod productivity and population dynamics. These considerations suggest that cod populations could be maintained in these areas if exploitation were reduced.

2.2.3 North Sea cod distributions

Georg Engelhard

Within the North Sea, a northward shift in the mean latitudinal distribution of cod has occurred over the past three decades, as demonstrated by several studies based on scientific trawl surveys (Hedger *et al.*, 2004; Perry *et al.*, 2005; Rindorf and Lewy, 2006). Perry *et al.* (2005) estimated that the centre of population shifted 117 km north between 1977 and 2001. Over the same period, cod distribution has, on average, shifted to deeper waters (Hedger *et al.*, 2004; Dulvy *et al.*, 2008). Two main hypotheses have been put forward: one related to climate warming and one to higher fishing effort in the southern North Sea than the northern North Sea. The popular press has given wide coverage to the former hypothesis, but scientific evidence supporting either of them (they are not mutually exclusive) remains equivocal.

Hedger *et al.* (2004) found that cod were caught in deeper water during the 1990s than in the 1980s, but demonstrated no change in their distribution with respect to temperature. This suggests that cod may respond to changing sea temperatures by seeking a “preferred temperature”, but the hypothesis that “cod swim north” is probably oversimplified (see discussion in Hedger *et al.*, 2004; also Heath, 2007) for three reasons. First, although the southern North Sea is typically warmer than the northern North Sea in summer, the opposite is true in winter. Second, within the North Sea, distinct subpopulations of cod appear to be reproductively isolated, implying little interbreeding and mixing (Hutchinson *et al.*, 2001; Wright *et al.*, 2006).

Third, data-storage tags, recovered from 129 individual cod throughout the North Sea, revealed that these fish actually experienced a warmer fraction of the sea than was potentially available to them (Neat and Righton, 2007). This was especially the case in the southern North Sea, where most of the individuals during summer experienced temperatures well above 14°C, which is considered superoptimal for growth. In the northern North Sea, temperatures recorded by the data-storage tags rarely exceeded 14°C, but were nevertheless generally close to the upper seasonal trend in local bottom temperature; a few cod moved into colder temperatures, confirming that cooler waters were within reach of the fish (Neat and Righton, 2007). Most did not, however, leading the authors to conclude that the changing thermal regime of the North Sea is not yet causing adult cod to move to cooler waters.

As a possible climate-driven mechanism for distribution shifts, Rindorf and Lewy (2006) suggested that, during a recent series of warm winters with southerly winds, increased northward transport of eggs and larvae may have occurred, leading to a northward shift in the distribution of juveniles the following year. Once settled at more northern locations, cod may “home” to the same spawning sites year after year, resulting in genetically distinct spawning aggregations (see Ruzzante *et al.*, 2001, for northern cod). This may make it difficult for the southernmost spawning sites, after they have become depleted, to be visited again once a more northern distribution shift of adolescent cod has occurred (Rindorf and Lewy, 2006).

Trawling effort in the southern and central North Sea has generally been far higher than in the northern North Sea (e.g. Jennings *et al.*, 1999). Hence, it is likely that unbalanced depletions of local cod concentrations (Hutchinson *et al.*, 2001) have taken place, so that greater depletion in the south may well have caused the overall distribution shifts (Heath, 2007). There is also some evidence that the general decline in North Sea cod recruitment took effect earlier in the reproductively segregated sub-stock in the southern North Sea than in the north, contributing to the greater decline in the south (Holmes and Wright, 2005; Heath, 2007).

Most recent studies on cod-distribution shifts have used data from surveys limited to the past three decades, and this has motivated our recent study on cod-distribution shifts over a much longer time-span (nine decades), but based on commercial cpue data (Engelhard *et al.*, see Appendix 1, Section A1.8). Preliminary results demonstrated that marked North Sea cod-distribution shifts have occurred throughout the 20th century. However, shifts in “centres of gravity” of distribution, that were temporarily located at more northerly or southerly latitudes, were not clearly linked to long-term climatic fluctuations, such as the warmer period of the 1920s–1930s or the colder period of the 1960s. The most recent northward latitudinal shift, documented by others (e.g. Perry *et al.*, 2005), was confirmed, but was also demonstrated to have a strong eastward longitudinal component. In fact, the distribution in the 1990s–2000s is particularly noteworthy as it is almost opposite (most cod in the eastern, northeastern, and far northern parts of the North Sea) to the situation during most of the 20th century (most cod in the northwestern and western–central parts of the North Sea; see Appendix 1, Section A1.8, Figure A15). Although this suggested that cod-distribution shifts were not straightforwardly linked to climate change, no clear link with fishing pressure was found either; for example, the near-absence of fishing during World War II hardly affected cod distributions.

More thorough statistical analyses may shed light on the relative impacts of climate change and fishing pressure on cod distributions. The effect of the severe decline in

abundance of cod since 1990 may, in itself, have affected their distribution, and this also needs to be investigated. Ideal free-distribution theory predicts that a declining population will contract into areas of highest habitat suitability. Blanchard *et al.* (2005) demonstrated that such “basins” of good habitat (based on bottom temperature) are fairly persistent and would be in the northeastern North Sea for age-1 cod and in the northwestern North Sea for age-2 cod. Finally, the effects of the marked age truncation in the current stock need to be investigated (B. Rothschild, pers. comm.), given the differences between the average distribution patterns of younger, smaller cod and older, larger cod. Indeed, the diminished North Sea stock may well have become increasingly confined to these sites.

The North Sea case suggests that cod populations are likely to demonstrate long-term distribution shifts. However, these may not necessarily be linked to climate (temperature) fluctuations in a direct and readily predictable fashion; rather, they may result from interplay between climate, (local) fishing pressures, (truncations in) age distributions, and/or density-dependent effects on population area sizes.

2.2.4 Lessons from Greenland

Kai Wieland

The occurrence of Atlantic cod at Greenland has been episodic in historical times. For West Greenland, two short periods of cod fishing are documented for the 17th and 19th centuries (Buch *et al.*, 1994; Dickson *et al.*, 1994), but in 1851, this fishery came to an abrupt end. Indications for a return of cod to West Greenland were first seen again in 1909 at southeast and southwest Greenland. In response to the large-scale North Atlantic-wide warming in the 1920s and 1930s (Rogers, 1985; Johannessen *et al.*, 2004), cod spread gradually northwards after 1917 and extended as far north as the Upernavik area at 73°N by the late 1930s (Jensen, 1939; Buch *et al.*, 1994). Catches increased to ca. 460 000 t in the early 1960s. The offshore spawning stock collapsed completely at the beginning of the 1990s, mainly as a result of overfishing. Fishing mortality far exceeded the sustainable level, even under favourable environmental conditions for growth and recruitment (Hovgård and Wieland, 2008). Warm conditions have prevailed again since the mid-1990s (Figure 2.3), but no substantial recovery of the stock has yet been observed (ICES, 2008c). The Greenland case demonstrates that cod populations can increase rapidly when environmental conditions are favourable, but the time taken for such an increase depends on how low the population level was at the start of the recovery and possibly also on the presence of subpopulations that are adapted to take advantage of the conditions.

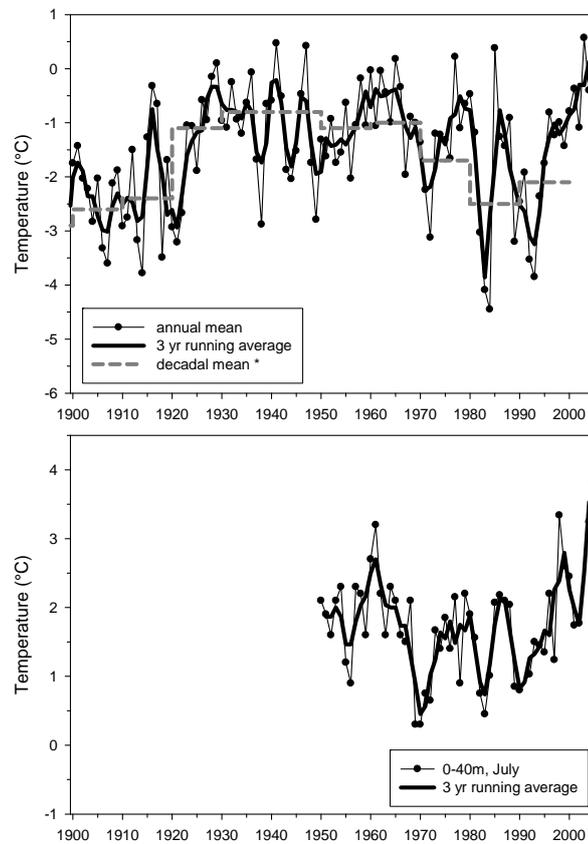


Figure 2.3. (Top panel) air temperature measured in Nuuk; (bottom panel) ocean surface layer temperature recorded at Fylla Bank (from Ribergaard, 2006). The decadal annual air temperatures in the top panel are derived from data collected at 12 locations along West Greenland (Vinther *et al.*, 2006).

3 Future climate projections

Corinna Schrum and Holger Pohlmann

The IPCC provides regular assessments of global climate change and its impacts, comprising detailed information on the current state of the art in palaeoclimatic reconstructions, data analyses from historical instrumental records, and understanding achieved by global and regional climate modelling. These assessments and model data typically provide the basis for regional and local climate-change impact studies. In the following, we discuss methods and knowledge based on the fourth IPCC assessment report on climate change (IPCC, 2007a, 2007b) and on the interpretation, reliability, and utility of existing climate scenarios for the assessment of climate-induced impacts on cod stocks.

3.1 Projections vs. predictions

In its fourth assessment report (IPCC, 2007a), the IPCC provided global climate-change scenarios (Meehl *et al.*, 2007) and some first regional downscaling results (Hegerl *et al.*, 2007). These projections are sometimes misinterpreted as future predictions or forecasts. Herein, the scenarios are consistently referred to as projections rather than predictions. A discussion on this issue was recently published in the Climate Feedback blog, hosted by *Nature* Reports: Climate Change (<http://blogs.nature.com/climatefeedback>). Further clarification and a personal opinion on IPCC scenarios for assessment of regional climate change were provided in http://blogs.nature.com/climatefeedback/2007/06/predictions_of_climate.html by Kevin Trenberth, a contributor to the fourth IPCC report (IPCC, 2007a). He pointed out that the IPCC did not provide predictions, but instead discussed “what if” scenarios, based on consistent “story lines” and a number of assumptions, and further influenced by the specific set-up, properties, and limitations of the models. He discussed specifically one main issue, viz. the lack of initialization of climate models to the present state and their consequently limited ability to deal with regional climate change. He postulated that regional climate change is impossible to deal with unless the climate models are properly initialized.

3.2 How skilful are climate models?

The quality and validity of impact assessments depend greatly on the quality of the climate-change scenarios and the ability of the climate models to correctly model the sensitivity of the climate system to changes in CO₂ forcing. The projections themselves cannot be validated; only the ability of the model to simulate the present-day climate state can be evaluated. This validation exercise can then be used to identify properties and limitations of climate models in order to accurately simulate the climate dynamics. Identification of bias and regional and temporal deviations of modelled time–space pattern from observed patterns could provide some indicators of the capability of the climate models to accurately simulate the climate system. In Chapter 8 of the fourth IPCC assessment report, Randall *et al.* (2007) describe such a validation exercise for a number of properties of the atmosphere and of the ocean.

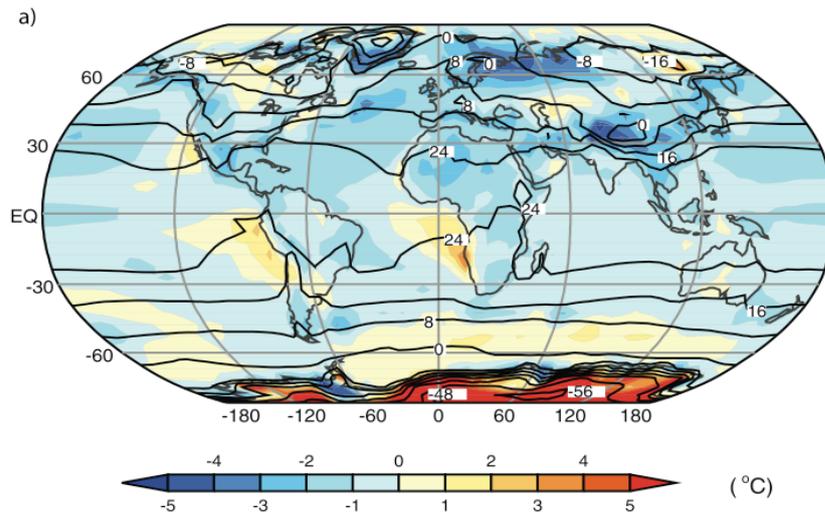


Figure 3.1. Climatic surface temperature (sea surface temperature and over-land surface air temperature; contour lines) and bias of the IPCC model ensemble mean (colours; Randall *et al.*, 2007).

Climate models are generally well tuned to reproduce the 20th-century global mean temperature trend; however, they do not reproduce the regional structure or other properties of the climate system, such as precipitation, radiation, and wind. The ensemble mean of the IPCC models (Figure 3.1) demonstrates substantial errors compared with the present-day climate, with pronounced regional patterns covering a range of -5 to $+5^{\circ}\text{C}$. Validations of single models demonstrate larger error margins (Randall *et al.*, 2007; IPCC, 2007a: supplementary material). In Figure 3.2, the zonally averaged sea surface temperature (SST) is presented. The errors of the model ensembles demonstrate the largest scatter in mid- to higher latitudes, with the spread ranging from below -4 to $+2^{\circ}\text{C}$; hence, the error margin for SST in mid- to higher latitudes is larger than 6°C .

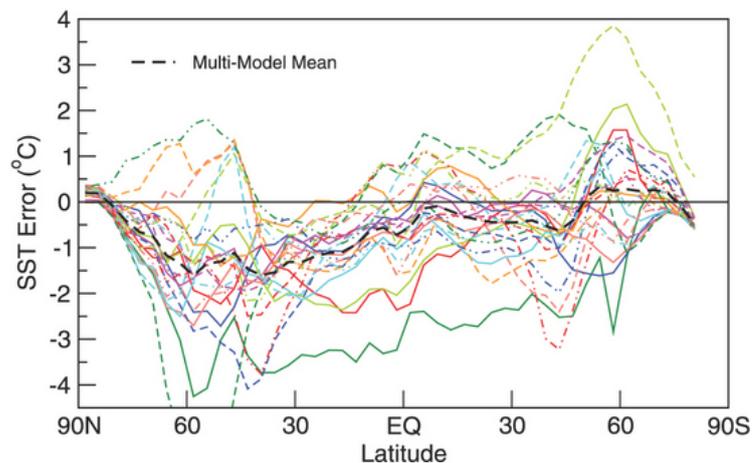


Figure 3.2. Zonally averaged SST error, i.e. simulated–observed. Results from the individual models (coloured lines) and the ensemble mean (dashed black line). (Figure from Randall *et al.*, 2007; for more details, see IPCC, 2007a.)

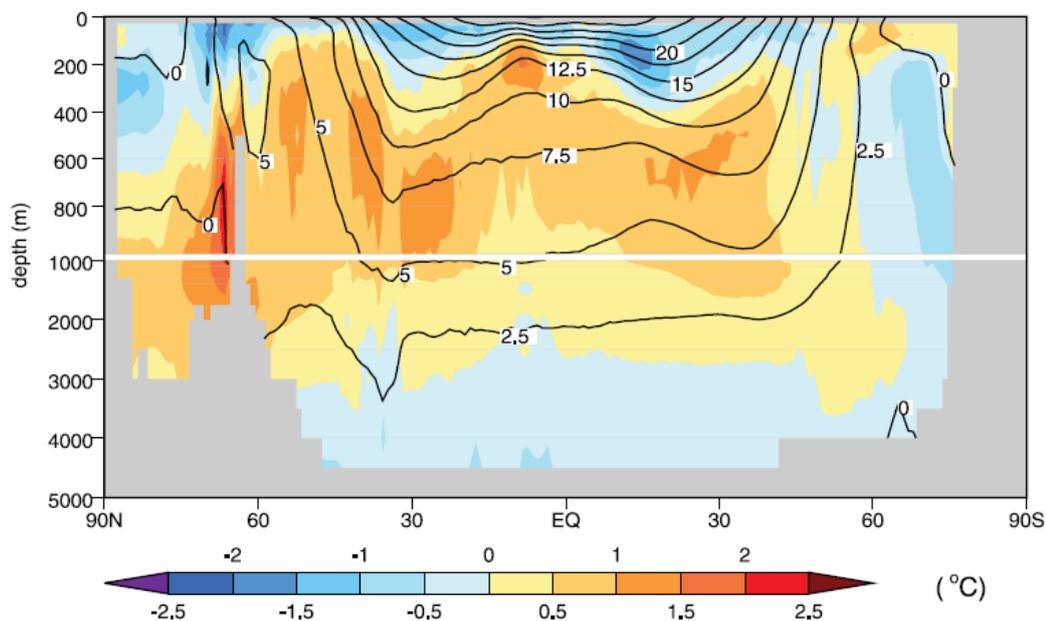


Figure 3.3. The simulated mean error, simulated–observed, in °C of the ocean’s zonally averaged potential temperature. The contour lines are the climatic mean potential temperature (from Levitus *et al.*, 2005). (Figure from Randall *et al.*, 2007.)

Significant deviations are found not only for ocean surface characteristics, but also for the deeper ocean. The bias of the ensemble mean ocean potential temperature varies from -1.5 to $+2.5$ °C (Figure 3.3), with systematic underestimation in temperature in the upper layers (first 100–400 m) and systematic overestimation of temperature in the lower layers. Similarly to the surface air temperature (ST) and SST bias, the individual models demonstrate substantially higher errors.

Zonally averaged windstress over the oceans (Figure 3.4) demonstrates good agreement in lower latitudes and substantial deviations in mid- to higher latitudes; twofold deviations and even a change in direction are identified in latitudes relevant to cod.

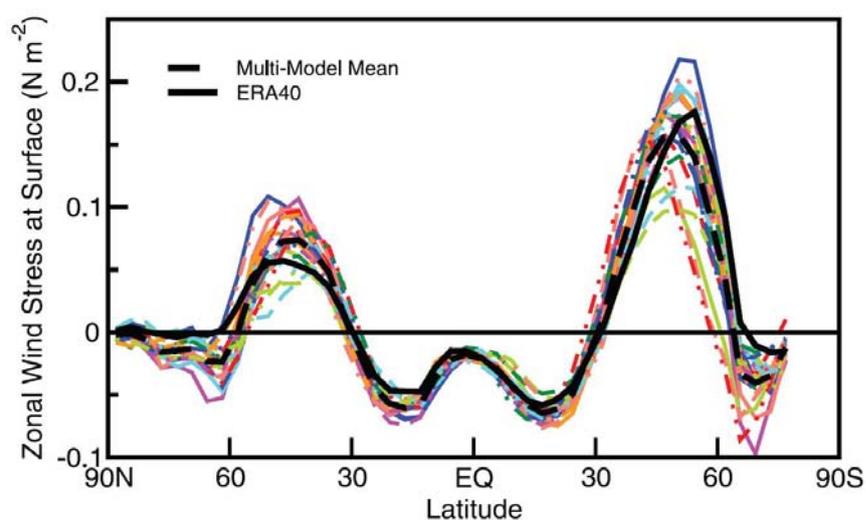


Figure 3.4. Zonally averaged windstress over the oceans. Results from the individual models (coloured lines), the ensemble mean (dashed black line), and observation-based data (ERA40, Uppala *et al.*, 2005) are compared here. (Figure from Randall *et al.*, 2007; for more details, see IPCC, 2007a.)

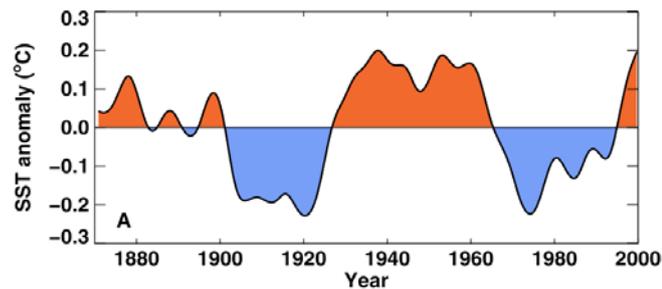


Figure 3.5. SST anomaly-based AMO index in the North Atlantic, de-trended. (Figure from Knight *et al.*, 2005.)

Validation of trends and variability of parameters other than the global mean temperature were not presented in the fourth IPCC report; hence, an assessment of the models' sensitivity to model change and variability of the climate system is not possible based on the material presented in the report, but the report does refer to the scientific literature. We will not discuss all of the conclusions in the scientific literature, but will concentrate on the two most relevant variability signals for those North Atlantic regions inhabited by Atlantic cod: (i) the AMO, with a period of ca. 60 years, which is responsible for ca. 50% of the observed SST increase in the past decades in the North Atlantic region (Knight *et al.*, 2005; Figure 3.5); and (ii) the NAO, which is the dominant signal most relevant to SST variability of the shelf seas. These two climate modes are represented in the IPCC GCMs; however, most models ascribe too much variability to the NAO (Miller *et al.*, 2006). Furthermore, the processes that give rise to the AMO are very different among the GCMs (Randall *et al.*, 2007). Because the IPCC models are not initialized with observed initial conditions, the phasing and variability of natural climate modes like the AMO and NAO do not match the observed climate. This results in large differences between the models in an aspect that is crucial to the skill of regional forecasting.

3.3 Global projections and regional downscaling

Projected global changes depend strongly on the chosen scenario and model. In general, all the models reveal a significant future warming, with an increase ranging from 0.5°C to 1.5°C for the average global surface air temperature in ca. 100 years. The uncertainty range in model spread is of the same order of magnitude as the projected change, and uncertainties in simulating the present-day climate pattern are significantly higher. The ensemble average projections reveal the highest temperature changes in the upper troposphere and the northern latitudes. Here, air temperature changes reach 4.5°C in the highest latitudes. These high, zonally averaged warming trends are, of course, not realized in the ocean, owing to the higher density and heat capacity of water. Here, the projected warming of the surface waters is <1°C in high latitudes from global models (A1B scenario, see Figure 3.6); however, stronger warming might be expected locally.

Although the global projections provide a certain frame of ranges for anticipated climate changes, they are not sufficient for climate-change impact studies regarding cod. Detailed assessment of the impact of climate change on cod can only be based on regional projections; global projections are too coarsely resolved to identify regional structures. Some regional climate-change projections are presented in chapter 11 of the fourth IPCC report (Christensen *et al.*, 2007). Two major drawbacks of the regional downscaling scenarios can be identified: (i) most of the scenarios are carried out with atmosphere-only models and, hence, do not provide regional ocean estimates or estimates of lower trophic-level productivity; (ii) owing to the complexity and

computational demands of regional models, there is a significant time-lag in providing the regional scenarios. The regional scenarios presented in the fourth IPCC report are based on global model runs and scenarios from previous IPCC reports or previous model runs. Hence, they are not necessarily consistent with the results in the fourth IPCC report and the present state-of-the-art in climate modelling. Furthermore, only very few of these scenarios were performed with coupled ocean–atmosphere models or ocean models on the regional scale. The only scenarios available for the regional oceans in the North Atlantic region are currently those produced by Meier *et al.* (2004, 2006) for the Baltic Sea, by Ellingsen *et al.* (2008) for the Barents Sea, and a scenario run produced by Bjørn Ådlandsvik for the North Sea and the adjacent Northeast Atlantic (Ådlandsvik and Bentsen, 2007; Ådlandsvik, 2008). The latter is the only scenario based on the fourth IPCC assessment report (IPCC, 2007).

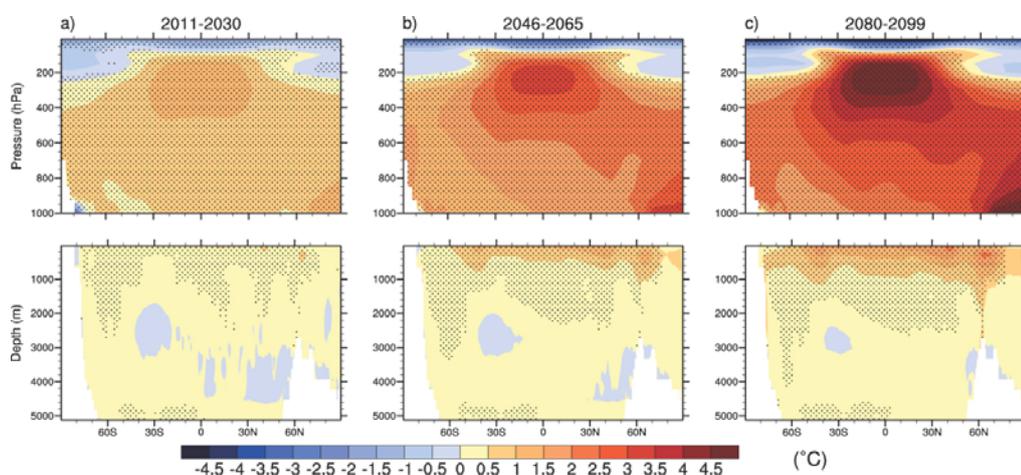


Figure 3.6. (Upper panels) Projected change in zonal mean air temperature; (lower panels) ocean temperature (for the IPCC scenario A1B, results from multimodel ensemble).

Only Markus Meier utilized different regional and global models for his scenarios. A consistently positive SST trend was modelled in all of the different scenarios, with an ensemble-averaged SST increase of 2.9°C. This is a significantly stronger temperature increase than the projected changes in the open ocean, which are in an order of magnitude of only 1°C (Meehl *et al.*, 2007). There are three possible explanations for this difference: (i) the scenarios are based on the less-mature global models from previous IPCC reports; (ii) there are additional biases in the regional atmospheric models; (iii) higher sensitivity of the regional sea.

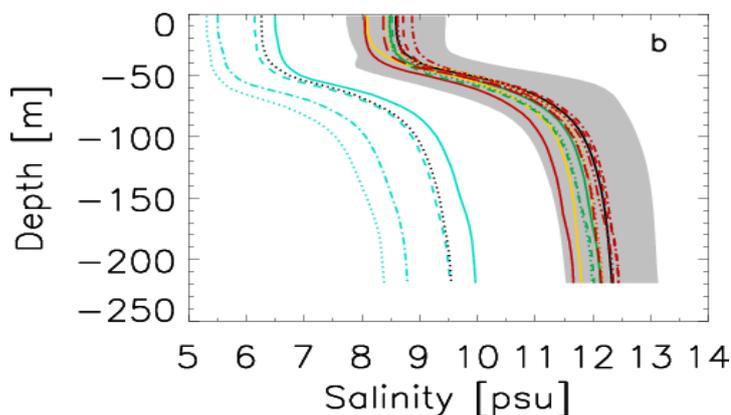


Figure 3.7. Projected changes in salinity at Gotland Deep for 2071–2100; the colours indicate different regional and global models. (For details, see Meier *et al.*, 2006.)

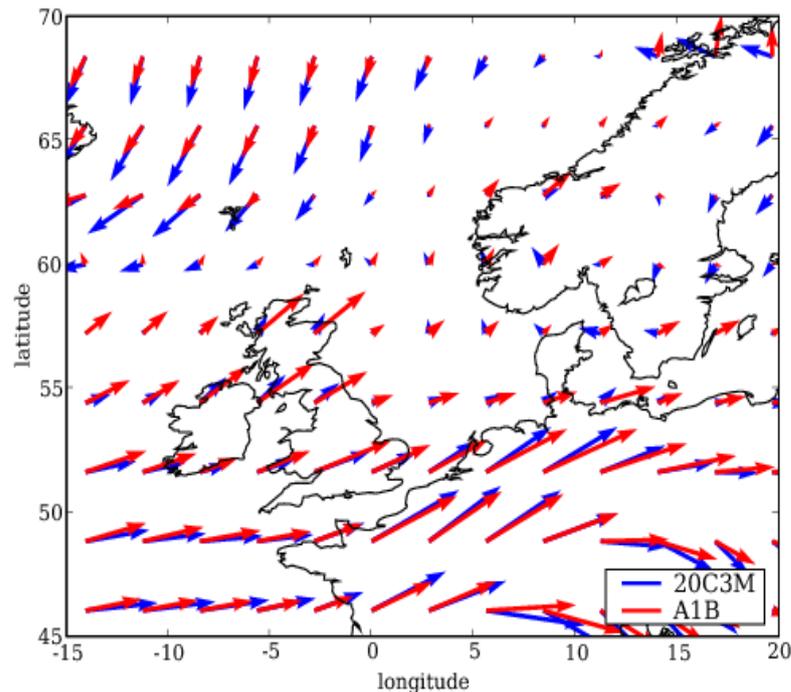


Figure 3.8. Windstress from the Bergen Climate Model (BCM) averaged over the period 1972–1997 (20C3M) and future scenario A1B. (Figure from Ådlandsvik, 2008.)

The projected changes in salinity within the Baltic Sea demonstrate significant differences, depending on which global model is used to force the regional scenarios (Figure 3.7). For example, a significant decrease in salinity (outside the present-day climatic variability) is found only for the runs forced by the Hamburg ecosystem model (ECHAM4). This clearly points to deviations in regional dynamics in the global models as one of the most significant factors for regional projections. Interesting as well are the results of Ådlandsvik (2008). He identified a major drawback in the characteristics of the global climate model that he selected, as the westerly winds were displaced too far south in the present-day 20th-century simulation and were in a similar location in future projection (Figure 3.8). Hence, the climate of the present-day reference simulation is quite unlike the observed climate over the North Sea. This GCM is, therefore, unlikely to provide a reliable projection of future climate change in the North Sea region.

One of the few regional scenarios using coupled biophysical models for the Northeast Atlantic is by Ellingsen *et al.* (2008) for the Barents Sea. Their climate simulations used atmospheric input from a hydrostatic regional climate model, REMO (Jacob, 2001) that was run for the ECHAM4/OPYC3 IPCC-SRES B2 scenario by the Max Planck Institute for Meteorology, Hamburg (Göttel *et al.*, 2008). These were applied to a coupled biophysical model (the hydrodynamic model SINMOD (The SINtef ocean MODEL) with an ecological module) to project future plankton scenarios. For the Baltic Sea, a few emission scenarios using a single ecosystem model (H. E. M. Meier, pers. comm.) are available based on the third IPCC assessment report (IPCC, 2001). Results of these model runs, and of the associated skill and validation exercise that document the performance of the regional ecosystem model, are currently unpublished. From complementary investigations comparing different ecosystem modules and their potential to simulate variability of primary production, the addition of the regional ecosystem models could be expected to increase the number of uncertainties (Skogen and Moll, 2005).

3.4 Regional projections at decadal and shorter time-scales

The initialization problem in climate models, mentioned previously as an important limitation of global climate models, has been addressed in two recent climate-modelling papers (i.e. Smith *et al.*, 2007, and Keenlyside *et al.*, 2008), both of which describe a significant step forward in climate science with respect to predictability.

The model runs presented in these two studies were initialized by the observed and present state, using different modelling techniques. The performed runs and predictions demonstrated a significantly better performance in the North Atlantic region (Keenlyside *et al.*, 2008) and a better performance in modelling the internal oscillations of the North Atlantic climate systems (Smith *et al.*, 2007). In both cases, the results demonstrated that the internal oscillations can locally offset the global warming trend for a couple of years (Figure 3.9).

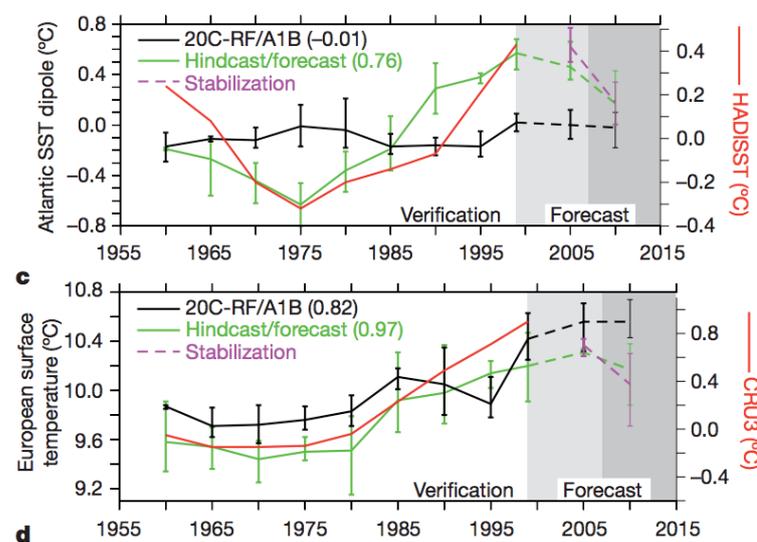


Figure 3.9. Modelled Atlantic SST dipole and European surface temperature with the decadal prediction systems of Keenlyside *et al.* (2008) and the IPCC 20th-century reference and an A1B projection run.

In addition, both model exercises demonstrated that the warming trend is resumed after a period ranging from several years to decades; however, interpretation of the conclusions is complicated by the fact that the decadal prediction systems lose performance after a couple of years. The model runs from Smith *et al.* (2007) were presented during the WKCFC (Figure 3.10 and see Appendix 1, Section A1.1), and time-series for North Sea and Baltic Sea SST were shown. From these results, the SST is predicted to increase in ca. 30 years, but demonstrates a modulation, and even a decrease, prior to this. Temperature and salinity resulting from the decadal prediction (Smith *et al.*, 2007) were provided to the WKCFC participants for impact studies. However, detailed three-dimensional model runs were not possible using these results because the full model output necessary to run three-dimensional regional models had not been stored. To enable future predictions, cooperation between regional and global modellers has been established.

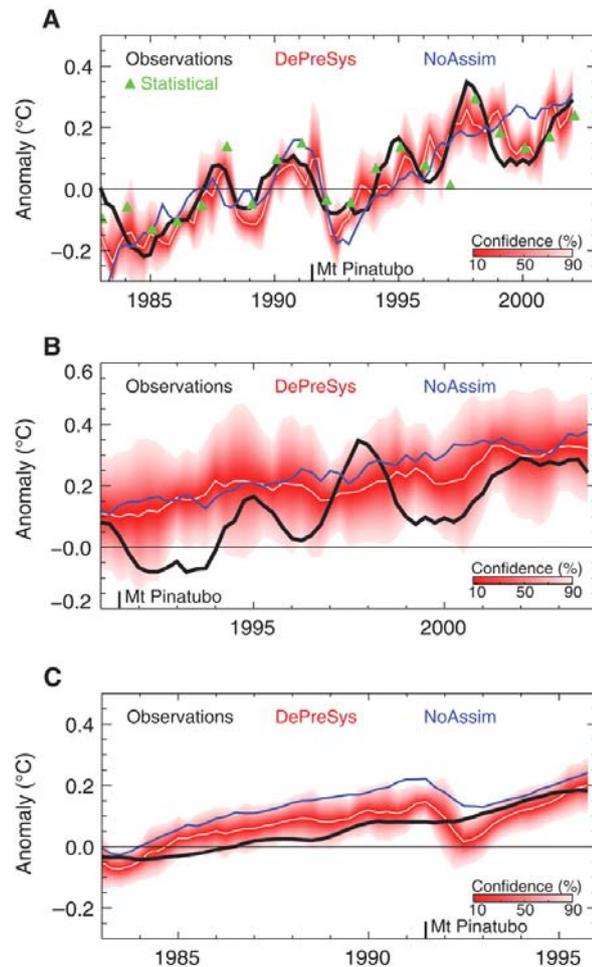


Figure 3.10. Results from the Decadal Climate Prediction System (DePreSys) compared with no-assimilation runs: (upper panel) the 1-year forecast; (middle panel) year 9 of the forecast; (lower panel) 9-year average of the forecast.

3.5 Present limitations

Uncertainties in the climate models arise from a combination of a number of sources and processes, which have been reported and discussed by IPCC and in the scientific literature. In addition to numerical errors and forcing-data uncertainties, the most important of these are the initialization problem for climate models, empirical parameterizations of key processes, lack of closure and simplification of climate models (e.g. carbon feedback mechanisms cannot be included until earth system models become available), parameterization of ocean mixing, and excluded tidal forcing.

Although present-day climate models are quite complex and (computationally) resource-demanding, they are still simple in many respects and currently far from being fully based on first principles. These limitations were mentioned and discussed briefly in the fourth IPCC report (IPCC, 2007). However, a detailed assessment of the empirical process and subsystem approximations with respect to their impact on climate-change projections was not performed. Hence, one of the burning questions with respect to assessment of limitations and potentials of climate models remains unanswered. However, from the previous discussions, it remains clear that uncertainty estimations based on validation provide ranges of uncertainties that are in the order of magnitude of the projected changes, or even larger. This strongly limits the potential for quantitative assessment of future impacts.

The establishment of fully coupled scenarios comprising regional ocean climate, lower trophic-level dynamics, and cod-recruitment dynamics for the next 20–50 years, as intended by the WKCFCC, was not possible owing to lack of reliable regional climate scenarios.

Alternatively, so-called “what if” scenarios can be performed, involving a range of different model approaches, in order to address the direct and indirect thermodynamic impacts, as well as wind-induced impacts on prey field variability. For these scenarios and model exercises, impacts of changes in wind, radiation, and temperature can be separated, and linear combinations and non-linear interactions can be identified. This kind of approach was presented at the WKCFCC by Daewel *et al.* (see Appendix 1, Section A1.3), using estimates of cod survival and sensitivity to changing climate variables in order to disentangle the direct effects from observed indicator relationships. These “what if” scenarios provide some insight into the sensitivity of cod recruitment to climate change and improve our understanding and identification of relevant climate controls.

Regional-scale modelling is time-consuming and cannot be performed using the ensemble approach currently chosen for global climate modelling. It is technically impossible to perform ensemble runs on the regional scale using all the available IPCC GCM output with all the different model concepts involved. Identification of regional bias and errors in global models is time-consuming, and correction techniques need to be developed regionally for different time- and spatial-scales. Hence, research is required to develop regional downscaling techniques for the regional hierarchy of models involved. The employment of coupled regional ocean–atmosphere climate models might be desirable. However, only a few of these research tools are currently available and validated with respect to climate variability, which is an essential precondition for quantitative climate-change assessment. Atmospheric regionalization alone does not seem to be a very important step forward in the simulation of regional marine climate impacts and delays the process of regionalization for the marine environment because of the technical work and manpower involved to proceed with climate-impact studies.

Major steps forward can be expected from coordinated regional climate-impact studies with coupled biophysical ecosystem models, such as those initiated by the European Union’s Seventh Framework Programme (EU-FP7) project, MEECE, and by other parallel national and international impact projects. For the time being, the uncertainties in regional environmental changes induced by global climate change strongly limit regional assessment of climate-change impact on regional ecosystems and key fish species.

4 Modelling biological impacts of climate change

4.1 Mechanistic coupled biophysical models

Ute Daewel and Corinna Schrum

Before briefly reviewing mechanistic coupled biophysical models, a short clarification of the terms “mechanistic” and “deterministic” is provided¹.

A **mechanistic** model is based on fundamental knowledge of (interacting) processes. Parameters indexing the processes are usually derived from experiments (observations, laboratory experiments, and model experiments) or the literature. A mechanistic model requires little input data, just initial and boundary conditions, but it does require a fundamental understanding of the physics, chemistry, and biology of the governing processes. Observed data for the output variables are used only to validate the model. Based on this validation, re-examination of process parameterizations may be required. As the mechanistic model does not require many data for development, it is not subject to data idiosyncrasies. The development of mechanistic models is usually very time-consuming.

A **deterministic** model is a model that provides a single solution for the one or more state variables. It is not able to explicitly simulate data uncertainty or variability. Changes in model solutions can, therefore, be directly attributed to changes in boundary and initial conditions (model input).

The complex, three-dimensional, coupled biophysical models used in ecosystem research, including three-dimensional individual-based models (IBMs), are commonly both mechanistic and deterministic. To address the question of how climatic, hydrodynamic, and biological processes interrelate to each other in a complex three-dimensional system, the use of a mechanistic–deterministic model approach appears to be expedient for the following reasons. First, using this approach, in contrast to observations, it is possible to cover a sufficient temporal and spatial resolution for all the modelled variables and combine them in a dynamically consistent approach. Second, having detailed knowledge of the process parameterization allows the different impacts to be disentangled in a three-dimensional context.

The parameterization and complexity of biophysical models vary with respect to the trophic levels and processes that are included, as well as to the scientific question being asked. The following is a very brief overview of the most important approaches.

4.1.1 NPZD models

Most of the currently running three-dimensional ecosystem modules used to study marine ecosystems and related environments are still quite simple. Typically, they include up to three nutrient cycles and one or two functional groups of phyto- and zooplankton (e.g. NORWECOM; Skogen *et al.*, 1995). Additionally, oxygen and a detritus class, or classes, are considered. The intermediate complexity models (e.g. ECOSMO, Schrum *et al.*, 2006a; SINMOD, Wassmann *et al.*, 2006; Slagstad and McClimans, 2005; and ERGOM, Neumann, 2000) are closed by prescribing

¹For more details, see <http://lorien.ncl.ac.uk/mining/dynamics/modeling.pdf> or http://www.epa.gov/ord/crem/library/CREM%20Modelling%Glossary%2912_03.pdf.

zooplankton mortality; simpler models are closed by prescribing phytoplankton mortality resulting from predation by zooplankton. The only more complex model currently used for the Northeast Atlantic in the coupling mode with three-dimensional hydrodynamic models is the ERSEM (European Regional Seas Ecosystem Model, Baretta *et al.*, 1995). The highest trophic level dynamically considered in this model is planktivorous fish. The model has been applied to the North Sea and British coastal waters (POLCOMS-ERSEM; Allen *et al.*, 2001, 2007a, 2007b; Blackford *et al.*, 2004; Holt *et al.*, 2005). The NEMURO-fish model, developed and applied in the North Pacific (Megrey *et al.*, 2007), and ATLANTIS, developed in Australia (Fulton *et al.*, 2004), are examples of models for areas outside the Northeast Atlantic that include upper trophic levels.

4.1.2 Spatially explicit IBMs

As a step towards understanding interannual variations of fish recruitment, IBMs for larval fish are utilized in order to examine processes affecting vital rates. Depending on the question being asked, IBMs vary in structure and complexity. Two main approaches have been developed, with different levels of complexity. The first approach includes information about one or two environmental factors (e.g. temperature, prey availability) and is based on empirically derived equations for these processes (e.g. Heath and Gallego, 1997). Although this approach provides estimates of spatial and temporal variability of growth that are particularly useful for some purposes (i.e. in drift modelling studies), growth variability resulting from changes in the prey field is usually ignored. Therefore, a more complex, mechanistic approach has been applied in a number of different studies (e.g. Letcher *et al.*, 1996; Lough *et al.*, 2005; Vikebø *et al.*, 2007b; Kristiansen *et al.*, 2009), including subroutines with functions describing factors affecting the underlying processes of energy gain (foraging) and energy loss (via metabolism).

By using a Lagrangian approach, IBMs have been coupled to three-dimensional hydrodynamic models, allowing the exploration of spatial-temporal variability of the interaction between marine organisms and their environment. Advances made in this area during the 1990s were reviewed by Werner *et al.* (2001). Some modelling studies focused on the role of currents and circulation patterns, yielding insight regarding fish spawning areas, nursery grounds, pathways of larval drift, and the general influence of tides, residual currents, and turbulence on the migration and spatial distribution of fish early life stages (e.g. Werner *et al.*, 1993). These studies clearly linked the physical properties of the environment to changes in the vital rates of individuals.

To address more complex questions, spatially explicit IBMs have been employed that incorporate three-dimensional fields of hydrographic properties (e.g. temperature, salinity, current velocity, and diffusion) experienced by individuals during early life (e.g. Hinckley *et al.*, 1996; Bartsch and Coombs, 2004). Utilizing a three-dimensional IBM is especially important within ocean shelf systems like the North Sea, where a complex topography and the presence of different frontal regimes lead to horizontal as well as vertical spatial variability of physical properties.

Recent efforts were also made in linking spatially explicit IBMs to three-dimensional zooplankton fields by using observed prey fields (Kühn *et al.*, 2008), and by developing links to nutrient-phytoplankton-zooplankton-detritus (NPZD) model results (Daewel *et al.*, 2008a). The advantage in using such a coupled model system, including dynamics throughout different trophic levels, is clearly the opportunity to

incorporate spatial and temporal dynamics into the investigation. However, it also increases the number of uncertainties that must be considered.

4.1.3 Limitations of coupled biophysical models

Spatially explicit IBM approaches still lack closure of the life cycle and, hence, are of limited applicability in resolving population dynamics. Scenarios based on these models cover only bottom-up control of the early life stages.

The simplicity of model approximations, the lack of closure, and the diversity of concepts are quite problematic when it comes to assessment of climatic variability impacts, marine resource management, and predictions of potential future scenarios. Results from impact studies carried out by Denman and Pena (2002) demonstrated that different ecosystem model concepts affect model predictions significantly. Moreover, the employed hydrodynamic model and the coupling mode were identified, in order to account for significant differences in ecosystem assessment, by Skogen and Moll (2005). These authors had to perform massive tuning before a simple ecosystem model could be used within another hydrodynamic framework. After new tuning, the best-fit simulations using two different ecosystem cores still demonstrated significant deviations in local annual mean primary production, with differences of twofold or more (Figure 4.1). Further results from their study demonstrated a clear impact on modelled interannual variability using the same hydrodynamic core (Figure 4.2). The two ecosystem modules that they used estimated different and even reversed trends in total productivity, a fact that would significantly affect scenario predictions based on these concepts. The relevant conclusion to draw from this study is that research is needed in order to identify valid model systems (i.e. to identify the necessary key processes to be included for estimation of total productivity) for respective regions and to ensure the scientific quality and value of scenario predictions.

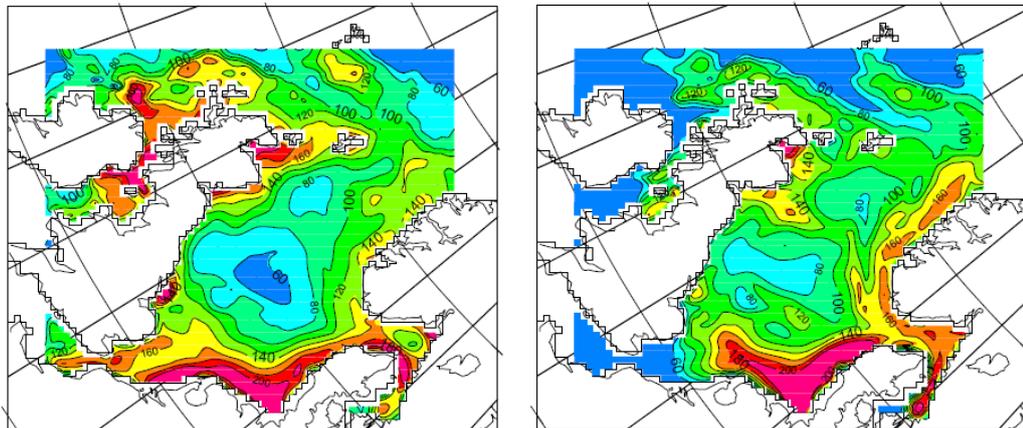


Figure 4.1. Mean annual production ($\text{g C m}^{-2} \text{ year}^{-1}$) from the NORWECOM model (left) and the ECOHAM1 model (right). (Figure from Skogen and Moll, 2005.)

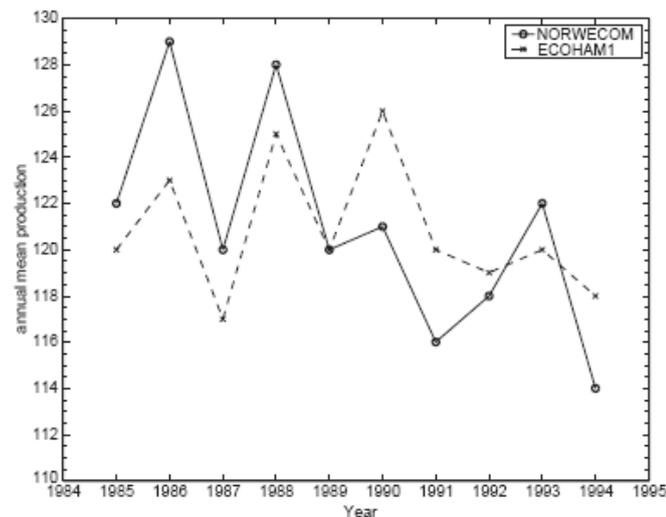


Figure 4.2. Mean annual production ($\text{g C m}^{-2} \text{ year}^{-1}$) from the NORWECOM model and the ECOHAM1 model. (Figure from Skogen and Moll, 2005.)

4.1.4 What can these models do?

The use of such complex model systems means large uncertainties in the outputs owing to inadequate parameterizations, the number of simplifications that have to be made, and the number of important processes that are probably not included. Nonetheless, these models provide useful tools for the understanding and identification of patterns in ecosystem dynamics. For lower trophic level dynamics, Schrum *et al.* (2006b) applied empirical orthogonal function (EOF) analyses to three-dimensional model results of phyto- and zooplankton production and biomass to identify both their relationship with hydrodynamic features, especially tidal-mixing fronts, and the corresponding time-scales and seasonal dynamics. Another example focused on bottom-up processes affecting larval cod on Georges Bank. A coupled biophysical model was applied by Lough *et al.* (2005) in combination with highly resolved *in situ* observations of zooplankton abundance. The focus of this study was on the vertical structure and temporal evolution of feeding and growth.

In addition to helping to identify patterns of ecosystem dynamics, mechanistic coupled biophysical models can provide information on processes and process interactions. In contrast to statistical models that find correlations or linear relationships between variables, mechanisms that directly or indirectly influence the abundance or biomass of marine organisms (“mediators”; see Dippner, 2006) can be determined from the mechanistic-model approach (Figure 4.3). It is clear that the knowledge of these mediators not only provides a deeper understanding of the processes observed in the field, but is also important for future predictions of ecosystem responses to climate variability.

The utility of biophysical models, in terms of identifying underlying mechanisms, can be illustrated by a number of examples. Variability of the flowfield, usually linked to changes in the large-scale atmospheric pressure system (e.g. the NAO), has a strong impact on larval fish survival, because it defines the environmental conditions experienced by a fish during its early life stages. An investigation concerning the impact of drift of mackerel (*Scomber scombrus*) was conducted by Bartsch and Coombs (2004), who studied environmental impacts on its growth and survival in the early life stages by combining an IBM with a hydrodynamic model. Another factor affecting growth and mortality of larval fish is turbulence, because of its strong impact on fish ingestion rates (MacKenzie *et al.*, 1994). The sensitivity of walleye

pollock (*Theragra chalcogramma*) growth and mortality to turbulence, studied by Megrey and Hinkley (2001), was also studied using an IBM approach. A third example pointed out the importance of individual larval behaviour for fish growth, mortality, and dispersion (Fiksen *et al.*, 2007).

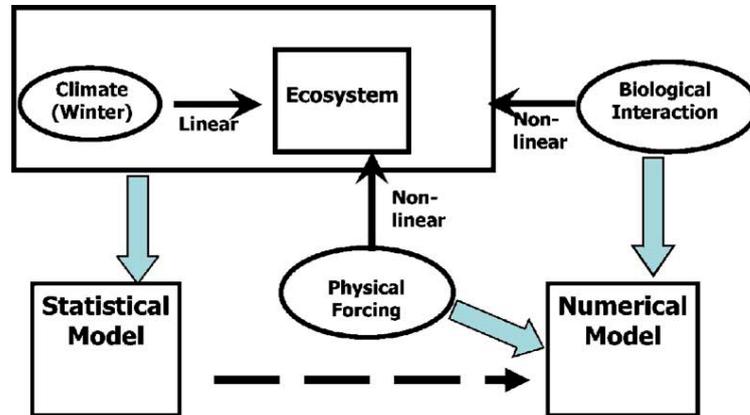


Figure 4.3. Schematic sketch (from Dippner, 2006) of the model application (large arrows), which depends on the property of the mediator (small arrows). The sketch indicates that, for linear mediators, the statistical model is appropriate. If the mediator is linear, the use of numerical models is necessary.

This process understanding can be further incorporated into biophysical models in order to test future climate scenarios. In contrast to observation-based studies, the models are able to reflect interactions between atmospheric forcing, physical environment, and ecosystem dynamics with a continuous spatial and temporal resolution (e.g. Daewel *et al.*, 2008a). Thus, the model provides a useful tool for performing scenario tests (e.g. by increasing the air temperature or changing the windfield). The model can also be used to develop “what if” scenarios that test the response of the marine ecosystem to predicted climate change.

4.1.5 What ecosystem models require from climate models

The development of a regional climate scenario using a downscaling approach that involves three-dimensional hydrodynamic and biophysical models requires that (i) the climate models be skilful in the region of interest, and the validity and skill of the models must have been tested with a present-day reference simulation; and (ii) the validation exercise must be performed regionally for the following variables:

- winds and air pressure (i.e. the correct location of the mean large-scale pressure systems is the single most important requirement);
- short-wave radiation (clouds) and air temperature;
- humidity;
- precipitation and run-off; and
- temperature and salinity in the ocean.

The regional models need to be skilful not only for the average climate signal, but also for the seasonal signal, the interannual variability, and the diurnal variability, because variability on all of these different time-scales can be an important driver of biological processes. To allow for reasonable predictions, the regional bias and model errors in dynamically active (non-linear processes) variables (temperature gradients, windfields) clearly need to be smaller than the climate-change signal, whereas error margins need to be given with reference to the present-day climate simulations.

Larger error margins have to be corrected, and specific corrections have to be developed.

Variables needed to force the regional ocean biophysical models are windfields (10 m), sea-level pressure, surface air temperature and dew-point temperature (humidity), short-wave radiation, cloud cover, atmospheric long-wave radiation, runoff, and sea ice. It may also be necessary to correct for resolution bias in the global models. Oceanic data requirements include the initial and boundary conditions in temperature, salinity, and sea level, although these and other data, such as currents, can be used for data assimilation in the models. The temporal resolution required is 3–6 h for the atmosphere and daily–weekly for the oceanic parameters.

4.2 Statistical models

Martin Lindgren and Jan Erik Stiansen

In contrast to mechanistic models, which are built up by representing and linking known processes, statistical models explore data for statistically significant relationships between two or more variables and, from this, infer an association between the variables, although the specific mechanisms may be unknown. The association between two variables may even be mediated by a third (often unknown) variable. Two common statistical models are correlation and regression. Correlation measures the degree of linear dependence between variables from the covariance of standardized descriptors. For multiple variables, a correlation matrix, whose elements are the coefficients of the linear correlation between each pair of variables respectively, can be constructed (Legendre and Legendre, 1998). The square of these coefficients is the coefficient of determination, that is, a measure of how much of the variance of each variable is explained by the other.

As with correlations, regression models generally assume linearity between response and predictor(s). In a simple linear regression, the model equation corresponds to a straight line defining the nature of the relationship between predicted (y) and explanatory (x) variables. In the case of several explanatory variables (x_1, x_2, \dots, x_n), a multiple linear regression is often used to represent a linear relationship between the predicted and all of the explanatory variables. When using such general linear models (GLMs), one must be aware that a linear model is imposed (Legendre and Legendre, 1998) and consider whether or not this is indeed valid.

Models have been developed to overcome the assumptions of linearity. These include polynomial regressions, partial linear regressions, and, if the actual function is known (e.g. logistic growth), non-linear regression. Generalized additive models (GAMs) provide a combination of both linear and non-linear techniques, as the linear predictor depends, in part, on a sum of smooth functions of predictors. The key idea here is that the dependence of the response on the predictors can be represented as a parametric submodel plus the sum of some smooth functions of one or more of the predictor variables.

Users of statistical models often neglect to identify and discuss the actual mechanisms of interactions between variables. However, a more theoretical–mechanistic approach to statistical models has been developed in the field of population dynamics. Log-linear, first-order autoregressive, or AR(1), models (Royama, 1992; Bjørnstad *et al.*, 1995; Stenseth *et al.*, 1996), provide a theoretically well-supported framework for modelling population dynamics under environmental stochasticity (Ives, 1995). Hjermann *et al.* (2004, 2007) effectively demonstrate how

such an approach can be used in modelling the Barents Sea cod stock dynamics in response to climate variability and fishing.

Elaborating from a single-species point of view, first-order multivariate autoregressive, or MAR(1), models provide a multispecies extension for modelling foodweb interactions at several trophic levels (Ives, 1995; Ives *et al.*, 1999, 2003). MAR(1) models can be viewed as a linear approximation to a non-linear, first-order stochastic process (Ives *et al.*, 2003) and, in general, function as a set of lagged multiple linear regression equations (one for each species of the foodweb), solved simultaneously to arrive at the most parsimonious model overall (Hampton *et al.*, 2006). Combined with internal species interactions, the MAR(1) framework allows any external forcing (e.g. climate variability or commercial fishing) to be included as a covariate (Ives, 1995; Ripa and Ives, 2003). Because the MAR modelling may integrate internal foodweb dynamics and external forcing, it can serve as an important tool in modelling and even in forecasting population responses to climate change. Surprisingly, it has hardly been extended beyond theory by applying it to real foodwebs (Ives *et al.*, 1999; Hampton *et al.*, 2006).

4.2.1 What can these models do?

The use of correlations and regressions in climate–fish relationships can be very useful. However, these approaches must be used with great care and may, in some cases, be misleading. Here, we discuss some of the possibilities and caveats.

Correlations and regressions can be useful in revealing possible relations between a climate variable and a fish-stock variable. Because they are simple to use, they are very suitable as a first test or approach. Multiple regressions that combine stock and climate variables can be useful for assessment purposes, especially if they have predictive power (i.e. the predictor variables precede the response variables in time). An example of this is given in Figure 4.4. For correlations and regressions or multiple regressions to be believable, they need to have a plausible cause–effect reasoning linked to them. In all cases, they should be treated with great care, because they are a very simple approach to describing parts of a generally complex structure of nature.

There are a number of limitations or caveats associated with the use of these methods. Here, we briefly mention a few that are primarily related to correlation and regression analysis.

Statistical relationships may be the result of pure coincidence. Significant correlation is a necessary, but not sufficient, criteria for a relationship.

- Multiple regressions often break the statistical assumptions that the explanatory variables should be independent (or for practical reasons, at least should be only weakly correlated).
- Autocorrelations in the explanatory and predicted variables need to be evaluated for determination of statistical significance.
- The relationships may be time-dependent, that is, a link may only hold for as long as the explanatory variable is the dominant influence. Often the relationships are only valid over a certain span or window of time and break down outside this interval.
- If the true relationship is non-linear, this may not demonstrate properly in linear regressions or correlations. (In some cases, the correlation may be zero, even if there is a clear non-linear relationship.)

- For multiple regressions, too many explanatory variables compared with the number of data points leads to pure curve-fitting, which reduces the analysis to a mathematical exercise, which is unlikely to be linked to a plausible cause and effect.
- The relationships may not be the result of a cause–effect response, but of an “undetected” cause to which both variables respond.

Although there are many traps for those that use statistical correlations and regressions, these approaches are still valid within their limitations. The greatest problem for practical use is the risk of breakdown of the relationship. Therefore, identified relations should be followed in time, and methods for continuous evaluation of the relations should be provided. In the time-window where the relations are valid, correlations and regressions can be valuable tools.

4.2.1.1 Example 1. Use of multiple regression to predict the number of Northeast Arctic (NEA) cod recruits

In present-day fish-stock assessments, climate is rarely taken into account. One of the most accessible places to add climate information is in the short-term projection of recruitment. In many assessment models, regression models may be substituted for the existing recruitment prognoses module.

Stiansen *et al.* (2005) suggested a model with a 2-year advanced prognosis.

$$R3 \sim \text{Temp}(-3) + \text{Age1}(-2) + \text{MatBio}(-2),$$

where R3 = the number of 3-year-old Northeast Atlantic (NEA) cod, Temp = the Kola annual mean temperature (averaged over 0–200 m), Age1 = the winter survey bottom-trawl index for age-1 cod, and MatBio = the maturing biomass of capelin. The numbers in parentheses represent the time-lag in years. The observed and modelled recruits of NEA cod using this model and applied to the years 1984–2005 are shown in Figure 4.4. The outlook for years 2006–2009 is also shown.

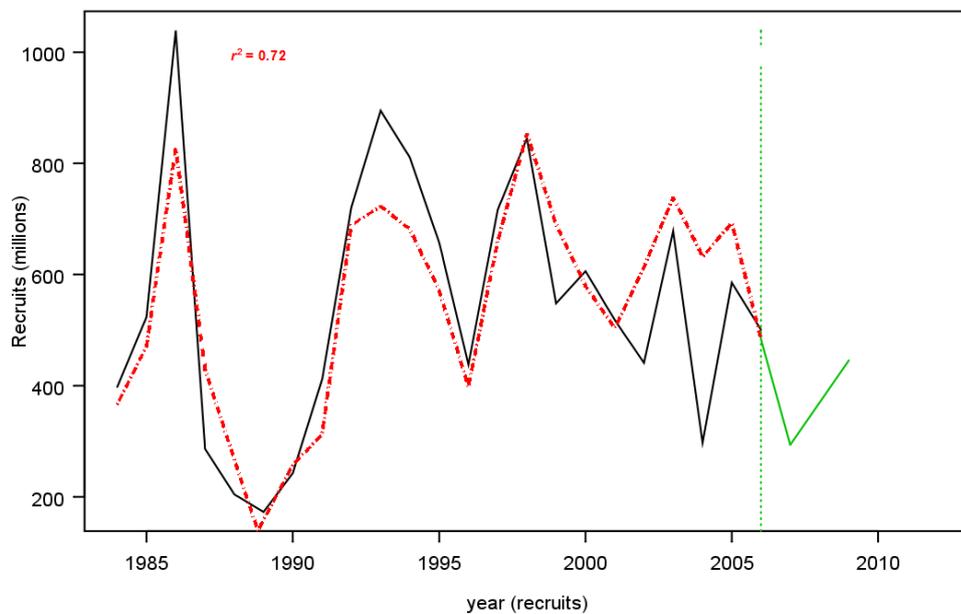


Figure 4.4. Northeast Arctic (NEA) cod recruitment projection using multiple regression. The black line is the number of recruits at age 3 from virtual population analysis (VPA) using data for 1985–2005; the red line is the number of recruits at age 3 estimated by the Stiansen *et al.* (2005) model shown above. The correlation between the observed and estimated recruits is $r^2 = 0.72$; the green line is the number of recruits at age 3 for 2006–2009 forecast by the model.

4.2.1.2 Example 2. Use of MAR(1) models in predicting Baltic cod stock dynamics in response to climate change

A fishing- and climate-driven multispecies model for the Baltic Sea that was able to accurately recreate the past dynamics of Baltic cod, sprat, and herring was developed as a first step in implementing MAR(1) modelling within fishery forecasting and management (Lindgren *et al.*, 2009). A simple climate model (Ripa and Lundberg, 1996) was used, based on “The assessment of climate change for the Baltic Sea Basin” (BACC, 2007), to simulate plausible climate scenarios for the 21st century. “Red-shifted” time-series (i.e. positively autocorrelated; see Steele and Henderson, 1984) of spring sea surface temperature (SST) and summer salinity were generated based on actual data for 1974–2004. A gradual trend in the mean over 100 consecutive years was applied in order to mimic a predicted increase in SST by 3.5°C and a salinity decrease of 0.8 or 5 psu, respectively. The impact of climate change on the future dynamics of Baltic cod was explored using the coupled foodweb and climate model. The effect of fishery management strategies in relation to climate change was explored by including different fishing scenarios for Baltic cod. The probability of the stock falling below the limiting stock size (B_{lim}) of 160 000 t was computed by running a large number of stochastic simulations for combinations of climate and fishing mortalities (Figure 4.5). Model runs demonstrate that, given even a relatively small decrease in salinity (~3 psu), recruitment of Baltic cod is impaired by an increase in egg and larval mortality (Nissling, 2004; Köster *et al.*, 2005). Only a drastic decrease in fishing mortality prevented stock collapse in the simulations and ensured the existence of Baltic cod for future generations.

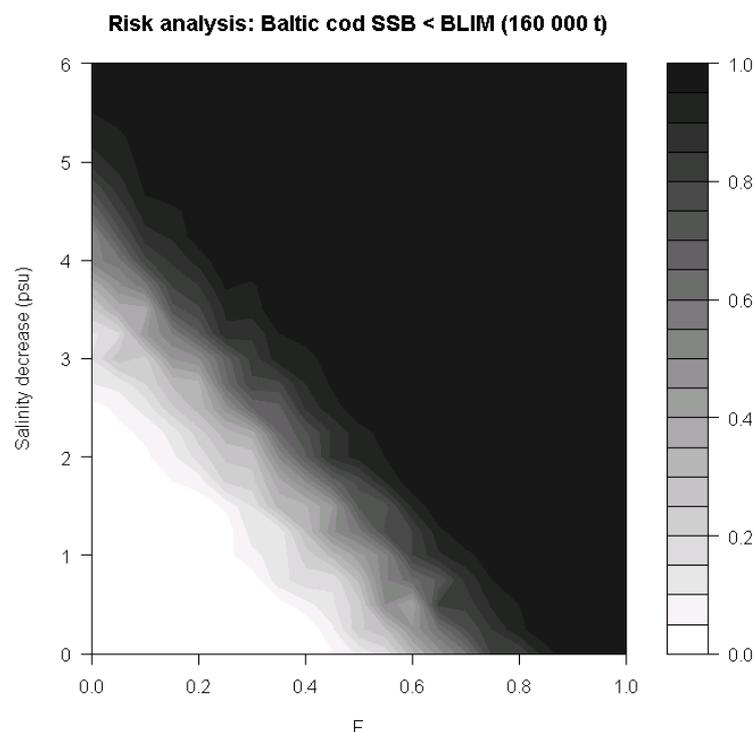


Figure 4.5. The probability of Baltic cod spawning-stock biomass (SSB) falling below the limiting stock size (B_{lim}) is computed as the percentage of model runs where the predicted SSB falls below 160 000 t. Simulations are run for all combinations of fishing mortality (F) from 0 to 1 and decreases in salinity from 0 to ~5 psu (relative to the mean salinity for 1974–2004). The risk of falling below B_{lim} increases rapidly and non-linearly as salinities decrease with increasing F .

4.3 Mechanistic–stochastic models

Irene Mantzouni

4.3.1 What can these models do?

The WKCFCC emphasized the need to broaden our insights into the processes that link climatic factors and their variability to cod life-history parameters and, hence, to population dynamics. This calls for the development of mathematical or empirical models that (i) describe and combine mechanisms through which environmental impacts operate at the stock level; (ii) incorporate the various sources of uncertainty; and, consequently, (iii) discern and illustrate patterns despite ecosystem complexity. A further advantage of such models is that their parameters have a meaningful interpretation and, thus, population characteristics of interest and their dynamics and/or variability can be directly obtained. Such examples include the stock–recruitment (SR) models, which are broadly used in fishery management in order to derive reference points. However, process modelling usually involves non-linear relationships which it may (e.g. Ricker SR model) or may not (e.g. Beverton–Holt or Deriso–Schnute SR models) be possible to express in a linear form. Empirical estimation can be hampered in such cases, especially when the data series are short and noisy, and the interannual variability in the forcing environmental factor is low, a situation not uncommon to natural fish populations.

4.3.2 Advantages of meta-analysis

The advantages and the potentials of joint/comparative studies in fishery science have long been advocated (e.g. Pauly, 1980; Brander, 1995) and have provided fundamental insights on spawner–recruit dynamics (Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971), especially in cases where single-stock inference does not have enough power to produce clear results (Myers, 1998, 2001; Brander, 2000). Theoretical and technological advances in recent years have allowed the more widespread use of synthetic approaches, such as meta-analysis, mixed (variance components) and Bayesian models, especially in stock assessments (e.g. Punt and Hilborn, 1997) and SR dynamics (see Myers and Mertz, 1998; Myers, 2001, 2002, for reviews). In particular, such analyses have revealed relationships between cod and environmental variables (e.g. Planque and Frédou, 1999; Brander, 2000; Dutil and Brander, 2003; Brander and Mohn, 2004; Stige *et al.*, 2006), based on the fact that stocks within species, or within related species with similar life histories, share common population dynamics patterns and respond to environmental effects in comparable ways (Brander, 2000; Myers *et al.*, 2002; MacKenzie *et al.*, 2003). Consequently, it is possible to “borrow strength” (Myers *et al.*, 2001), or to “stand on the shoulders of giants” (Hilborn and Liermann, 1998), by combining data across stocks. Such approaches can yield superior parameter estimates, thereby reducing uncertainty for management reference points, allowing inference at a higher level, and improving estimations for stocks with limited data (Myers *et al.*, 2001).

4.3.3 Hierarchical modelling

To couple the needs for both mechanistic, possibly non-linear, models and robust parameter estimation for the empirical research of natural phenomena, hierarchical or multilevel models can provide a useful and flexible toolbox, describing stochastic processes of various forms and allowing for inference across stocks (Gelman and Hill, 2007). Hierarchical modelling is a rigorous probabilistic framework offering two mutually implicative advantages: (i) the explicit incorporation and, thus, isolation of

uncertainty sources; and (ii) the combination of data across various independent sources (Hilborn and Liermann, 1998; Gelman and Hill, 2007). Uncertainty arises, mainly from two sources of variation or error: (i) observation, and (ii) systematic model error (e.g. Hilborn and Walters, 1992). Observational process uncertainty arises from non-systematic effects, such as measurement error in recruitment and/or spawner biomass, resulting in random model or sampling error (Hilborn and Walters, 1992). Systematic model error can be decomposed into process variation and parameter uncertainty. The former is the result of insufficient or improper specification of the model functional form. Defining the process generating the data is, in general, the most fundamental step in model development. Errors of this type arise from mis-specification or oversight of stochastic, usually environmental, factors affecting the basic model mechanism, so affecting recruitment success probabilities (e.g. Bakun, 1996; Jarre-Teichmann *et al.*, 2000). Finally, parameter variability across stocks, apart from observation error, also stems from the fact that parameters do differ across stocks (Hilborn and Liermann, 1998), and is possibly the result of differences in the size and magnitude of dynamics response to underlying processes.

4.3.4 Case study: hierarchical development of the Beverton–Holt SR model

Hierarchical implementation is based on the decomposition of the model into three stages, or levels, according to the probability theory (Clark, 2007); here, it is illustrated for SR models.

On the first level, the data model is specifying the data distribution, given the model (i.e. the functional form of the SR model and the associated parameters). For example, the hierarchical Beverton–Holt SR model can be written as

$$y_{it} = \alpha_{it}^{BH} + \beta_{it}^{BH} - \log(\exp(\beta_{it}^{BH}) + x_{it}) + \varepsilon_{it}, \quad (1)$$

where $y_{it} = \log(R_{it} / S_{it})$ and $x_{it} = S_{it}$. Parameters α_{it}^{BH} (maximum reproductive rate) and β_{it}^{BH} (log of S giving half of asymptotic recruitment) can be assumed to depend on stock i specific temperature (T) time-series, thus, being time-varying:

$$\alpha_{it}^{BH} = c_{oi}^{BH} + c_{T1}^{BH} T_{it} + c_{T2}^{BH} T_{it}^2; \quad (2)$$

$$\beta_{it}^{BH} = d_{oi}^{BH} + d_{T1}^{BH} T_{it} + d_{T2}^{BH} T_{it}^2 \quad (3)$$

Equation (1), incorporating the above relationships, is the data-level model, represented by the likelihood in the Bayesian framework and expressing the probability of observing the data, given the functional model and its parameters:

$$y_{it} \sim N(\alpha_{it}^{BH} + \beta_{it}^{BH} - \log(\exp(\beta_{it}^{BH}) + x_{it}), \sigma_{yi}^2) \quad (4)$$

On the second level, the process models describe the mechanism based on the associated parameters. In the present context, they specify the distribution of the SR model parameters across the cod stocks and can also be extended to account for the factors generating the among-stock differences. Thus, they are referred to as the “stock-level models”, acting as priors for the coefficients in Equations (2) and (3). Models for the temperature-related terms allow for the possibility that *alpha* and *beta* have different degrees of sensitivity to temperature effects in the individual stocks. These across-stock distributions are of the form

$$c_{Tii}^{BH} \stackrel{iid}{\sim} N(\mu_{c_{T1}}^{BH}, (\sigma_{c_{T1}}^{BH})^2) = p[c_{Tii}^{BH} | \mu_{c_{T1}}^{BH}, \sigma_{c_{T1}}^{BH}] \quad (5)$$

The stock-level models for the intercepts account for among-stock differences in Beverton–Holt *alpha* and *beta* parameters, arising from additional effects not included in the data-level model. For parameter *beta*, representing carrying capacity (CC), variation is partly the result of differences in the habitat size occupied by the individual stocks. Therefore, the intercepts in Equation (3) can be modelled as a function of *H*, and the corresponding priors become stock-specific:

$$d_{oi}^{BH} \stackrel{iid}{\sim} N(k_o^{BH} + f_{H1}^{BH} H_i + f_{H2}^{BH} H_i^2, (\sigma_{d_o}^{BH})^2) = p[d_{oi}^{BH} | k_o^{BH}, f_{H1}^{BH}, f_{H2}^{BH}, \sigma_{d_o}^{BH}]. \quad (6)$$

The third level is known as the parameter model and concerns the hyper-parameters used to specify the probability distribution of the parameters in the previous stages. The second and third levels, which are based on the assumption that certain SR model parameters are connected across stocks, lie at the core of the hierarchical meta-analytic inference. The common probability distribution and the process generating these parameters, or describing the differences among them, which are both described by the hyper-parameters of the third level, form the interface for the combination of the individual datasets and, thus, for exchange of estimation strength across stocks (Gelman *et al.*, 1995).

4.3.5 Perspectives

Hierarchical approaches offer multiple advantages for the modelling of climate-change effects on cod stocks by bringing together the sources of variability within and among stocks and a broader range of environmental conditions across the distribution of the species. Environmental factors acting on local scales clearly differ across regions. The flexibility of the Bayesian framework, apart from multilevel structures, allows the simulative implementation of mechanistic models incorporating complex processes for single stocks. Thus, patterns inferred at the species level, coupled with models describing the stock-specific dynamics, either directly or as priors, can provide further insights into the future of cod under the climate-change perspective.

5 Improving management strategies by evaluating climate impacts

5.1 Management advice on sustainable yield – Barents Sea

Anatoly Filin

Management of fisheries is always based on decision-making under uncertainty. Incorporating data on ocean climate in management procedures should reduce the uncertainty of scientific recommendations for harvest levels. The first aim of fishery strategy is to ensure a sustainable harvest, and precautionary and ecosystem approaches should be used.

Environmental information related to future climate change ought to play an important role in the design of management strategies. Environmental information can be used to exploit a stock either more efficiently or more carefully, according to prevailing environmental conditions. Environmental impacts, ascribable to climate change, should also be taken into account in the evaluation of a management strategy.

The existing ICES advisory system was designed to provide advice on a very short-term basis: one year ahead based on the recent past. As we now move towards the provision of longer term advice in a more rapidly changing environment, there is a need to alter the way that we consider the future and to provide advice that is both more robust and more adaptive to change. In the face of global warming, we need to take into account not only stochastic variability, but also trends and shifts in the environment as we develop scientific advice. Exploitation rates estimated from observations taken over several climate-regime changes will not be optimal for any specific set of environmental conditions.

The existing management strategies for cod stocks are based on the precautionary approach and use biological reference points expressed in terms of fishing mortality and spawning-stock biomass. Today, the reference points on which cod-harvesting rules are based are constant and independent of the state of the ecosystem. For this reason, they are inconsistent with the ecosystem approach. If we see a long-lasting change in the productivity of cod stocks induced by a climate-regime change, or are able to identify good qualitative relationships between environmental factors and growth or recruitment, we may imagine that the reference points will be set as a function of the state of the environment. This would allow stocks to be harvested more heavily in more productive periods than in poor periods.

The stock-management strategy is based on an expected estimate of long-term yield. Such estimates are used to set optimal harvest intensity according to the accepted management targets. The only method for estimation of expected long-term yield is mathematic modelling. Therefore, in order to move from the constant biological reference points for harvesting control of cod stocks that are used today to biological reference points that will depend on the ecosystem regime, it is necessary to develop relevant cod ecosystem-coupled models. Such models should be region-specific as well as ecosystem-specific. On the other hand, they can be based on the same approaches to the simulation of growth, maturation, cannibalism, and other population variability of cod.

The cod ecosystem-coupled models require a relevant prognosis of the state of the environment that corresponds to expected climate changes. Where there is no basis for predicting future environmental drivers, management strategies should be based

on scenario testing. This implies the development of scenarios of temperature changes as well as dynamics of cod prey and predator abundance.

Simulations should be based on a stochastic approach. Taking into account uncertainties, the probability can be expressed in terms of a risk estimate of the undesirable consequences for the stock and harvest that implements a testing strategy. It especially concerns the probability of declines in stock level below the established threshold level. Alternative future scenarios should be used to evaluate future risks and uncertainties for management.

At present, a complete procedure for estimating environmental-dependent biological reference points for harvest control of cod stocks is lacking. However, existing models demonstrate their power not only to evaluate cod responses to climate change, but also to test management and recovery strategies for cod stocks under different climate scenarios. One example, using MAR(1), is provided in Section 4.2.1.2. Another example of such models is STOCOBAR, which describes the STOCk dynamics of COd in the BARents Sea, taking into account trophic interactions and temperature influences (Filin and Oganin, see Appendix 1, Section A1.7).

Projections of the consequences of expected warming in the Barents Sea for cod and its harvesting from the STOCOBAR model are shown in Figure 5.1. The stochastic Ricker recruitment equation was used to couple spawning-stock biomass and recruitment at age 1. Available observations on the Kola section were the basis for development of the temperature scenarios for the long-term simulations. The alternation of cold, moderate, and warm periods was introduced into the temperature scenario. In addition to temperature, changes in biomass of capelin in the Barents Sea were considered in these evaluations as an element of the ecosystem scenario. The harvest-control rule for cod in the simulations was used as the management strategy, which is based on the precautionary approach. The total allowable catch (TAC) was calculated using existing values of the biological reference points for the Barents Sea cod stock. Long-term simulations were performed for five temperature regimes: present temperature and temperature increases of 1, 2, 3, and 4°C.

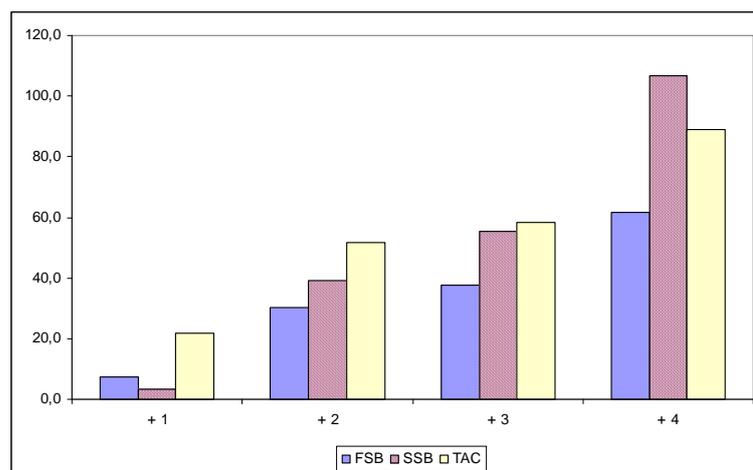


Figure 5.1. Relative changes (y-axis; % to simulated values under the current temperature regime) of cod spawning-stock biomass and catches at temperature increases (x-axis) in the Barents Sea of 1–4°C according to the STOCOBAR simulations. FSB is fishable stock biomass.

The results of simulations demonstrate temperature increases in the Barents Sea of 1–4°C, which will lead to acceleration of cod growth and cod maturation rates. This will have a positive effect on the general production of the cod stock. On the other

hand, cannibalism in cod will also probably increase in response to expected warming in the Barents Sea. This will have a negative effect on cod recruitment and total abundance. The simulation results also demonstrate that, with warming, the cod stock can be harvested more heavily (Figure 5.1).

Another example of environmental impact on the harvesting potential of cod in STOCOBAR simulations is presented in Figure 5.2. It demonstrates the dependence of cod recovery rate on temperature regime and capelin abundance in the Barents Sea. Thus, models can be viewed as a potential tool for scenario testing of cod-rebuilding strategies.

Further development of existing cod ecosystem-coupled models should ensure a transition from theoretical studies of improvement in cod management to their practical implementation through updating and reevaluation of reference points for controlling the harvest of cod stocks.

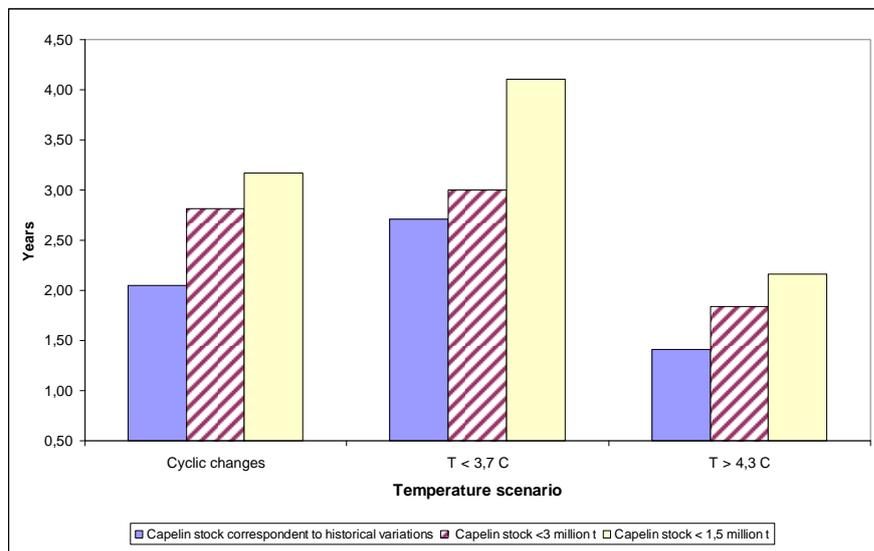


Figure 5.2. Mean recovery period for the Barents Sea cod stock in the STOCOBAR simulations for different temperature scenarios.

5.2 Time-scales: centennial, decadal, interannual

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5.2.1 Climate periodicities and their ecosystem effects

Variations in the signals of sea surface temperature in the North Atlantic have occurred over interannual to multidecadal time-scales. Within the 20th century, the amplitudes of these variations have exceeded those of the human-induced climate-change signal. During the 20th century, the long-term average increase in sea surface temperature in the North Atlantic region has been ca. 0.2°C. In contrast, the AMO demonstrates rates of changes of 0.4°C over a 30-year time interval averaged over the entire North Atlantic (Sutton and Hodson, 2005). The AMO signal increases with latitude (Johannessen *et al.*, 2004). For the European waters of the Northeast Atlantic (e.g. the Kola section of the Barents Sea), the rate of temperature change is typically ca. 0.7°C over a 30-year time interval. Interannual to decadal-scale climate variations have larger amplitudes than the multidecadal signal. Typically, the rate of change of the decadal-scale signal is up to 1.5°C over a time interval of 4 years for the Kola section of the Barents Sea. The amplitude of the observed ocean temperature changes

during the 20th century, as a function of periodicity, is shown in Figure 5.3. The figure may give the impression of a logarithmic relationship. However, it should be strongly emphasized that this is only valid for the observations of the limited time-span of the 20th century, and that extrapolation to longer time-scales cannot be justified. On a millennial time-scale, we know that there will be a further increase in temperature. Moreover, what is expected of anthropogenic sea temperature changes of the northern North Atlantic during the present century, i.e. in the order of 2°C, will exceed any earlier observed changes on a centennial time-scale.

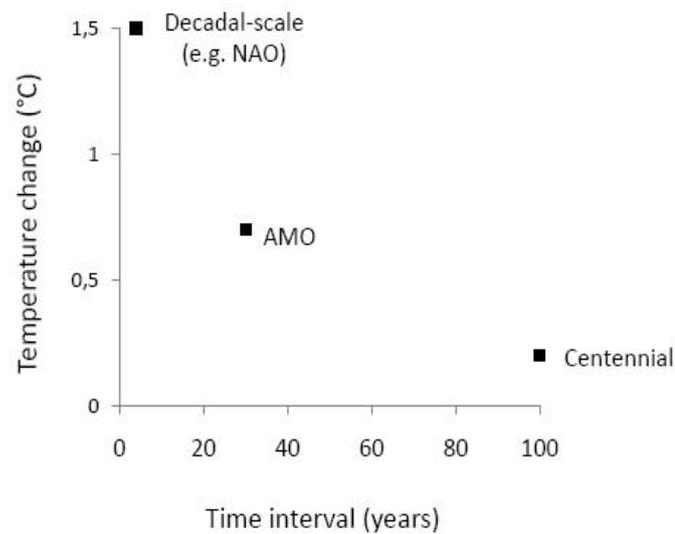


Figure 5.3. Change in sea temperature for three periods, from interannual to centennial, in the Northeast Atlantic during the 20th century.

The marine ecosystems of the northern North Atlantic have responded to the natural climate periodicities experienced during the past century in a multitude of ways. These responses provide some insight into how marine ecosystems might respond to the predicted climate change of the 21st century. The amplitudes of the interannual to decadal-scale temperature changes are expected to be similar to those during the 20th century. However, as mentioned above, on a centennial time-scale, the amplitude of the anthropogenic climate change will far exceed that experienced during the 20th century, specifically by one order of magnitude. Therefore, the lesson on the effects of climate change on marine ecosystems learned from the 20th century needs to be treated with care when applied to the climate projections of the 21st century.

Interannual to decadal-scale temperature changes have been demonstrated to have strong effects on individual growth, survival, and recruitment in fish. Particularly, its effects on Atlantic cod have been documented frequently (Elizarov, 1963; Koslow *et al.*, 1985; Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989; deYoung and Rose, 1993; Brander, 1995; Ottersen and Sundby, 1995; Rodionov, 1995; Svendsen *et al.*, 1995; Campana, 1996; Planque and Fox, 1998; Planque and Frédou, 1999; Ottersen and Loeng, 2000; Rindorf *et al.*, 2008; Sandeman *et al.*, 2008). Moreover, it has been demonstrated that the geographical distribution of adult cod in the Barents Sea varies on an interannual time-scale according to climate variations (Nakken and Raknes, 1987; Ottersen *et al.*, 1998). These shorter time responses to climate change seem to be associated with processes linked to population ecology as indicated by the responses of individual populations in terms of growth, reproduction, recruitment, and distribution (Sundby and Nakken, 2008). The mechanisms behind these responses, particularly growth rates, may be directly linked to temperature change (e.g. Brander, 1995). However, there is often an indirect link, where the apparently direct

temperature response is a proxy for other processes, such as variability in ocean currents, which, in turn, influence advection of zooplankton-rich water masses (e.g. Sundby, 2000). Flux variability of ocean currents typically acts on interannual to decadal-scales, and in the northern North Atlantic, is influenced by the NAO (Sundby and Drinkwater, 2007).

The shorter term ecosystem responses described above (i.e. interannual to decadal-scale responses) indicate a relatively direct mechanistic link between climate variability and the response of the biological processes in the ecosystem. Temperature-dependent growth rates of individuals, from larvae to juveniles to adult fish, are such direct short-term responses. Early focus on recruitment of fish stocks demonstrated large interannual variations (Hjort, 1914). Recruitment processes, such as the match–mismatch hypothesis of the abundance of prey for larval fish (Cushing, 1974) and the bigger-is-better hypothesis (Leggett and DeBlois, 1994), are other examples of short-term responses involving the direct effects of temperature and a direct link to the trophic level below (the abundance of the copepod prey).

Another type of ecosystem response is associated with longer term climate variability (i.e. the multidecadal climate variability as exemplified by the AMO). Drinkwater (2006) demonstrated how the general warming of the North Atlantic from the 1920s towards the end of the 1930s resulted in a substantial northward shift in distributions of Atlantic fish species. For example, most of the cod stocks in the North Atlantic demonstrated a more northerly distribution by the end of the 1940s compared with the situation at the beginning of the 20th century, when the climate was cooler (Tåning, 1953). During the recent warming since the cool 1960s and 1970s, there has been a distinct northward shift in Northeast Atlantic zooplankton (Beaugrand *et al.*, 2002). The spawning areas of Arcto-Norwegian cod along the Norwegian coast have oscillated northwards and southwards with the AMO during the 20th century (Sundby and Nakken, 2008). These examples demonstrate that long-term climate variations exert a different influence on North Atlantic marine ecosystems than short-term variations. Despite the moderate temperature amplitude compared with the amplitudes of interannual periodicity (Figure 5.3), the change in species habitats is considerable. Sundby and Nakken (2008) suggested that these kinds of ecosystem responses are more indirect and act through the foodweb. This implies that such changes are associated with system ecology rather than population ecology.

5.2.2 Some considerations about effects of future climate change in the 21st century

The projected climate change in the 21st century is expected to generate ecosystem responses similar to those generated by the multidecadal climate oscillation during the 20th century. This means that zooplankton species, as well as pelagic and demersal fish species, will probably continue to move northwards. However, the uncertainty of such assessments is that the amplitude of the projected change is substantially larger than that resulting from changes in the AMO, and will probably exceed the maximum temperatures that will be experienced before the mid-21st century. It is highly uncertain whether or not this might cause abrupt responses of the ecosystem and, thus, are impossible to predict. Understanding such abrupt changes depends on understanding the mechanisms behind the changes. Simple correlations between sea temperature (or NAO) and ecosystem variables will not be a successful approach towards this understanding. We need to understand the linkage with a range of climate variables, i.e. temperature, salinity, wind mixing, stability, advection, ice cover, and light. Then, we need to understand how these climate

variables influence fish stocks directly and indirectly through the foodweb. Such an approach is only possible by combining experimental studies in the laboratory and the field, time-series, and basin-scale to local-scale biophysical modelling. This approach was described during the initiation of the ICES Cod and Climate Change (CCC) programme (ICES, 1990). The CCC programme has indeed developed in this direction, but there is still a considerable lack of process understanding, particularly because there is still a long way to go in combining experimental studies with biophysical modelling.

6 Suggestions for future work and recommendations

In order to predict the impact of climate change on cod stocks over the next 20–50 years, we require adequate and credible climate forecasts and biological models that respond correctly to the climate drivers and consider both direct and indirect biological processes. The impact of climate will also depend on our management of cod stocks and the marine ecosystems in which they occur. It is clear that neither climatic nor biological models are currently adequate to produce credible forecasts over this time-scale.

Regional models must be consistent with and based on global models by statistical, dynamic, and blended downscaling from the global circulation models (GCMs). However, for the latter to be useful for regional downscaling, they should at least be able to re-create the current regional climate reasonably well. This is a necessary condition for credible forecasting, but unfortunately is not in itself sufficient, because the ability to match the observational record does not necessarily entail good predictive skill. Improved initialization of GCMs using the observational record is nevertheless a key requirement for future models. Downscaling should be performed using the results from several GCMs, not just one.

Research should continue into shorter term forecasting (<20 years) using assimilation of multidecadal and recent data, because skill in forecasting over shorter periods can also be extremely valuable in fishery management and in the anticipation of possible qualitative and quantitative changes in productivity (including “regime”).

Even in the absence of detailed and credible regional forecasts, it is valuable to carry out impact assessments based on the best available global projections and a variety of “what if” scenarios. These will help our understanding of the potential influences of climate change on cod and their ecosystems and will provide a good basis for using regional forecasts when they become available. They will also allow the exploration of interactions between climate and fishing mortality in developing robust and responsive management strategies.

In order to ensure that future global and regional climate models deliver the critical information required for impact studies, the impacts community needs to interact routinely with the climate-modelling community in order to develop and convey their requirements.

The effect of size-selective mortality on size-at-age should be further investigated, covering more stocks. In addition, examination of the effects of age structure and geographical substructure of the spawning stock on 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 mean age of the female spawning stock). The effects of small-scale features, such as fronts and eddies, on cod productivity appear to be important in several areas. These are often not even incorporated into regional models, although this is improving. Continued work to further improve the models in this regard is suggested.

7 References

- Ådlandsvik, B. 2008. Marine downscaling of a future climate scenario for the North Sea. *Tellus*, 60A: 451–458.
- Ådlandsvik, B., and Bentsen, M. 2007. Downscaling a twentieth century global climate simulation to the North Sea. *Ocean Dynamics*, 57: 453–466.
- Alheit, J., Möllmann, C., Dütz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES Journal of Marine Science*, 62: 1205–1215.
- Allen, J. I., Blackford, J., Holt, J., Proctor, R., Ashworth, M., and Siddorn, J. 2001. A highly spatially resolved ecosystem model for the North West European Continental Shelf. *Sarsia*, 86: 423–440.
- Allen, J. I., Somerfield, P. J., and Gilbert, F. J. 2007a. Quantifying uncertainty in high-resolution coupled hydrodynamic ecosystem models. *Journal of Marine Systems*, 64: 3–14.
- Allen, J. I., Holt, J. T., Blackford, J., and Proctor, R. 2007b. Error quantification of a high-resolution coupled hydrodynamic-ecosystem coastal-ocean model: Part 2. Chlorophyll-*a*, nutrients and SPM. *Journal of Marine Systems*, 68: 381–404.
- Andrews, J. M., Gurney, W. S. C., Heath, M. R., Gallego, A., O'Brien, C. M., Darby, C., and Tyldesley, G. 2006. Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 1027–1048.
- Axenrot, T., and Hansson, S. 2003. Predicting herring recruitment from young-of-the-year densities, spawning stock biomass, and climate. *Limnology and Oceanography*, 48: 1716–1720.
- BACC. 2007. Assessment of climate change for the Baltic Sea Basin – the BACC Project. International Conference, Gothenburg, Sweden, 22–23 May, 2006. IKSS, Geestacht, Germany. Available online at http://www.gkss.de/baltex/BACC/Climate_change_report_07.pdf.
- Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. BCS Mexico, California Sea Grant System, NOAA, and Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico. 323 pp.
- Bakun, A., and Weeks, S. J. 2006. Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish and Fisheries*, 7: 316–333.
- Baretta, J. W., Ebenhöf, W., and Ruardij, P. 1995. The European Regional Seas Ecosystem Model (ERSEM), a complex marine ecosystem model. *Netherlands Journal of Sea Research*, 33: 233–246.
- Bartsch, J., and Coombs, H. 2004. An individual-based model of the early life history of mackerel (*Scomber scombrus*) in the eastern North Atlantic, simulating transport, growth and mortality. *Fisheries Oceanography*, 13: 365–379.
- Baumann, H., Peck, M. A., and Herrmann, J. P. 2005. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, *Sprattus sprattus*. *Marine and Freshwater Research*, 56: 539–547.
- Baumann, H., Hinrichsen, H-H., Möllmann, C., Köster, F. W., Malzahn, A. M., and Temming, A. 2006. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 2191–2201.
- Beaugrand, G., Ibanez, F., and Lindley, J. A. 2001. Geographical distribution and seasonal and diel changes in the diversity of calanoid copepods in the North Atlantic and North Sea. *Marine Ecology Progress Series*, 219: 189–203.

- Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, 296: 1692–1694.
- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. *Fisheries Investigations (London) Series 2*, 19. 533 pp.
- Bigg, G. R., Cunningham, C. W., Ottersen, G., Pogson, G. H., Wadley, M. R., and Williamson, P. 2008. Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. *Proceedings of the Royal Society of London, Series B*, 275: 163–172.
- Bjørnstad, O. N., Falck, W., and Stenseth, N. C. 1995. Geographic gradient in small rodent density-fluctuations – A statistical modeling approach. *Proceedings of the Royal Society of London, Series B*, 262: 127–133.
- Blacker, R. W. 1957. Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fisheries Investigations (London) Series 2*, 20: 1–49.
- Blackford, J. C., Allen, J. I., and Gilbert, F. J. 2004. Ecosystem dynamics at six contrasting sites: a generic modelling study. *Journal of Marine Systems*, 52: 191–215.
- Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., and O'Brien, C. M. 2005. Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 2001–2009.
- Brander, K. (Ed). 1994. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 205. 150 pp.
- Brander, K. M. 1995. The effects of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 52: 1–10.
- Brander, K. M. 2000. Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. *Oceanologica Acta*, 4: 485–496.
- Brander, K. M. 2003. What kinds of fish stock predictions do we need and what kinds of information will help us to make better predictions? *In Fish Stock Assessments and Predictions: Integrating Relevant Knowledge*, pp. 21–33. Ed. by Ø. Ulltang and G. Blom. *Scientia Marina*, 67(Suppl. 1). 370 pp.
- Brander, K. (Ed). 2005. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 274. 152 pp.
- Brander, K. M. 2007. The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. *ICES Journal of Marine Science*, 64: 211–217.
- Brander, K. M., and Mohn, R. K. 2004. Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1558–1564.
- Buch, E., Horsted, S. Å., and Hovgård, H. 1994. Fluctuations in the occurrence of cod in Greenland waters and their possible causes. *ICES Marine Science Symposia*, 198: 158–174.
- Campana, S. E. 1996. Year class strength and growth rate in young Atlantic cod (*Gadus morhua*). *Marine Ecology Progress Series*, 135: 21–26.
- Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J. C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine system. *Proceedings of the Royal Society of London, Series B*, 275: 1795–1801, doi:10.1098/rspb.2007.1752.
- Cheung, W. W. I., Lam, V. W. Y., and Pauly, D. 2008. Modelling present and climate-shifted distribution of marine fishes and invertebrates. *University of British Columbia Fisheries Centre Research Report*, 16(3). 72 pp.
- Christensen, J. H., Hewitson, B., Bueuloc, A., Chen, A., Gao, X., Held, I., Jones, R., *et al.* 2007. Chapter 11: Regional climate projections. *In Climate Change 2007: The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment of the*

- Intergovernmental Panel on Climate Change, pp. 847–940. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, *et al.* Cambridge University Press, Cambridge, UK. 996 pp.
- Clark, J. S. 2007. *Models for Ecological Data: An Introduction*. Princeton University Press, Princeton, NJ. 632 pp.
- Clark, R. A., Fox, C. J., Viner, D., and Livermore, M. 2003. North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biology*, 9: 1–12.
- Cooper, H., and Hedges, L. V. (Eds). 1994. *The Handbook of Research Synthesis*. Russell Sage Foundation, New York. 573 pp.
- Cushing, D. H. 1971. The dependence of recruitment on parent stock in different groups of fishes. *Journal du Conseil International pour l'Exploration de la Mer*, 33: 340–362.
- Cushing, D. H. 1974. The natural regulation of fish populations. *In Sea Fisheries Research*, pp. 399–412. Ed. by F. R. Harden Jones. Elek Science, London. 510 pp.
- Daewel, U., Peck, M. A., Kühn, W., St John, M. A., Alekseeva, I., and Schrum, C. 2008a. Coupling ecosystem and individual-based models to simulate the influence of climate variability on potential growth and survival of larval sprat (*Sprattus sprattus*) in the North Sea. *Fisheries Oceanography*, 17: 333–351.
- Daewel, U., Peck, M. A., Schrum, C., and St John, M. A. 2008b. How best to include the effects of climate-driven forcing on prey fields in larval fish individual based models. *Journal of Plankton Research*, 30: 1–5.
- Denman, K. L., and Peña, M. A. 2002. The response of two coupled 1-D mixed layer/planktonic ecosystem models to climate change in the NE Subarctic Pacific Ocean. *Deep-Sea Research Part II*, 49: 5739–5757.
- deYoung, B., and Rose, G. A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 2729–2741.
- Dickson, R. R., Briffa, K. R., and Osborn, T. J. 1994. Cod and climate: the spatial and temporal context. *ICES Marine Science Symposia*, 198, 280–286.
- Dippner, J. W. 2006. Future aspects in marine ecosystem modelling. *Journal of Marine Systems*, 61: 246–267.
- Döscher, R., and Meier, H. E. M. 2004. Simulated sea surface temperature and heat fluxes in different climates of the Baltic Sea. *Ambio*, 33: 242–248.
- Drinkwater, K. F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 62: 1327–1337.
- Drinkwater, K. F. 2006. The regime shift of the 1920s and 1930s in the North Atlantic. *Progress in Oceanography*, 68: 134–151.
- Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45: 1029–1039.
- Dutil, J. D., and Brander, K. M. 2003. Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production. *Fisheries Oceanography*, 12: 502–512.
- Eide, A. 2008. An integrated study of economic effects of and vulnerabilities to global warming on the Barents Sea cod fisheries. *Climatic Change*, 87: 251–262.
- Elizarov, A. A. 1963. On oceanographic conditions influencing year-class strength of commercially important species in the Northwest Atlantic. *Oceanologiya*, 3: 1065–1078 (In Russian).

- Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relations between temperature and survival of eggs and first feeding larvae of the North-East Arctic cod (*Gadus morhua* L.). *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 191: 209–219.
- Ellingsen, I. H., Dalpadado, P., Slagstad, D., and Loeng, H. 2008. Impact of climatic change on the biological production in the Barents Sea. *Climatic Change*, 87: 155–175.
- Engelhard, G. H. 2005. Catalogue of Defra historical catch and effort charts: six decades of detailed spatial statistics for British fisheries. Science Series Technical Report, Cefas, Lowestoft, No. 128. 42 pp.
- Enghoff, I. B., MacKenzie, B. R., and Nielsen, E. E. 2007. The Danish fish fauna during the warm Atlantic period (ca. 7000–3900 BC): forerunner of future changes? *Fisheries Research*, 87: 285–298.
- Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., and Huse, G. 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Marine Ecology Progress Series*, 347: 195–205.
- Fogarty, M., Incze, L., Hayhoe, K., Mountain, D., and Manning, J. 2007. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the northeastern USA. *Mitigation and Adaptation to Global Change*, 13: 453–466.
- Frank, K. T., Perry, R. I., and Drinkwater, K. F. 1990. Predicted response of Northwest Atlantic invertebrate and fish stocks to CO₂-induced climate change. *Transactions of the American Fisheries Society*, 119: 353–365.
- Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308: 1621–1623.
- Fulton, E. A., Smith, A. D. M., and Johnson, C. R. 2004. Effects of spatial resolution on the performance and interpretation of marine ecosystem models. *Ecological Modelling*, 176: 27–42.
- Gelman, A., and Hill, J. 2007. *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York. 648 pp.
- Gelman, A., Carlin, J. B., Stern, H. S., and Rubin, D. B. 1995. *Bayesian Data Analysis*. Chapman and Hall, London. 552 pp.
- Gordon, C., Cooper, C., Senior, C. A., Banks, H., Gregory, J. M., Johns, T. C., Mitchell, J. F. B., *et al.* 2000. The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, 16: 146–168.
- Göttel, H., Alexander, J., Keup-Thiel, E., Rechid, D., Hagemann, S., Blome, T., Wolf, A., *et al.* 2008. Influence of changed vegetation fields on regional climate simulations in the Barents Sea Region. *Climatic Change*, 87: 35–50, doi:10.1007/s10584-007-9341-5.
- Greenstreet, S. P. R., Spence, F. B., Shanks, A. M., and McMillan, J. A. 1999. Fishing effects in Northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. II. Trends in fishing effort in the North Sea by UK registered vessels landing in Scotland. *Fisheries Research*, 40: 107–124.
- Hampton, S. E., Scheuerell, M. D., and Schindler, D. E. 2006. Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. *Limnology and Oceanography*, 51: 2042–2051.
- Hare, S. R., and Mantua, N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47: 103–145.
- Heath, M. R. 2007. Responses of cod to climate change in the North Sea and implications for management. ICES Working Document (3 April 2007).

- Heath, M., and Gallego, A. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. *Journal of Fish Biology*, 51(Suppl. A): 1–29.
- Heath, M. R., and Lough, R. G. 2007. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fisheries Oceanography*, 16: 169–185.
- Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Bridson, J. 2004. Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using generalised additive models. *Fisheries Research*, 70: 17–25.
- Hegerl, G. C., Zwiers, F. W., Braconnot, P., Gillett, N. P., Luo, Y., Marengo Orsini, J. A., Nicholls, N., *et al.* 2007. Chapter 9: Understanding and attributing climate change. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment of the Intergovernmental Panel on Climate Change*, pp. 665–745. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, *et al.* Cambridge University Press, Cambridge, UK. 996 pp.
- Hilborn, R., and Liermann, M. 1998. Standing on the shoulders of giants: learning from experience. *Reviews in Fish Biology and Fisheries*, 8: 273–283.
- Hilborn, R., and Walters, C. J. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. Chapman and Hall, New York. 592 pp.
- Hinckley, S., Hermann, A., and Megrey, B. 1996. Development of spatially explicit, individual-based model of marine fish early life history. *Marine Ecology Progress Series*, 139: 47–68.
- Hjermann, D. O., Stenseth, N. C., and Ottersen, G. 2004. The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1747–1755.
- Hjermann, D. O., Bogstad, B., Eikeset, A. M., Ottersen, G., Gjøsæter, H., and Stenseth, N. C. 2007. Food web dynamics affect Northeast Arctic cod recruitment. *Proceedings of the Royal Society of London, Series B*, 274: 661–669.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 20: 1–228.
- Holden, M. J. 1981. The North Sea international 0-group gadoid surveys 1969–1978. ICES Cooperative Research Report No. 99. 73 pp.
- Holmes, S. J., and Wright, P. J. 2005. Regional variability in cod dynamics in the North Sea and West of Scotland and its implications to management. ICES Document CM 2005/AA:08.
- Holt, J. T., Allen, J. I., Proctor, R., and Gilbert, F. 2005. Error quantification of a high-resolution coupled hydrodynamic–ecosystem coastal–ocean model. Part 1: Model overview and assessment of the hydrodynamics. *Journal of Marine Systems*, 57: 167–188.
- Hovgård, H., and Wieland, K. 2008. Fishery and environmental aspects relevant for the emergence and decline of Atlantic cod (*Gadus morhua*) in West Greenland waters. In *Resilience of Gadoid Stocks to Fishing and Climate Change*, pp. 89–110. Ed. by G. H. Kruse, K. Drinkwater, J. N. Ianelli, J. S. Link, D. L. Stram, V. Wespestad, and D. Woody. Alaska Sea Grant College Program, University of Alaska Fairbanks, AK, AK-SG-08–01. 375 pp.
- Hugall, A., Moritz, C., Moussalli, A., and Stanisci, J. 2002. Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). *Proceedings of the National Academy of Science USA*, 99: 6112–6117.
- Hutchinson, W. F., Carvalho, G. R., and Rogers, S. I. 2001. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters as revealed by microsatellites. *Marine Ecology Progress Series*, 223: 251–260.

- ICES. 1990. Report of the ICES Study Group on Cod Stock Fluctuations. Cod and Climate Change (CCC), Framework for the Study of Global Ocean Ecosystem Dynamics. ICES Document CM 1990/G:50. 29 pp.
- ICES. 2006. Report of Working Group for Regional Ecosystem Description (WGRED), 30 January–3 February 2006. ICES Document CM 2006/ACE:03. 129 pp.
- ICES. 2007. Report of the Workshop on the Integration of Environmental Information into Fisheries Management Strategies and Advice (WKEFA), 18–22 June 2007. ICES Document CM 2007/ACFM:25. 182 pp.
- ICES. 2008a. Report of the Workshop on Cod and Future Climate Change (WKCFC), 17–20 June 2008. ICES Document CM 2008/OCC:09. 98 pp.
- ICES. 2008b. Cod in Subdivisions 25–32. *In* Report of the ICES Advisory Committee, 2008, pp. 56–68. ICES Advice, 2008. Book 8. 133 pp.
- ICES. 2008c. Report of the North-Western Working Group (NWWG), 21–29 April 2008. ICES Document CM 2008/ACOM:03. 604 pp.
- IPCC. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, *et al.* Cambridge University Press, Cambridge, UK. 881 pp.
- IPCC. 2007a. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, *et al.* Cambridge University Press, Cambridge, UK. 996 pp.
- IPCC. 2007b. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by M. Parry, O. Canziani, J. Palutikof, P. van der Linden, and C. Hanson. Cambridge University Press, Cambridge, UK. 976 pp.
- Ives, A. R. 1995. Predicting the response of populations to environmental change. *Ecology*, 76: 926–941.
- Ives, A. R., Carpenter, S. R., and Dennis, B. 1999. Community interaction webs and zooplankton responses to planktivory manipulations. *Ecology*, 80: 1405–1421.
- Ives, A. R., Dennis, B., Cottingham, K. L., and Carpenter, S. R. 2003. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, 73: 301–330.
- Jacob, D. 2001. A note to the simulation of the annual and inter-annual variability of the water budget over the Baltic Sea drainage basin. *Meteorological and Atmospheric Physics*, 77: 61–73.
- Jarre-Teichmann, A., Wieland, K., MacKenzie, B. R., Hinrichsen, H-H., Plikshs, M., and Aro, E. 2000. Stock-recruitment relationships for cod (*Gadus morhua callarias* L.) in the central Baltic Sea incorporating environmental variability. *Archive of Fishery and Marine Research*, 48: 97–123.
- Jennings, S., Alvsvåg, J., Cotter, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., *et al.* 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. *Fisheries Research*, 40: 125–134.
- Jensen, A. S. 1939. Concerning a change of climate during recent decades in the Arctic and Subarctic regions from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. *Det Kongelige Danske Videnskabelige Selskab, Biologiske Meddelelser*, 14: 1–77.

- Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semenov, V. A., Alekseev, G. V., Nagurnyi, A. P., *et al.* 2004. Arctic climate change: observed and modelled temperature and sea-ice variability. *Tellus*, 56A: 328–341.
- Keenlyside, N. S., Latif, M., Jungclauss, J., Kornblueh, L., and Roeckner, E. 2008. Advancing decadal-scale climate prediction in the North Atlantic sector. *Nature*, 453: 84–88.
- Kell, L. T., Pilling, G. M., and O'Brien, C. M. 2005. The implications of climate change for the management of North Sea cod (*Gadus morhua*). *ICES Journal of Marine Science*, 62: 1483–1491.
- Kjørboe, T., Munk, P., Richardson, K., Christensen, V., and Paulsen, H. 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Marine Ecology Progress Series*, 44: 205–219.
- Knight, J., Allan, R. J., Folland, C. K., Vellinga, M., and Mann, M. E. 2005. Natural variations in the thermohaline circulation and future surface temperature. *Geophysical Research Letters*, 32, L20708, doi: 10.2929/2005GL024233.
- Koslow, J. A., Brault, S., Dugas, J., Fournier, R. O., and Hughes, P. 1985. Condition of larval cod off southwest Nova Scotia in 1983 in relation to plankton abundance and temperature. *Marine Biology*, 86: 113–121.
- Köster, F. W., and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science*, 57: 310–323.
- Köster, F. W., Möllmann, C., Hinrichsen, H-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment—the impact of climate variability on key processes. *ICES Journal of Marine Science*, 62: 1408–1425.
- Kristiansen, T., Vikebø, F., Sundby, S., Huse, G., and Fiksen, Ø. 2009. Modeling growth of larval cod (*Gadus morhua*) in large-scale seasonal and latitudinal environmental gradients. *Deep-Sea Research Part II*, 56: 2001–2011.
- Kühn, W., Peck, M. A., Hinrichsen, H-H., Daewel, U., Moll, A., Pohlmann, T., Stegert, C., *et al.* 2008. Defining habitats suitable for larval fish in the German Bight (southern North Sea): an IBM approach using spatially- and temporally-resolved, size-structured prey fields. *Journal of Marine Systems*, 74: 329–342.
- Lees, K., Pitois, S., Scott, C., Frid, C., and Mackinson, S. 2006. Characterizing regime shifts in the marine environment. *Fish and Fisheries*, 7: 104–127.
- Legendre, P., and Legendre, L. 1998. *Numerical Ecology*, 2nd edn (English). Elsevier Science BV, Amsterdam. 853 pp.
- Leggett, W. C., and DeBlois, E. 1994. Recruitment in marine fishes: is it regulated by starvation or predation in the egg and larval stages? *Netherlands Journal of Sea Research*, 32: 119–134.
- Letcher, B. H., Rice, J. A., Crowder, L. B., and Rose, K. A. 1996. Variability in survival of larval fish: disentangling components with a generalized individual-based model. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 787–801.
- Levitus, S., Antonov, J. I., Boyer, T. P., and Stephens, C. 2005. Warming of the world ocean. *Science*, 287: 2225–2229.
- Lilly, G. R., Wieland, K., Rothschild, B. J., Sundby, S., Drinkwater, K. F., Brander, K. M., Ottersen, G., *et al.* 2008. Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic. *In Resilience of Gadoid Stocks to Fishing and Climate Change*, pp. 39–66. Ed. by G. H. Kruse, K. Drinkwater, J. N. Ianelli, J. S. Link, D. L. Stram, V. Wespestad, and D. Woody. Alaska Sea Grant College Program, University of Alaska Fairbanks, AK, AK-SG-08-01. 375 pp.

- Lindegren, M., Möllmann, C., Nielsen, A., and Stenseth, N. C. 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences*, 106: 14722–14727.
- Lindegren, M., Möllmann, C., Nielsen, A., Brander, K., MacKenzie, B., and Stenseth, N. C. 2010. Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal Society of London, Series B*, 277: 2121–2130, doi:10.1098/rspb.2010.0353.
- Lochmann, S. E., Taggart, C. T., Griffin, D. A., Thompson, K. R., and Maillet, G. L. 1997. Abundance and condition of larval cod (*Gadus morhua*) at a convergent front on Western Bank, Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1461–1479.
- Loeng, H., Brander, K., Carmack, E., Denisenko, S., Drinkwater, K., Hansen, B., Kovacs, K., *et al.* 2005. Chapter 8: Marine systems. p. 451–538. *In Arctic Climate Impact Assessment*. Cambridge University Press, New York. 1042 pp.
- Lough, R. G., Buckley, L. J., Werner, F. E., Quinlan, J. A., and Edwards, K. P. 2005. A general biophysical model of larval cod (*Gadus morhua*) growth applied to populations on Georges Bank. *Fisheries Oceanography*, 14: 241–262.
- MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate: sprat in the Baltic Sea. *Ecology*, 85: 784–794.
- MacKenzie, B. R., and Schiedek, D. 2007a. Daily ocean monitoring since the 1860s shows unprecedented warming of northern European seas. *Global Change Biology*, 13: 1335–1347.
- MacKenzie, B. R., and Schiedek, D. 2007b. Long-term sea surface temperature baselines – time series, spatial covariation and implications for biological processes. *Journal of Marine Systems*, 68: 405–420.
- MacKenzie, B. R., Miller, T. J., Cyr, S., and Leggett, W. C. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography*, 39: 1790–1799.
- MacKenzie, B. R., St John, M. A., and Wieland, K. 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. *Marine Ecology Progress Series*, 134: 265–281.
- MacKenzie, B. R., Myers, R. A., and Bowen, K. G. 2003. Spawner–recruit relationships and fish stock carrying capacity in aquatic ecosystems. *Marine Ecology Progress Series*, 248: 209–220.
- MacKenzie, B. R., Gislason, H., Möllmann, C., and Köster, F. W. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biology*, 13: 1348–1367.
- Marasco, R. J., Goodman, D., Grimes, C. B., Lawson, P. W., Punt, A. E., and Quinn, T. J. 2007. Ecosystem-based fisheries management: some practical suggestions. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 928–939.
- Matthäus, W., and Schinke, H. 1994. Mean atmospheric circulation patterns associated with major Baltic inflows. *Deutsche Hydrographische Zeitschrift*, 46: 321–339.
- Megrey, B. A., and Hinckley, S. 2001. The effect of turbulence on feeding of larval fishes: a sensitivity analysis using an individual-based model. *ICES Journal of Marine Science*, 58: 1015–1029.
- Megrey, B. A., Rose, K. A., Klumb, R. A., Hay, D. E., Werner, F. E., Eslinger, D. L., and Smith, S. L. 2007. A bioenergetics-based population dynamics model of Pacific herring (*Clupea harengus pallasii*) coupled to a lower trophic level nutrient–phytoplankton–zooplankton model: description, calibration and sensitivity analysis. *Ecological Modelling*, 202: 144–164.

- Meehl, G. A., Stocker, T. F., Colline, W. D., Friedlingstein, P., Gaye, A. T., Gregory, J. M., Kitoh, A., *et al.* 2007. Chapter 10: Global climate projections. *In* Climate Change 2007: The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment of the Intergovernmental Panel on Climate Change, pp. 747–845. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, *et al.* Cambridge University Press, Cambridge, UK. 996 pp.
- Meier, H. E. M., Broman, B., and Kjellström, E. 2004. Simulated sea level in past and future climates of the Baltic Sea. *Climate Research*, 27: 59–75.
- Meier, H. E. M., Kjellström, E., and Graham, L. P. 2006. Estimating uncertainties of projected Baltic Sea salinity in the late 21st century. *Geophysical Research Letters*, 33: L15705, doi:10.1029/2006GL026488.
- Miller, R. L., Schmidt, G. A., and Shindell, D. T. 2006. Forced variations of annular modes in the 20th century IPCC AR4 simulations. *Journal of Geophysical Research*, 111, D18101, doi:10.1029/2005JD006323.
- Möllmann, C., Köster, F. W., Kornilovs, G., and Sidrevics, L. 2003. Interannual variability in population dynamics of calanoid copepods in the central Baltic Sea. *ICES Marine Science Symposia*, 219: 220–230.
- Möllmann, C., Müller-Karulis, B., Kornilovs, G., and St John, M. A. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES Journal of Marine Science*, 65: 302–310.
- Munk, P. 1997. Prey size spectra and prey availability of larval and small juvenile cod. *Journal of Fish Biology*, 51(Suppl. A): 340–351.
- Munk, P. 2007. Cross-frontal variation in growth rate and prey availability of larval North Sea cod *Gadus morhua*. *Marine Ecology Progress Series*, 334: 225–235.
- Munk, P., and Nielsen, T. G. 1994. Trophodynamics of the plankton community at Dogger Bank: predatory impact by larval fish. *Journal of Plankton Research*, 16: 1225–1245.
- Myers, R. A. 1998. When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8: 1–21.
- Myers, R. A. 2001. Stock and recruitment: generalisations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science*, 58: 937–951.
- Myers, R. A. 2002. Recruitment: understanding density-dependence in fish populations. *In* Handbook of Fish Biology and Fisheries, 1: Fish Biology, pp. 123–148. Ed. by P. J. B. Hart and J. D. Reynolds. Blackwell Publishing, Malden, MA. 424 pp.
- Myers, R. A., and Barrowman, N. J. 1996. Is fish recruitment related to spawners abundance? *Fishery Bulletin US*, 94: 707–724.
- Myers, R. A., and Mertz, G. 1998. Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations; a synthesis. *Fisheries Research*, 37: 51–60.
- Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series*, 138: 293–308.
- Myers, R. A., MacKenzie, B. R., Bowen, K. G., and Barrowman, N. J. 2001. What is the carrying capacity of fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1464–1476.
- Myers, R. A., Barrowman, N. J., Hilborn, R., and Kehler, D. G. 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. *North American Journal of Fisheries Management*, 22: 351–364.

- Nakken, O., and Raknes, A. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978–1984. *Fisheries Research*, 5: 243–252.
- Neat, F., and Righton, D. 2007. Warm water occupancy by North Sea cod. *Proceedings of the Royal Society of London, Series B*, 274: 789–798.
- Neumann, T. X. 2000. Towards a 3-D ecosystem model of the Baltic Sea. *Journal of Marine Systems*, 25: 405–419.
- Nielsen, E. E., Hansen, M. M., Schmidt, C., Meldrup, D., and Grønkjær, P. 2001. Genetic differences among cod populations. *Nature*, 413: 272.
- Nielsen, E. E., Hansen, M. M., Ruzzante, D. E., Meldrup, D., and Grønkjær, P. 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology*, 12: 1497–1508.
- Nissling, A. 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. *Hydrobiologia*, 514: 115–123.
- Nissling, A., and Westin, L. 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. *Marine Ecology Progress Series*, 152: 261–271.
- Nissling, A., Kryvi, H., and Vallin, L. 1994. Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. *Marine Ecology Progress Series*, 110: 67–74.
- Ottersen, G. 1996. Environmental impact on variability in recruitment, larval growth and distribution of Arcto-Norwegian cod. PhD Thesis, University of Bergen, Norway.
- Ottersen, G., and Loeng, H. 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock and herring: the environmental link. *ICES Journal of Marine Science*, 57: 339–348.
- Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. *Fisheries Oceanography*, 4: 278–292.
- Ottersen, G., Michalsen, K., and Nakken, O. 1998. Ambient temperature and distribution of North-east Arctic cod. *ICES Journal of Marine Science*, 55: 67–85.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia*, 128: 1–14.
- Paine, R. T. 1980. Food webs – linkage, interaction strength and community infrastructure – the 3rd Tansley Lecture. *Journal of Animal Ecology*, 49: 667–685.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer*, 39: 175–193.
- Pepin, P., Orr, D., and Anderson, J. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 54(Suppl. 1): 2–10.
- Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. *Science*, 308: 1912–1915.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. *Science*, 305: 346–347.
- Planque, B., and Fox, C. J. 1998. Interannual variability in temperature and the recruitment of Irish Sea cod. *Marine Ecology Progress Series*, 172: 101–105.
- Planque, B. and Frédou, T. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2069–2077.

- Plikshs, M., Kalejs, M., and Grauman, G. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES Document CM 1993/J:22.
- Punt, A. E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries*, 7: 35–63.
- Randall, D. A., Wood, R. A., Bony, S., Colman, R., Fichfet, T., Fyfe, J., Kattsov, V., *et al.* 2007. Chapter 8: Climate models and their evaluations. *In Climate Change 2007: The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment of the Intergovernmental Panel on Climate Change*, pp. 589–662. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, *et al.* Cambridge University Press, Cambridge, UK. 996 pp.
- Reid, P. C., Borges, M. D., and Svendsen, E. 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research*, 50: 163–171.
- Ribergaard, M. H. 2006. Oceanographic observations off West Greenland 2005. Northwest Atlantic Fisheries Organization Scientific Council Research Document 06/001. 36 pp.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11: 559–623.
- Rindorf, A., and Lewy, P. 2006. Warm, windy winters drive cod north and homing of spawners keeps them there. *Journal of Applied Ecology*, 43: 445–453.
- Rindorf, A., Jensen, H., and Schrum, C. 2008. Growth, temperature, and density relationships of North Sea cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 456–470.
- Ripa, J., and Ives, A. R. 2003. Food web dynamics in correlated and autocorrelated environments. *Theoretical Population Biology*, 64: 369–384.
- Ripa, J., and Lundberg, P. 1996. Noise colour and the risk of population extinctions. *Proceedings of the Royal Society of London, Series B*, 263: 1751–1753.
- Rodionov, S. 1995. Atmospheric teleconnections and coherent fluctuations in recruitment to North Atlantic cod (*Gadus morhua*) stocks. *In Climate Change and Northern Fish Populations*, pp. 45–55. Ed. by R. J. Beamish. Canadian Special Publication on Fisheries and Aquatic Sciences, 121.
- Rogers, J. 1985. Atmospheric circulation changes associated with the warming over the northern North Atlantic in the 1920s. *Journal of Climate and Applied Meteorology*, 24: 1303–1310.
- Rothschild, B. J. 2007. Coherence of Atlantic cod stock dynamics in the Northwest Atlantic Ocean. *Transactions of the American Fisheries Society*, 136: 858–874.
- Rothschild, B. J., and Mullen, A. J. 1985. The information-content of stock-and-recruitment data and its nonparametric classification. *Journal du Conseil International pour l'Exploration de la Mer*, 42: 116–124.
- Royama, T. 1992. *Analytical Population Dynamics*. Chapman and Hall, London. 392 pp.
- Ruzzante, D. E., Taggart, C. T., Doyle, R. W., and Cook, D. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. *Conservation Genetics*, 2: 257–269.
- Sætersdal, G., and Loeng, H. 1987. Ecological adaptation of reproduction in Northeast Arctic cod. *Fisheries Research*, 5: 253–270.
- Sandeman, L. R., Yaragina, N. A., and Marshall, C. T. 2008. Factors contributing to inter- and intra-annual variation in condition of cod *Gadus morhua* in the Barents Sea. *Journal of Animal Ecology*, 77: 725–734.

- Schinke, H., and Matthäus, W. 1998. On the causes of major Baltic inflows – an analysis of long time series. *Continental Shelf Research*, 18: 67–97.
- Schrum, C., Hübner, U., and Janssen, F. 2000. Recent climate modelling in North Sea and the Baltic Sea. Part A: model description and validation. *Berichte des Zentrums Meeres- und Klimaforschung, Reihe B*, 37. 59 pp.
- Schrum, C., Alekseeva, I., and St John, M. 2006a. ECOSMO, a coupled ecosystem model of the North Sea and Baltic Sea. Part I: Model description and simulation of annual characteristics in the North Sea. *Journal of Marine Systems*, 61: 79–99.
- Schrum, C., Alekseeva, I., and St John, M. 2006b. ECOSMO, a coupled ecosystem model of the North Sea and Baltic Sea. Part II. Spatial seasonal characteristics in the North Sea as revealed by EOF analysis. *Journal of Marine Systems*, 61: 100–113.
- Sclafani, M., Taggart, C. T., and Thompson, K. R. 1993. Condition, buoyancy and the distribution of larval fish, implication for vertical migration and retention. *Journal of Plankton Research*, 1514: 413–435.
- Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R. K., and Duplisea, D. E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 235–238.
- Sinclair, A. F. 1996. Recent declines in cod species stocks in the Northwest Atlantic. *Northwest Atlantic Fisheries Organization Scientific Council Studies*, 24: 41–52.
- Skogen, M. D., and Moll, A. 2005. Importance of ocean circulation in ecological modelling: an example from the North Sea. *Journal of Marine Systems*, 57: 289–300.
- Skogen, M. D., Svendsen, E., Berntsen, D. A., Aksne, D., and Ulvestad, K. B. 1995. Modelling the primary production in the North Sea using a coupled three-dimensional physical–chemical–biological model. *Estuarine, Coastal and Shelf Science*, 41: 545–565.
- Slagstad, D., and McClimans, T. A. 2005. Modeling the ecosystem dynamics of the Barents Sea including the marginal ice zone. I. Physical and chemical oceanography. *Journal of Marine Systems*, 58: 1–18.
- Smith, D. M., and Murphy, J. M. 2007. An objective ocean temperature and salinity analysis using covariances from a global climate model. *Journal of Geophysical Research*, 112: C02022, doi:10.1029/2005JC003172.
- Smith, D. M., Cusack, S., Colman, A. W., Folland, C. K., Harris, G. R., and Murphy, J. M. 2007. Improved surface temperature prediction for the coming decade from a global climate model. *Science*, 317: 796–799, doi:10.1126/science.1139540.
- Sohlenius, G., Emeis, K-C., Andrén, E., Andrén, T., and Kohly, A. 2001. Development of anoxia during the Holocene fresh-brackish water transition in the Baltic Sea. *Marine Geology*, 177: 221–242.
- Steele, J. H., and Henderson, E. W. 1984. Modeling long-term fluctuations in fish stocks. *Science*, 224: 985–987.
- Stenevik, E. K., and Sundby, S. 2007. Impacts of climate change on commercial fish stocks in Norwegian waters. *Marine Policy*, 31: 19–31.
- Stenseth, N. C., Bjørnstad, O. N., and Saitoh, T. 1996. A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of the Royal Society of London, Series B*, 263: 1117–1126.
- Stiansen, J. E., Bogstad, B., Budgell, P., Dalpadado, P., Gjørseter, H., Hiis Hauge, K., Ingvaldsen, R., et al. 2005. Status Report on the Barents Sea Ecosystem, 2004–2005. *Fisken og Havet*, 3-2005, Technical Report Series. Institute of Marine Research, Bergen.
- Stige, L. C., Ottersen, G., Brander, K. M., Chan, K-S., and Stenseth, N. C. 2006. Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Marine Ecology Progress Series*, 325: 227–241.

- Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, 85: 277–298.
- Sundby, S., and Drinkwater, K. 2007. On the mechanisms behind salinity anomaly signals of the northern North Atlantic. *Progress in Oceanography*, 73: 190–202.
- Sundby, S., and Nakken, O. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, 65: 953–962.
- Sutton, R. T., and Hodson, D. L. R. 2005. Atlantic Ocean forcing of North American and European summer climate. *Science*, 309: 115–118.
- Svendsen, E., Aglen, A., Iversen, S. A., Skagen, D. W., and Smedstad, O. 1995. Influence of climate on recruitment and migration of fish stocks in the North Sea. *In Climate Change and Northern Fish Populations*, pp. 641–653. Ed. by R. J. Beamish. Canadian Special Publication on Fisheries and Aquatic Sciences, 121.
- Tåning, A. V. 1953. Long term changes in hydrography and fluctuations in fish stocks. *Annual Proceedings of the International Commission for the Northwest Atlantic Fisheries*, 3: 69–77.
- Uppala, S. M., Kallberg, P. W., Simmons, A. J., Andrae, U., Bechtold, V. D., Fiorino, M., Gibson, J. K., *et al.* 2005. The ERA-40 re-analysis. *Quarterly Journal of the Royal Meteorological Society*, 131: 2961–3012.
- Vallin, L., Nissling, A., and Westin, L. 1999. Potential factors influencing reproductive success of Baltic cod, *Gadus morhua*: a review. *Ambio*, 28: 92–99.
- Vikebø, F. B., Sundby, S., Ådlandsvik, B., and Otterå, O. H. 2007a. Impacts of a reduced thermohaline circulation on transport and growth of larvae and pelagic juveniles of Arcto-Norwegian cod (*Gadus morhua*). *Fisheries Oceanography*, 16: 216–228.
- Vikebø, F. B., Jørgensen, C., Kristiansen, T., and Fiksen, Ø. 2007b. Drift, growth and survival of larval Northeast Arctic cod with simple rules of behaviour. *Marine Ecology Progress Series*, 347: 207–219.
- Vilhjálmsson, H. 1997. Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. *Rit Fiskideildar*, 15: 7–29.
- Vinther, B. M., Andersen, K. K., Jones, P. D., Briffa, K. R., and Cappelen, J. 2006. Extending Greenland temperature records into the late eighteenth century. *Journal of Geophysical Research*, 111: D11105. 13 pp.
- Wassmann, P., Slagstad, D., Riser, C. W., and Reigstad, M., 2006. Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone. II. Carbon flux and interannual variability. *Journal of Marine Systems*, 59: 1–24.
- Werner, F., Page, F., Lynch, D., Loder, J., Lough, R., Perry, R., Greenberg, D., *et al.* 1993. Influence of mean 3-d advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. *Fisheries Oceanography*, 2: 43–64.
- Werner, F. E., Perry, R. I., Lough, R. G., and Naimie, C. E. 1996. Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep-Sea Research Part II*, 43: 1793–1822.
- Werner, F., Quinlan, J., Lough, R., and Lynch, D. 2001. Spatially explicit individual based modeling of marine populations: a review of the advances in 1990s. *Sarsia*, 86: 411–421.
- Wieland, K., Waller, U., and Schnack, D. 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana*, 10: 163–177.

Wright, P. J., Neat, F. C., Gibb, F. M., and Gibb, I. M. 2006. Evidence for metapopulation substructuring in cod from the West of Scotland and North Sea. *Journal of Fish Biology*, 69(Suppl. C): 181–199.

Appendix 1: Extended abstracts of presentations

A1.1 Decadal simulations at the Met Office Hadley Centre

Holger Pohlmann

This extended abstract summarizes results from the Decadal Climate Prediction System (DePreSys), which is described in more detail in Smith *et al.* (2007). The skill of decadal predictions is examined using the DePreSys, which is based on the Hadley Centre Coupled Model, version 3 (HadCM3; Gordon *et al.*, 2000), a dynamic global climate model (GCM). Initial conditions are generated by applying HadCM3, relaxing oceanic temperature and salinity, and atmospheric horizontal winds, temperature, and surface pressure, to analyses of observations. The ocean analyses (Smith and Murphy, 2007) are created by a four-dimensional, multivariate optimal interpolation technique. The DePreSys is designed to avoid trends during forecasts caused by systematic model errors. This is achieved by assimilating the observed anomalies added to the model climatology and removing the model climatology to produce forecast anomalies. The accuracy of DePreSys is assessed in a set of ten-year hindcasts (forecasts made retrospectively using only data that would have been available at that time), starting from the first day of March, June, September, and December from 1982 to 2001.

The impact of initial condition information is assessed by comparing DePreSys against an additional hindcast set (hereafter referred to as NoAssim), which is identical with DePreSys but does not assimilate the observed state of the atmosphere or ocean. The global annual mean surface temperature and heat content of the upper (113 m) ocean are predicted with significantly more skill by DePreSys than by NoAssim throughout the range of the hindcasts. The increased skill of DePreSys over NoAssim results from an improved ability to predict *El Niño* for the first 15–18 months and, thereafter, mainly from initializing the low-frequency variability of the oceanic heat content. Regional improvements in surface temperature are found in many regions. Much of the regional improvement in DePreSys relative to NoAssim is coincident with improvements in upper ocean heat content.

Once the predictive skill of DePreSys has been established, climate forecasts for the decade starting in 2005 are analysed. The DePreSys forecast is closer to the verified changes observed since the forecast start date. Both NoAssim and DePreSys, however, predicted further warming during the coming decade, with the year 2014 predicted to be $0.30 \pm 0.21^\circ\text{C}$ (5–95% confidence interval) warmer than the observed value for 2004. Furthermore, at least half of the years after 2009 are predicted to be warmer than 1998, the warmest year currently on record. In the DePreSys forecast, internal variability offsets the effects of anthropogenic forcing in the first few years, leading to no net warming before 2008. In contrast, the NoAssim forecast predicted warming during this period. An updated forecast, starting in 2007 and extending over a period of 30 years, confirms these findings, with DePreSys global annual mean temperature being cooler than NoAssim over the coming decade. However, the Atlantic meridional overturning circulation is stronger in DePreSys than in NoAssim for the whole 30-year period, with associated increased warming in the North Atlantic. Regional improvements are demonstrated in terms of the surface temperature of the North and Baltic seas. Especially for the Baltic Sea, initial errors which are present in the NoAssim experiment are removed in the DePreSys, allowing the forecasts to start from the observed state (Figure A1). However, analysing climate

changes in terms of the annual means can hide the effect that the temperature increase will be greater in summer than in winter (Figure A2).

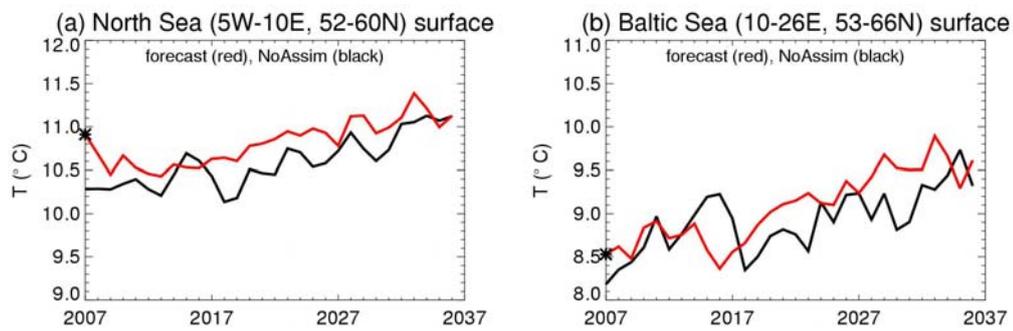


Figure A1. Surface temperature of (a) the North Sea and (b) the Baltic Sea for the forecast (red) and NoAssim (black) experiments. The forecast starts (per definition) from the observed values.

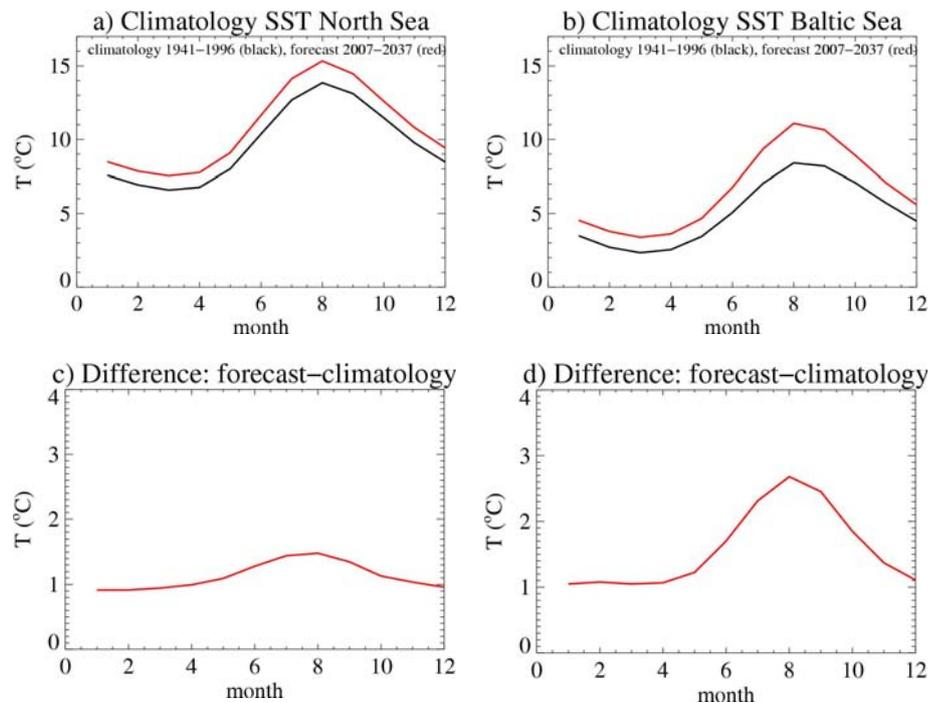


Figure A2. Surface temperature climatology of (a) the North Sea and (b) the Baltic Sea average over the period 1941–1996 from a 20th-century experiment (black) and 2007–2037 from the forecast experiment (red), together with the differences (forecasted temperature anomalies) of the time-series for (c) the North Sea and (d) the Baltic Sea.

A1.2 Challenges in modelling regional climate change: uncertainties and predictability

Corinna Schrum

The presentation focused on three related aspects: (i) interpretation of IPCC climate scenarios, predictions vs. projections; (ii) evaluation of uncertainties of climate model projections based on their skill in modelling present-day climate and on the model spread of future projections; and (iii) discussion of some aspects of regional climate projections, including the lack of regional scenarios.

The following conclusions relevant to the WKCFCC's terms of reference were presented.

- Uncertainty resulting from global, regional, and biological models is larger than the expected signal resulting from climate change models.
- Available regional scenarios are largely based on the third IPCC report (IPCC, 2001) and are likely to be out of date.
- Only a few regional climate models (RCMs) employ more than one general circulation model (GCM) and perform ensembles.
- IPCC scenario-model projections (and consequently the RCMs based on these) are only of limited use for regional climate-change assessment.
- It may be possible to learn more while performing controlled sensitivity tests with validated regional models.
- Decadal-scale predictions from GCMs might provide improved forcing data, but performance declines significantly after approximately one decade.
- Decadal-scale predictions demonstrate improvements in modelling the AMO, but NAO variability is still not modelled sufficiently well in these models.

The establishment of regional predictions based on global decadal prediction systems is faced with several practical problems. Regional model predictions with coupled physical and biological models for North Atlantic waters are as resource-demanding as global climate models; hence, we have to accept a delay in obtaining regional predictions. In addition, regional climate projections are still a matter for research; many aspects and problems relevant to regional downscaling are not yet solved, and a significant international research effort is necessary to improve the situation.

A1.3 Response of larval cod to environmental changes: scenario modelling in the North Sea

Ute Daewel, Irina Alekseeva, Myron Peck, and Corinna Schrum

The dynamics of an ecosystem depend on the complex interplay of a number of different factors, and not only biotic (e.g. prey, predators), but also abiotic (hydrodynamic, meteorological) and anthropogenic factors need to be considered. In order to disentangle the impact of different processes affecting cod (*Gadus morhua*) eggs and larvae in the North Sea, we developed and utilized a three-dimensional interlinked model system (Daewel *et al.*, 2008a; Schrum *et al.*, 2006a, 2006b). Based on a three-dimensional hydrodynamic model, two model systems were applied in order to assess (i) the processes important for larval cod survival; and (ii) variability and interactions between environmental factors (Figure A3).

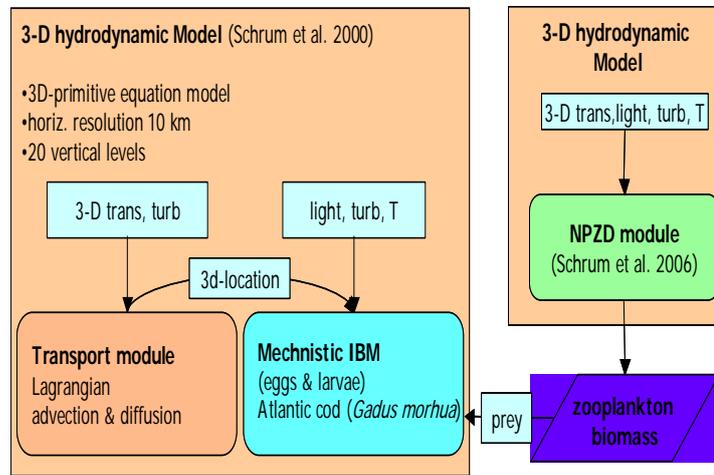


Figure A3. Schematic diagram of the coupled model system to simulate cod eggs and larvae. Left panel: online coupling of hydrodynamic Lagrangian transport model and mechanistic IBM; right panel: coupled hydrodynamic-NPZD model (Schrum *et al.*, 2000, 2006a) providing prey for the IBM (Daewel *et al.*, 2008a, 2008b).

Three types of experiments were performed in order to investigate a number of processes affecting larval survival:

- 1) assessment of interannual differences using the fully coupled model system;
- 2) assessment of changes in environmental variables and prey biomass, applying the changes separately to only the IBM part of the coupled model system;
- 3) assessment of changes in environmental variables affecting lower trophic-level production, applying the changes only to the coupled nutrient-phytoplankton-zooplankton-detritus (NPZD) part of the model system.

For the first set of experiments, four climatically different years (cold, 1986 and 1996; median, 1992; warm, 1990) were chosen, and potential larval survival was calculated based on prey fields obtained from the NPZD module for the relevant year.

The second set of experiments was designed to investigate single environmental factors on cod larval survival by separately changing three parameters of environmental forcing: (i) $T_{\text{air}} \pm 1$ and $\pm 2^\circ\text{C}$; (ii) west wind +30%; and (iii) prey biomass $\pm 20\%$, based on calculations for the intermediate year (1992).

The third set of experiments dealt with interrelationships between environmental factors and was applied only to the ecosystem model (ECOSMO). Again, air temperature (T) and west-windforcing were increased: (i) $T_{\text{air}} \pm 2^\circ\text{C}$; (ii) west wind +30%).

The results from the first set of experiments demonstrated a strong relationship between recent larval survival and winter water temperature year, indicating water temperature to be a major factor in determining recruitment. Two basic internal processes of the IBM are affected by temperature: (i) the duration of the non-feeding phase, and (ii) metabolism. Associated with these are the responses of larval survival and growth to changes in temperature and prey biomass. A scenario with increased air temperature indicated the importance of these processes to interannual variability.

In the second set of experiments, the results from the temperature scenario (Figure A4) demonstrated that, even if survival is related to temperature, the temperature dependence of fish vital rates is not the dominant process, explaining the high correlation of natural variability in modelled potential survival.

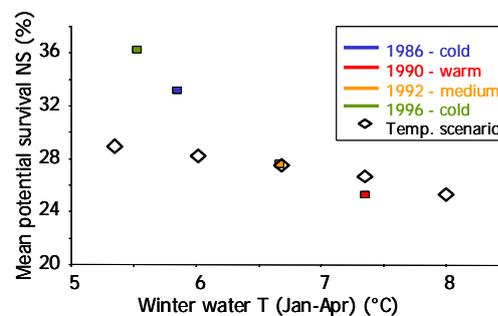


Figure A4. North Sea averaged potential survival calculated by the coupled model system vs. mean winter (January–April) water temperature. Colours = model calculations for four years; diamonds = temperature scenario tests for 1992.

The two other scenarios tested with the IBM resulted in similarly important changes in larval fish survival relative to changes in west wind as well as zooplankton biomass.

The results from the third set of experiments indicate that strong interrelationships among the environmental factors contribute to the strong temperature relationship modelled for the simulated years. Although a relationship between temperature and west wind has already been reported for the North Sea in combination with changes in the NAO index, the scenarios also calculated an earlier start of the zooplankton bloom with increasing west wind. In contrast, an increase in air temperature did not significantly affect the calculated zooplankton production.

In conclusion, the results point to complex ecosystem dynamics affecting larval fish survival in the North Sea. We can confidently state that any correlation with temperature is not necessarily the result of a single temperature-dependent process; instead, temperature may be acting as a “proxy” for a combination of interrelated processes.

A1.4 The future of Baltic cod: modelling interactions between climate, foodweb dynamics, and fisheries

Martin Lindegren

Atlantic cod (*Gadus morhua*) is one of the most commercially important fish species in the North Atlantic and has been subjected to excessive fishing pressure for many years (Brander, 2007). Partly because of overfishing, many of the stocks have declined dramatically and are now at historically low levels (Myers *et al.*, 1996; Lilly *et al.*, 2008). Additionally, climate variability has influenced cod stocks, principally through effects on recruitment (Brander and Mohn, 2004; Stige *et al.*, 2006), but also through effects on growth (Brander, 1995, 2007). The climate effect generally works through a suite of different physical and biological processes, mainly related to effects of temperature, salinity, oxygen, turbulence, and advection (Ottersen *et al.*, 2001).

In several areas, the collapses of Atlantic cod stocks were major drivers of large-scale reorganizations of ecosystems (Frank *et al.*, 2005). These so-called “regime shifts” are frequently caused by climatic changes (Hare and Mantua, 2000; Beaugrand *et al.*, 2001; Reid *et al.*, 2001; Alheit *et al.*, 2005) or by overexploitation resulting in cascading trophic interactions (Frank *et al.*, 2005; Lees *et al.*, 2006). Such changes in ecosystem structure will necessarily affect species interactions, eventually influencing foodweb dynamics (Paine, 1980) by producing positive and negative feedback loops that determine the ultimate response of populations to environmental changes (Ives, 1995; Bakun and Weeks, 2006). The recognition of this ecosystem context of the collapse of fish stocks has led to the development of more holistic ecosystem-based fishery management (EBFM) approaches. EBFM considers both the effects of fishing on foodwebs and the effects of physical oceanic conditions on ecosystems and, hence, fish stock dynamics (Pikitch *et al.*, 2004; Marasco *et al.*, 2007).

Multivariate autoregressive models (MAR(1)) provide a framework for modelling foodweb interactions at multiple trophic levels (Ives *et al.*, 1995, 1999, 2003). Within the MAR(1) framework, external forcing by climate variability and commercial fishing may be included as covariates (Ives, 1995; Ripa and Ives, 2003). Because MAR modelling can integrate internal foodweb dynamics and external forcing, it has the potential to serve as an important tool in modern EBFM. Surprisingly, its applications have remained largely theoretical and have seldom been extended to real foodwebs (Ives *et al.*, 1999; Hampton *et al.*, 2006).

By statistically fitting a MAR(1) model to time-series data from the Baltic Sea, we developed a fishing- and climate-driven multispecies model for the Baltic Sea (Lindegren *et al.*, 2009) that was able to accurately recreate the past dynamics of Baltic cod (*Gadus morhua*), sprat (*Sprattus sprattus*), and herring (*Clupea harengus*; Figure A5). Based on the findings of “The Assessment of Climate Change for the Baltic Sea Basin” (BACC, 2007), we used a simple climate model (Ripa and Lundberg, 1996) to simulate plausible climate scenarios for the 21st century. Taking into account that marine climate is “red-shifted” (i.e. positively autocorrelated; Steele and Henderson, 1984), we generated “red-shifted” time-series of spring sea surface temperature (SST) and summer salinity based on actual data for 1974–2004. To mimic the predicted increase in SST of 3.5°C and a salinity decrease of 0.8 or 5.5 psu, a gradual trend in the mean over 100 consecutive years was applied.

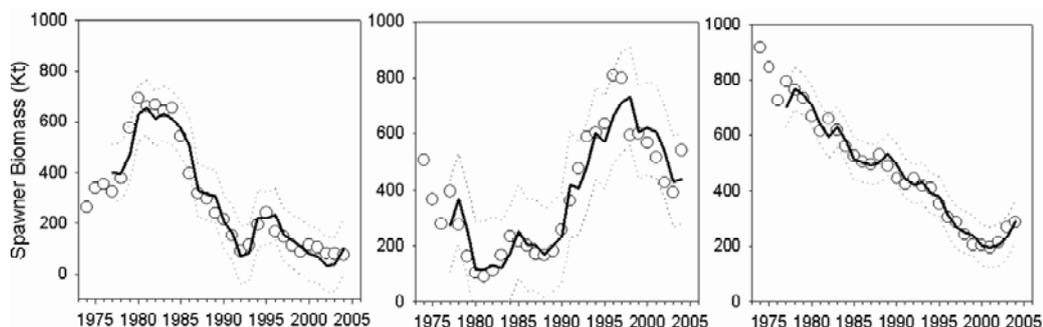


Figure A5. Development of Baltic cod, sprat, and herring fish populations. Observed (circles) and fitted spawning-stock biomass (SSB) values (black line) for (left) cod, (middle) sprat, and (right) herring for 1974–2004. Upper and lower 95% prediction intervals are displayed by dotted lines.

Using these scenarios as inputs, we forced our foodweb model bottom–up, exploring the impact of climate change on the future dynamics of Baltic cod (Lindegren *et al.*, 2010). Further, by including different fishing scenarios for Baltic cod, we elaborated on the role of management in relation to climate change. Running a vast number of stochastic simulations for combinations of climate and fishing mortalities, the probability of the stock falling below the limiting stock size (B_{lim}) of 160 000 t was computed (Figure A6). Model runs demonstrate that, given even a relatively weak decrease in salinity (>3 psu), thus impairing recruitment of Baltic cod through increased egg and larvae mortality (Nissling, 2004; Köster *et al.*, 2005), only a drastic decrease in fishing mortality could avoid future stock collapses and ensure the existence of Baltic cod for future generations.

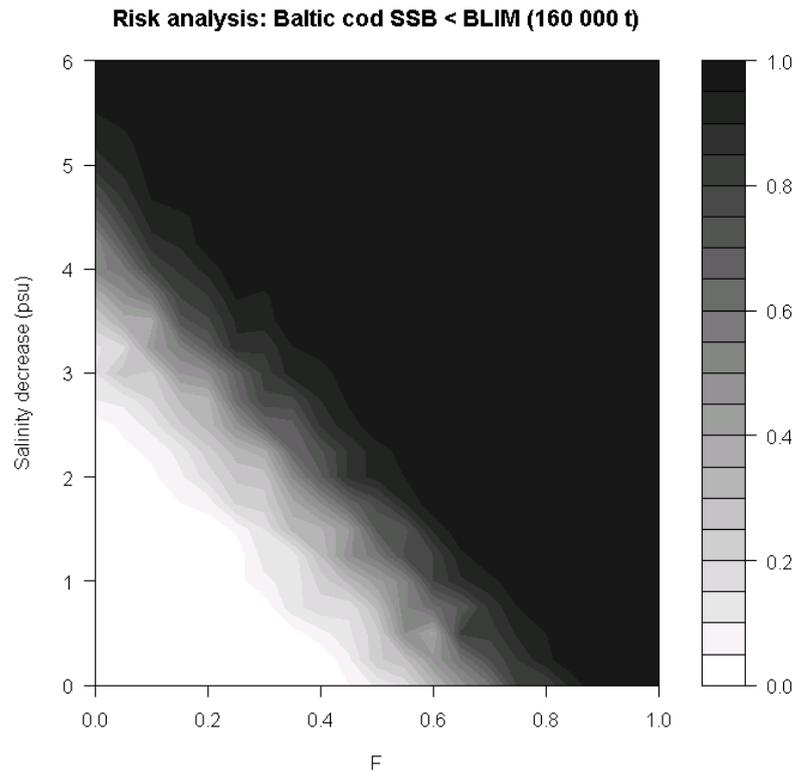


Figure A6. The probability of Baltic cod spawning-stock biomass (SSB) falling below the limiting stock size (B_{lim}) is computed as the percentage of model runs where the predicted SSB falls below 160 000 t. Simulations are run for all combinations of fishing mortality (F) from 0 to 1 and decreases in salinity from 0 to 6 psu (relative to the mean salinity for 1974–2004). The risk of falling below B_{lim} increases rapidly and non-linearly as salinities decrease with increasing fishing mortalities.

A1.5 The response of Atlantic cod (*Gadus morhua*) to future climate change

Kenneth F. Drinkwater

Global circulation models (GCMs) predict significant warming throughout the globe under higher levels of greenhouse gases (IPCC, 2007a). Although the amplitude of the warming varies according to the particular GCM used, they all demonstrate proportionately greater warming in the Subarctic and Arctic regions. In this presentation (based on Drinkwater, 2005), knowledge of the impact of climate variability on Atlantic cod (*Gadus morhua*) is coupled with predictions of future climate change. The focus is restricted to the impact of temperature changes on cod, and a pan-Atlantic perspective is adopted, considering the effects of warming on all of the major cod stocks from Georges Bank and the Gulf of Maine in the southwest, around the continental shelves of the North Atlantic covering Canada, Greenland, Iceland, Barents Sea, and south to the Celtic Sea, southern North Sea, and the Baltic. These areas cover temperatures ranging from $<-1^{\circ}\text{C}$ to $>20^{\circ}\text{C}$, although adult cod are usually found in bottom temperatures with annual means of between 0 and 12°C , and are expected to experience some of the largest anthropogenic-induced climate changes in the world.

Climate scenarios

For quantitative analysis of the response of each of the cod stocks to anthropogenically induced warming, we need coupled atmosphere–ocean regional models to determine the extent of the warming. These are not yet available, so the IPCC (2001) multimodel scenarios were used to simulate the rise in temperature expected in the waters occupied by cod. If we assume similar changes in the upper-layer ocean temperatures, as Loeng *et al.* (2005) suggested might be the case, and that the amplitude of the temperature anomalies are relatively similar with depth over the ranges occupied by cod (mostly 50–400 m), which is based on examination of depth-dependent temperature anomalies throughout the cod regions, we can use these temperature changes as, at least, an indication of what could be experienced by cod stocks. Therefore, the mean temperature change by the year 2100 ranges from a minimum of $2\text{--}3^{\circ}\text{C}$ to $>6^{\circ}\text{C}$ in the northern and eastern Barents Sea. In most of the areas inhabited by cod, the modelled temperature changes range from 2°C to 4°C , with the uncertainties comparable with the means (IPCC, 2001).

Cod stock responses to warming temperatures

This prediction of the abundance response of present-day cod stocks to future warming relies on the following. First, because today's cod stocks are not observed much above annual mean bottom temperatures of 12°C (Dutil and Brander, 2003), it is assumed that this relationship will continue to hold into the future. Thus, if bottom temperatures warm beyond 12°C , it is assumed that cod will disappear. Second, the temperature–recruitment relationships found by Planque and Frédou (1999; Figure A7) were converted into a change in recruitment as a function of surface-temperature change and plotted against the mean annual bottom temperature of the stock (Figure A8). At bottom temperatures $<5^{\circ}\text{C}$, recruitment increases with increasing temperature, and at temperatures $>8.5^{\circ}\text{C}$, recruitment decreases. At temperatures between these two values, there is little change in recruitment. This provides a clue as to what will happen to recruitment under the predicted temperature changes. For example, Georges Bank cod live in bottom waters with an annual average temperature of approximately 8°C , and

there is currently no relationship between sea surface temperature (SST) and recruitment (Figure A8). However, if mean bottom temperatures were to increase by only 1°C, recruitment is expected to become temperature-dependent, such that the warmer temperatures would result in decreasing recruitment. If the higher temperatures were to continue, this would tend to reduce the stock.

With a sustained 1°C change, several of the southern cod stocks would become stressed. It is predicted that the cod stocks in the Celtic Sea and English Channel would eventually disappear as the waters warmed to 12°C and above (Figure A9). Stocks in the Irish Sea, southern North Sea, and Georges Bank would decline owing to decreasing recruitment with increasing temperatures. On the other hand, the cold-water stocks, (e.g. most of the stocks off eastern Canada and Greenland, and in the Barents and Kara seas), would benefit from increased recruitment resulting from warmer waters. The recruitment levels of the remaining stocks would not change appreciably.

With a temperature increase of 1–2°C above present-day values, we would expect the Irish Sea stock to disappear. The Georges Bank and North Sea stocks would continue to decline, and the stocks in the Kattegat, off West Scotland, and around the Faroes would begin to decline owing to decreasing recruitment. The stocks that increased under a 1°C change would continue to increase, with the exception perhaps of the Flemish Cap stock, whose recruitment would level off. The remaining stocks would not experience any change in recruitment.

With a temperature increase of 2–3°C above present-day values, we would expect to see the disappearance of the Kattegat and North Sea stocks. The southernmost stocks on the western Atlantic (Georges Bank, Gulf of Maine, and Browns Bank/Bay of Fundy) would all be in decline. Icelandic stocks would begin to show signs of declining recruitment, joining the Faroes and the West Scotland stocks on the eastern side of the Atlantic. Recruitment in the Barents Sea stocks would level off, as would the southern Grand Banks stocks, but most of the Canadian stocks, as well as those off West Greenland and in the Kara Sea, would continue to improve.

With an increase of 3–4°C above present-day values, the Georges Bank stock would probably disappear. The Norwegian coastal cod stocks would begin to see declining recruitment, along with the Flemish Cap stock. Recruitment in the eastern Scotian Shelf, northern Gulf of St Lawrence, southern Newfoundland, Greenland, and the Kara Sea stocks would no longer increase. Only in the southern Gulf of St Lawrence and southern Labrador/northern Newfoundland stocks would recruitment continue to increase.

Possible additional changes

The above analysis suggests the possible disappearance and decline in abundance of the southern stocks, and the increased recruitment and abundance of the northern stocks. Warming temperatures should also result in improved growth rates in general (Brander, 2000) and improved cod production (Dutil and Brander, 2003), resulting in higher biomass, especially in the northern regions. There should also be a northward range extension, as observed in past warm periods (Jensen, 1939; Blacker, 1957), perhaps including beyond the Barents Sea farther into the Arctic. Spawning locations will also move northwards, as observed in the past (Vilhjálmsson, 1997; Sundby and Nakken, 2008), and there will be changes in migration times for those stocks undertaking annual movements from overwintering grounds to summer feeding and spawning areas.

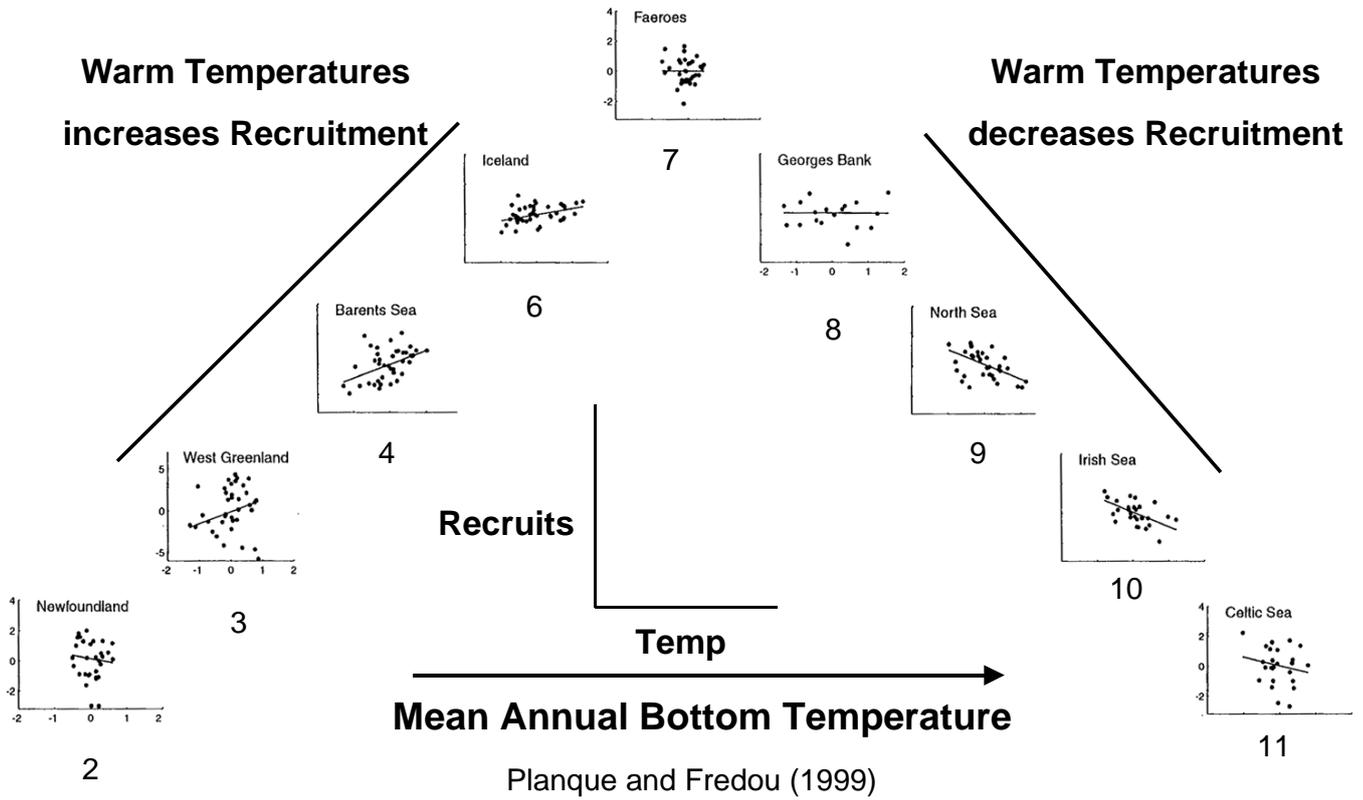


Figure A7. The relationship between recruitment and temperature for various cod stocks. The numerical values at the bottom of the plots represent mean annual bottom temperatures. Note that the relationship is generally positive for the cold-water stocks, but is negative for the warm-water stocks. There is no relationship in the mid-temperature range. (Based on Planque and Frédou, 1999.)

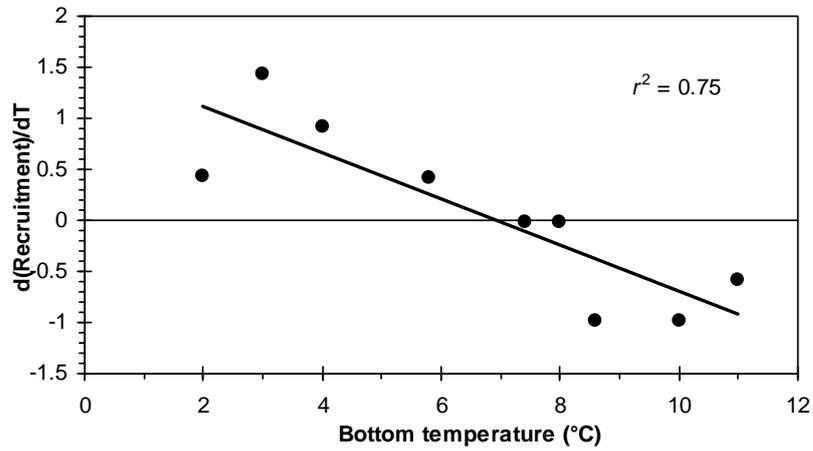


Figure A8. The change in recruitment with surface temperature for various stocks as a function of the mean bottom temperature.

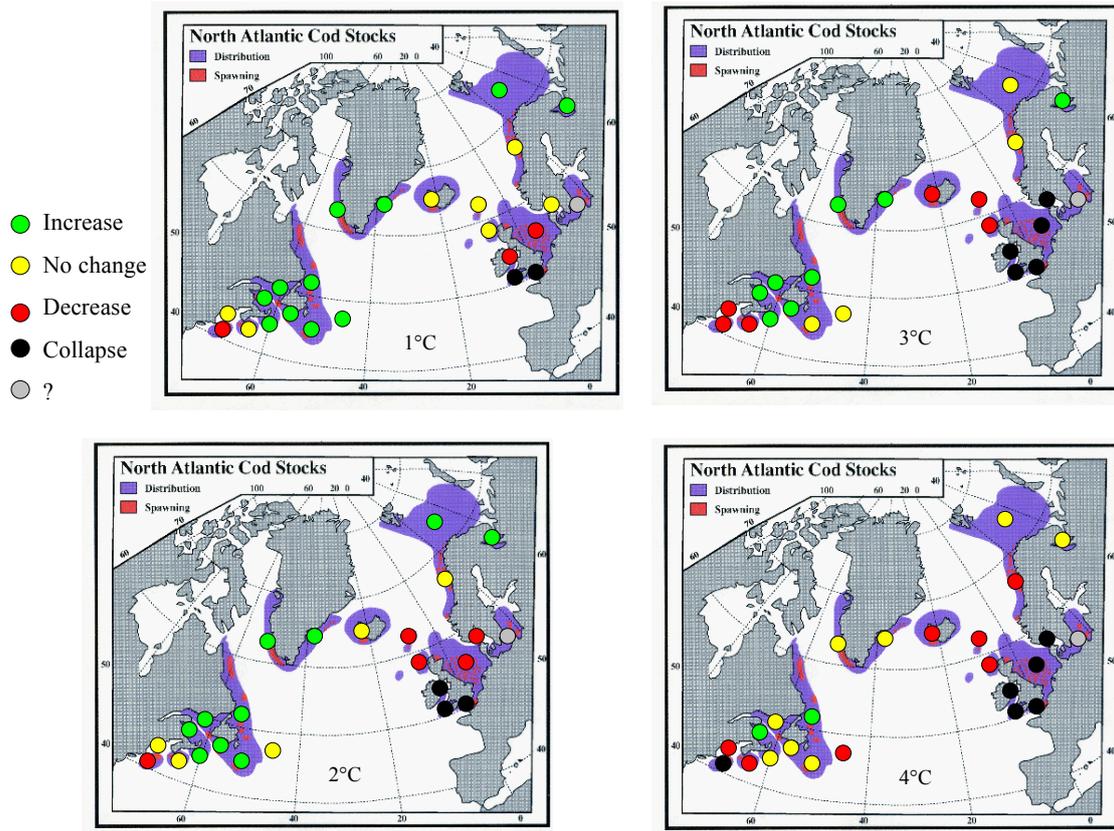


Figure A9. Expected changes in abundance of cod stocks with temperature increases above present-day values of: (upper left) 1°C; (lower left) 1–2°C; (upper right) 2–3°C; and (lower right) 3–4°C.

Concluding remarks

These projections have not taken into account industrial fishing, which we know will play a strong and, in some cases, dominant role on fish abundance, distribution, and growth. Future changes to cod will also depend on changes to other parts of the ecosystem, including overall primary and secondary production in the North Atlantic and, more specifically, in the specific food for larval, juvenile, and adult cod, such as *Calanus finmarchicus* for the more northern stocks, and *Paracalanus* and *Pseudocalanus* for several of the more southern stocks (Heath and Lough, 2007). Only changes in ocean temperatures associated with local atmospheric heating have been considered. Temperature may also change substantially because of variations in the circulation patterns, as well as in the strength of mixing and stratification. Thus, although these predictions of what might happen to Atlantic cod under future warming are consistent with our present understanding, the actual response remains highly uncertain.

A1.6 Could warmer years mean good years for cod? A pan-Atlantic meta-analytic perspective

Irene Mantzouni and Brian R. MacKenzie

This study aims to identify the effect of temperature on cod (*Gadus morhua*) population dynamics by meta-analysing data across the species distributional range in the North Atlantic. Our dataset consists of spawner (S), recruitment (R), and temperature (T) time-series for 21 eastern and western cod stocks. Regarding T , we use annual spring (spawning season) estimates in the upper water layer (0–100 m). We employ a twofold approach, aimed at different, but complementary issues: (i) the identification of the general pan-Atlantic pattern of T impacts, with special focus on extreme temperature and/or recruitment events; and (ii) the incorporation of these climatic effects in the spawner–recruit (SR) models, in order to improve the predictive capacity and investigate the possibility that SR parameters depend on ecosystem characteristics.

The first approach focuses on the identification of the influence exerted on R or R survival ($\log(R/S)$) during years of extreme low or high T . It is, therefore, largely based on the classification of exceptional population observations according to the exceptional T events. Similar non-parametric, classification approaches have provided insights into both stock-specific and broadscale comparative analyses of SR data (e.g. Rothschild and Mullen, 1985; Myers and Barrowman, 1996). Within stocks, we define these extremes as corresponding to observations below the 25th or above the 75th percentiles, respectively. In a similar way, we have defined years of weak or strong R year classes.

Also, we expect the T effects to be stronger at the extremes of the cod thermal distribution (Myers, 1998). Therefore, we have defined two sets of stocks: “hot” and “cool”, including stock data within either the upper or the lower temperature intervals, respectively. The interval limits were approximated by the 25th ($T_{25\%ile}$) and the 75th ($T_{75\%ile}$) percentiles of temperature across the species range. For every hot and cool stock, we estimate effect sizes (ESs) quantifying: (i) the probability of strong R year classes during years of low T vs. the probability during low T years; (ii) whether or not R strength differs significantly between years of high and low T ; and (iii) the correlation between the entire time-series of R or $\log(R/S)$ and T . The ESs on an across-stocks basis are analysed using random effects meta-analysis (Cooper and Hedges, 1994), a conservative approach that allows ESs to differ, not only because of the varying amounts of data available for each stock, but also because of variability in their responses to environmental forcing.

The results provide strong evidence that extremely warm years result in extremely strong R year classes for the cool stocks and vice versa. As Figure A10a suggests, for the cool stocks, the probability of a strong R is higher at high T . In Figure A10b, for the hot stocks, we plot the stock-specific estimates of the log ratio between mean $\log(R/S)$ during extreme high and extreme low T . Using the non-parametric Wilcoxon test, it is seen that, in the upper thermal limit, this log ratio is negative.

The second approach involves the study and integration of T effects on the parameters of the SR models. To this end, we develop the models using hierarchical (mixed models and Bayesian inference) approaches that allow the parameters to be modelled across cod stocks (Gelman and Hill, 2007). The method offers various advantages and can be especially useful with fisheries data, which are usually limited and characterized by high variability (Myers, 2001). The SR parameters, maximum

reproductive rate at low stock size (*alpha*), and habitat carrying capacity (CC) are biologically and ecologically meaningful, and thus depend both on species traits, which are common across stocks, and on the ecosystem conditions experienced by individual populations.

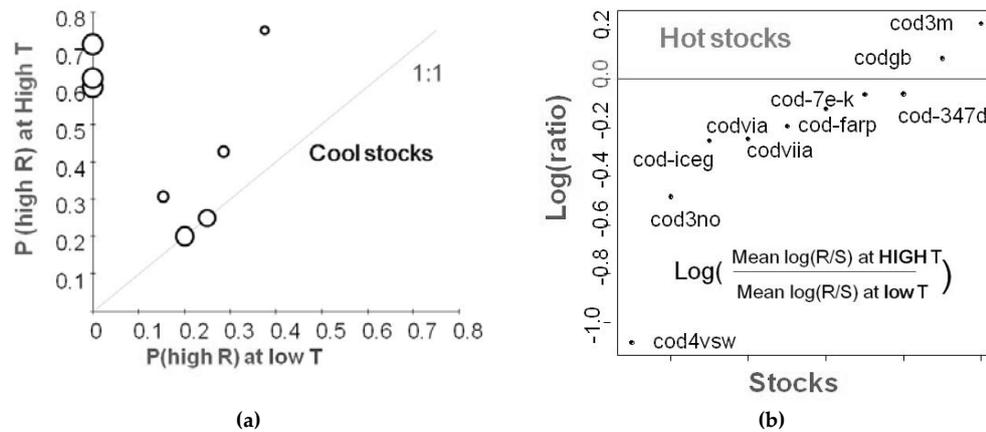
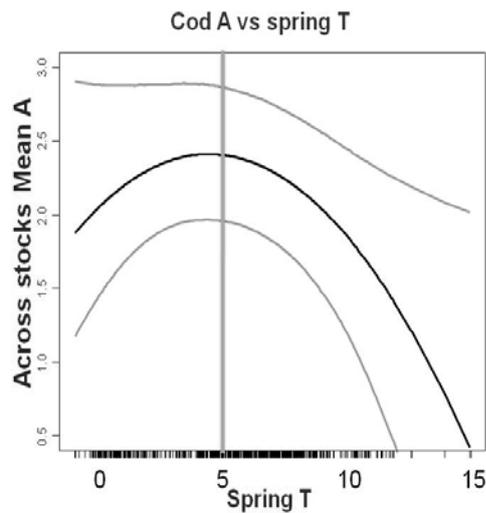


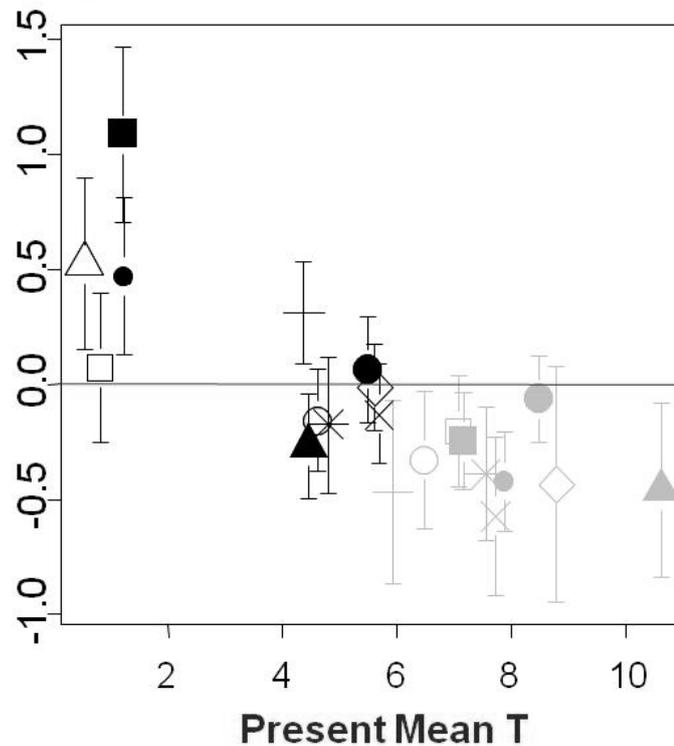
Figure A10. (a) Probability of strong *R* year classes during years of extreme high *T* plotted against the corresponding probability during low *T* years for the cool stocks. (b) The log ratio of mean *R* survival between years of high and low *T* (formula on the plot) for the hot stocks.

These cross-stocks relationships in the parameters can be integrated into the hierarchical model structure and thus “strength is borrowed” across stocks (Hilborn and Liermann, 1998). The CC is shown to depend on the stock-specific habitat size (40–300 m), which can explain almost half of the variability observed across the species range. More importantly, by combining data across the cod distributional range, and thus from the whole thermal range, it is proven that *T* has significant effects on *R* survival (parameter *alpha*). The relationship is shown to be non-linear; on average, survival increases with *T* up to almost 5°C, above which negative effects prevail (Figure A11a). The critical *T* varies among stocks between 3°C and 5°C. Differences in *T* across the cod range can explain 60% of the variability across stocks in *alpha*. The variability left unexplained is greater in the lower thermal range compared with stocks in warmer waters. Thus, temperature seems to be the limiting factor for stocks experiencing a higher-than-average *T*, whereas at the lower limit, other factors can have a substantial influence.



(a)

Change in A with 3°C increase in mean



(b)

Figure A11. (a) The mean quadratic relationship of parameter α (slope at the origin in the Ricker model) with T . (b) The expected change in stock-specific α s following an increase of 3°C in mean T . Grey (black) symbols correspond to stocks in warmer (or colder) waters.

In Figure A11a, the expected change in α following an increase of 3°C in mean T is shown. Climatic effects on α also have implications for the CC, defined either as the maximum R or as R at equilibrium; for stocks in warmer waters, the expected reduction can be up to 30%. The hierarchical SR models can be extended to include additional factors that influence R strength and CC on a pan-Atlantic or regional basis. The technique could also be applied to growth models incorporating T effects. Coupled SR and growth models can provide further insight into a climate-change-sensitive management approach (Kell *et al.*, 2005).

A1.7 Modelling the consequences of expected warming in the Barents Sea on the Atlantic cod stock

Anatoly Filin and Ivan Oganin

The aim of this study was to conduct a quantitative analysis of the response of the cod stock in the Barents Sea to future climate changes using the STOCOBAR (STOCK of COd in the BAREnts Sea) model, which has been developed at PINRO. This is a fish–ecosystem coupled model that describes stock dynamics of cod in the Barents Sea and takes into account trophic interactions and environmental influences. It can be used for predictions and historical analysis of cod-stock development, as well as for estimating the effectiveness of different harvest and rebuilding strategies.

The STOCOBAR model has no geographical resolution, i.e. the processes are simulated without area differentiation. The time-step of the model is 1 year. The model includes cod as a predator and seven of its prey species: capelin (*Mallotus villosus*), shrimp (*Pandalus borealis*), polar cod (*Boreogadus saida*), herring (*Clupea harengus*), krill (euphausiids), haddock (*Melanogrammus aeglefinus*), and young cod (cannibalism). In our study, we included only capelin and juvenile cod as prey species. The standard Ricker recruitment equation was used to couple the cod spawning stock and recruitment at age 1. The stochastic nature of the recruitment processes was realized by including residues in the simulated data.

Long-term estimations of the influence of ecosystem factors on cod-stock development are realized in the model by using stochastic ecosystem scenarios generated within the model. Kola Section observations were the basis for development of the temperature scenarios for our simulations. We introduced the alternation of cold, moderate, and warm periods in the modelled temperature scenarios. This may be regarded as a deterministic component in long-term year-to-year dynamics of water temperature. In this study, we recognized three temperature periods: cold periods (<3.7°C); moderate periods (3.7–4.3°C); and warm periods (>4.3°C). The duration of these periods was set to 5 years. The actual values of temperature for cold, moderate, and warm periods were selected randomly from the historical data of the various periods.

In addition to temperature scenarios, the long-term simulations of cod dynamics in the Barents Sea require a scenario of year-to-year variations in the capelin stock. This was developed taking into account the observed relationship between changes in cod and capelin stocks. Historical data indicate that the probability of the appearance of a large capelin stock in any particular year is much higher if the cod spawning stock in the previous year was lower than 400 000 t. Therefore, we set the scenarios for capelin stock dynamics on the basis of a random selection of values from historical data of the cod spawning-stock biomass calculations in the model. In our analysis, we used such an approach for the development of the capelin stock dynamics scenario at the current temperature regime and at a temperature increase of 1 or 2°C. For ecosystem scenarios at temperature increases of 3 or 4°C, we applied another approach. Taking into account that capelin is a cold-water species, we assumed that, at a high temperature, the capelin stock size in the Barents Sea will decrease independently of the cod stock. We also assumed that, at a temperature increase of 3–4°C, the capelin stock will be at an historically low level. Therefore, in this case, we set the capelin scenario by random selection of values from available historical data that were less than 2 million t.

For the analysis of the impact of expected warming on cod in the Barents Sea, we conducted long-term simulations at five temperature regimes: the current temperature and temperature increases of 1, 2, 3, and 4°C. To obtain temperature scenarios for temperature increases of 1–4°C, we simply added an expected temperature increment to the current temperature regime. The harvest-control rule for cod in our simulations corresponds to the management strategy based on the precautionary approach. Cod yield at all temperature scenarios was calculated using existing values of the biological reference points for the Barents Sea cod stock.

For every temperature regime, we carried out ten runs, each with a modelled period of 250 years. The mean long-term values for the following parameters in the cod stock were estimated as follows: (i) growth rate (increments in body weight and in body length); (ii) maturation rate (proportion of mature fish by age, mean age of fish in spawning stock); (iii) annual consumption of young cod by adult cod (cannibalism); (iv) recruitment at age 3; (v) abundance and biomass of fishable and spawning cod stocks; and (vi) total allowable catch (TAC).

The results of the simulations show that a 1–4°C increase in temperature in the Barents Sea will lead to an acceleration of cod growth and maturation rates. This will positively affect the general production of the cod stock. On the other hand, cannibalism will also increase in response to expected warming in the Barents Sea. This will have a negative effect on cod recruitment and total abundance. The consequences of temperature increase in the Barents Sea for the cod stock and catches are summarized in Figures A12 and A13.

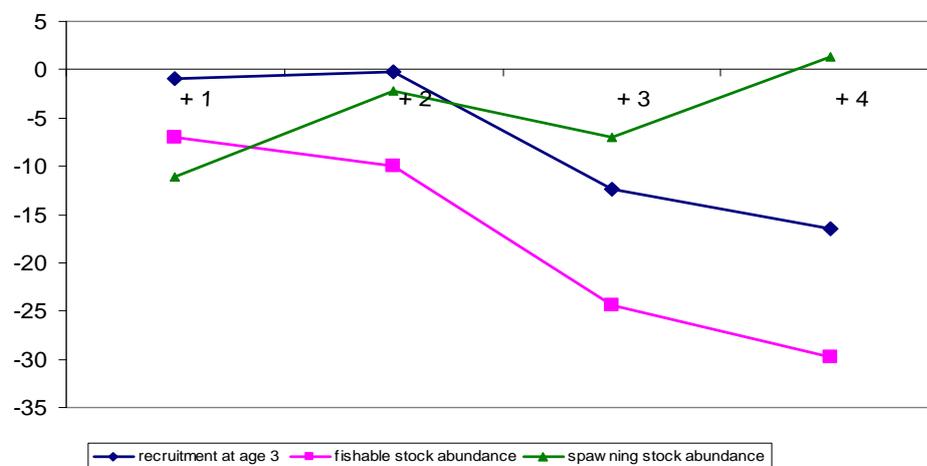


Figure A12. Relative changes (in % relative to the current temperature regime) of recruitment, fishable abundance, and spawning-stock abundance of cod at temperature increases in the Barents Sea of 1–4°C, according to the STOCOBAR simulations.

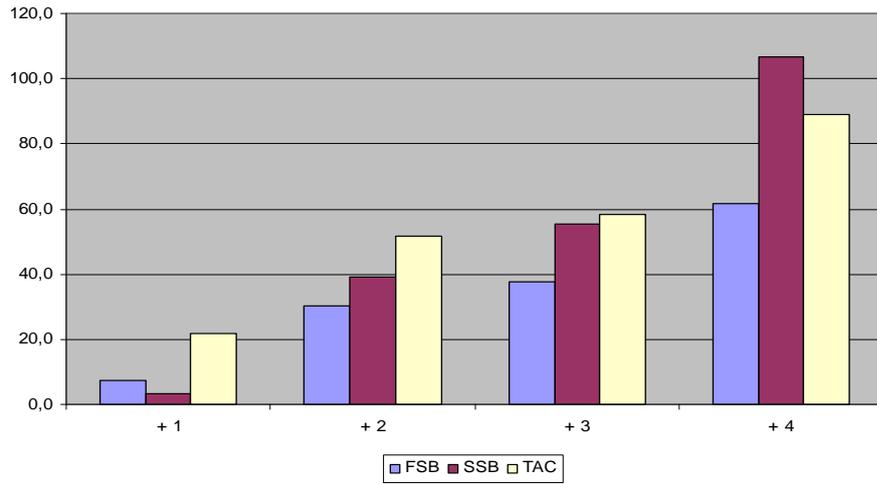


Figure A13. Relative changes (% change of simulated values under the current temperature regime) of cod stock biomass and catches at temperature increases in the Barents Sea of 1–4°C, according to the STOCOBAR simulations.

A1.8 Climate and North Sea cod distribution: a long-term approach

Georg H. Engelhard, Andrew B. South, and John K. Pinnegar

Recent studies, based mainly on International Bottom Trawl Survey (IBTS) data, have highlighted that cod (*Gadus morhua*) within the North Sea, over the past three decades, have demonstrated a northward shift in mean distribution (Hedger *et al.*, 2004; Perry *et al.*, 2005; Rindorf and Lewy, 2006). Two main hypotheses have been put forward, one related to climate warming and one to higher fishing effort in the southern North Sea compared with the northern North Sea; but the rather short time-span of the survey data has complicated the disentanglement of these hypotheses. This has motivated the current study, which is based on British commercial catch per unit of effort (cpue) data over a far longer time-span (past nine decades), covering both warming and cooling periods and including periods of contrasting levels of fishing effort.

For the period 1913–1980 (except the war years), data were from historical fisheries “statistical charts” (catalogued in Engelhard, 2005), which were produced by the UK Ministry of Agriculture, Fisheries and Food (MAFF, now the Department for Environment, Food and Rural Affairs, or Defra). These show fishing effort (hours fished) and fish landings by British otter trawlers (either steam or motor driven) for each ICES rectangle in the North Sea, into England and Wales (1913, 1967–1980) or into England, Scotland, and Wales (1920–1967). For 1968–2007, data on otter-trawler landings into Scotland were from the Scottish Sea Fisheries System (SSFS), held by the Fisheries Research Services (FRS, Aberdeen) database (e.g. Greenstreet *et al.*, 1999). For 1982–2007, data on otter-trawler landings into England and Wales were from the Fisheries Activity Database (FAD) of Defra. Combined, these data represent almost all British trawling effort in the North Sea during 1920–1938 and 1947–2007 (and ca. 10% of the effort in 1913), spatially detailed by rectangle (specialized trawling fleets such as *Nephrops* trawlers were not included in the analysis).

Indeed, long-term cpue data indicate that marked shifts in North Sea cod distribution have occurred throughout the 20th century. We are assuming that relative cpue by the commercial fleet gives a reasonably good indication of the spatial distribution of the species. We acknowledge that potential bias might arise from uneven distribution of effort by more or less powerful vessels within the North Sea.

Figure A14 shows, by decade, the distribution of cod cpue over the North Sea, from the 1920s to the 2000s. We have normalized the data for each period in order to overcome the confusing effect of the increase in fishing power of trawlers, particularly after the 1960s. Thus, cod cpue tended to be highest around the Orkneys and Shetlands in the 1920s and 1980s, to the northeast of England from the 1930s to 1950s, and in the eastern half of the North Sea in the 1990s and 2000s. Interestingly, the spatial distribution of cod in the 2000s appears almost opposite to that during most decades of the 20th century.

A marked southward (and less marked eastward) shift occurred from the 1920s to the 1950s, followed by a generally more northward shift from the 1950s onwards, but with fairly irregular changes in latitudinal centre of gravity of distribution during the 1980s and 1990s (e.g. relatively south in the late 1990s; Figure A15). A noticeable eastward shift occurred in the 1980s–1990s. Finally, in the 2000s, there was again a north- and westward shift (related to cod becoming somewhat more numerous off Shetland and very rare in the southern North Sea). The trend in depth distribution of

cod (cf. Dulvy *et al.*, 2008) closely mimics that of the latitudinal distribution, which is unsurprising given the general north–south depth gradient in the North Sea. Meanwhile, temperatures were generally low in the 1920s, increased up to the 1940s, then decreased until the 1960s, when the current period of substantial warming began.

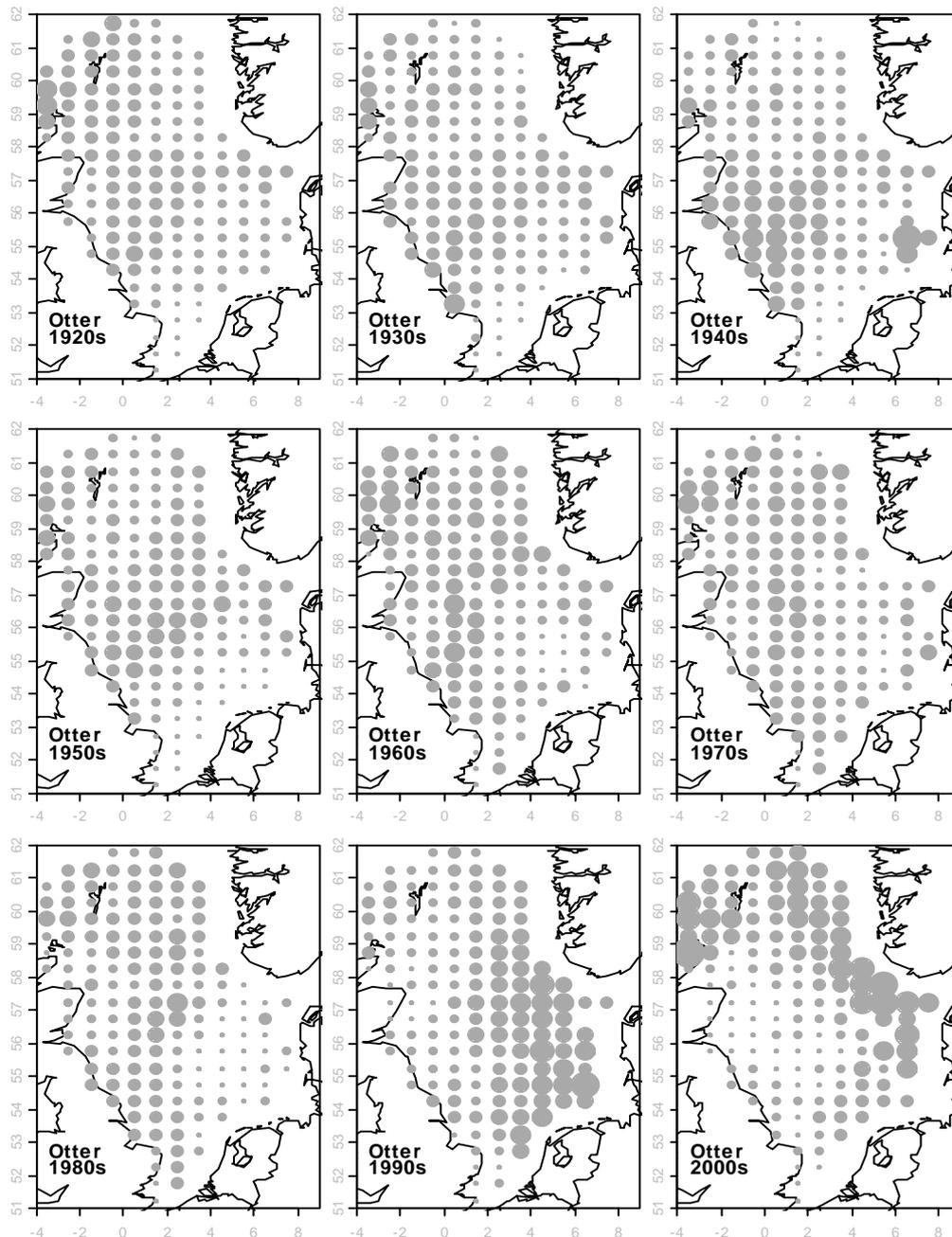


Figure A14. Long-term changes in relative cod catch per unit of effort (cpue) within the North Sea. For each decade, maps show spatial distribution of cod cpue by British trawlers landing in England, Scotland, and Wales.

Initial analysis suggests that long-term cod-distribution shifts are not straightforwardly linked to either climate change or fishing pressure. A more thorough statistical analysis will be needed for a firmer conclusion about the factors behind the long-term cod-distribution shifts, including interpretation in the light of recent process-oriented studies. This may include additional environmental variables,

as suggested during the 2008 ICES Workshop on Cod and Future Climate Change (WKCFC; ICES, 2008a; e.g. marine monitoring data described by Mackenzie and Schiedek, 2007a).

Acknowledging this, the preliminary results strongly suggest that it would be too simplistic to solely attribute the recent northward distribution shift of North Sea cod to global warming.

The study was supported by Cefas Seedcorn project DP233 (Spatial Analysis of Historical Fisheries Data) and the European Union's Sixth Framework Programme (FP6) project RECLAIM (Resolving Climatic Impacts on Fish Stocks). Joyce Petrie, Bill Turrell, and Phil Kunzlik (FRS) provided Scottish fisheries data from 1967 onwards. Suzy Baldry contributed to the digitizing of Cefas historical fisheries data, and Peter Robinson extracted the data from the England and Wales FAD.

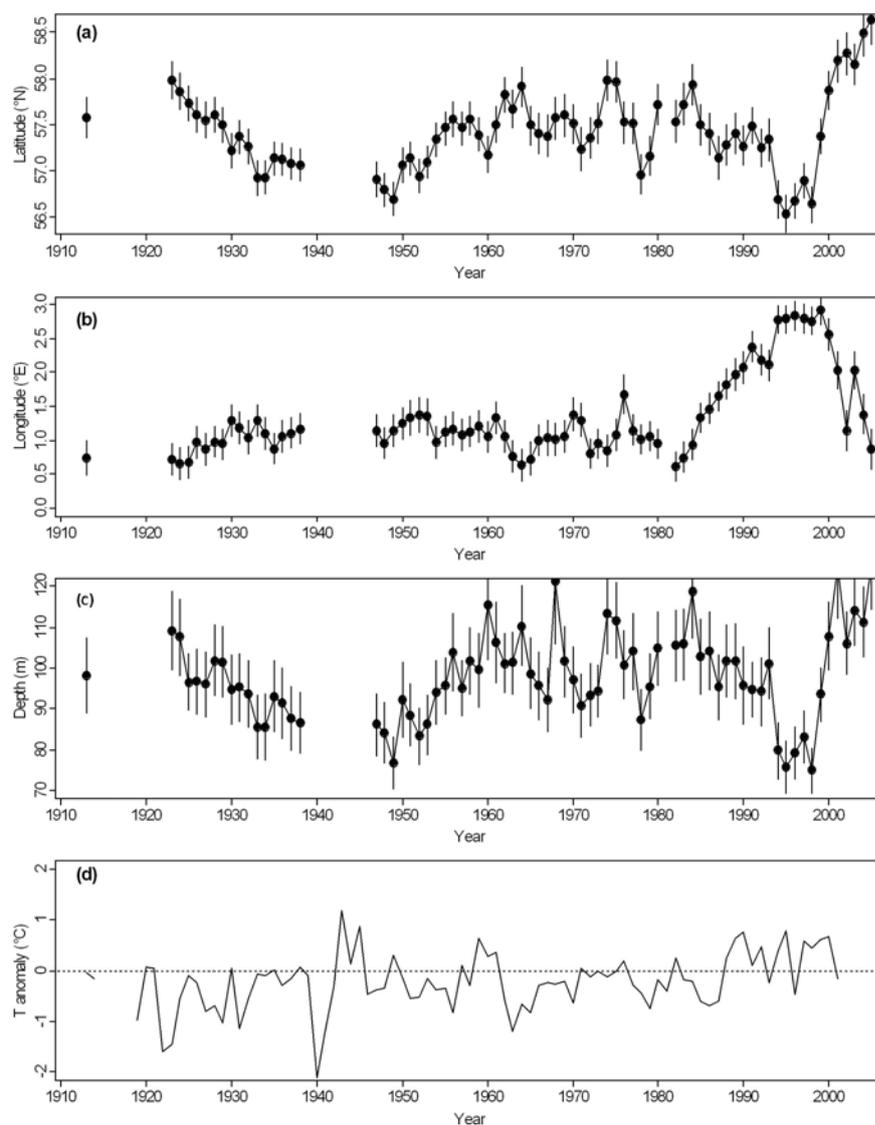


Figure A15. Long-term changes in (a) latitudinal and (b) longitudinal centre-of-gravity of estimated North Sea cod distribution, based on commercial landings (calculated as the mean latitude and longitude weighted with cod cpue; bars indicate s.e. of weighted means). Long-term changes in (c) mean depth distribution of North Sea cod (with s.e.), and (d) variability in mean gridded SST in the North Sea (data from Ken F. Drinkwater, IMR), expressed as annual anomalies against a 1971–2000 baseline.

A1.9 Influence of oceanographic changes at the nursery grounds of 0-group North Sea cod

Peter Munk

Consideration of realistic spatial heterogeneity is important when interpreting vital rates and population structure of marine organisms. In the marine environment, fronts, boundary layers, pycnoclines, gyres, and other smaller spatial features play a significant role in determining conditions for marine life. Specifically, processes related to hydrographic fronts appear to play an important role in the advection and/or retention of fish eggs/larvae and other planktonic organisms. This has been demonstrated by a number of field studies (Kjørboe *et al.*, 1988; Munk and Nielsen, 1994; Lochmann *et al.*, 1997), and by biophysical modelling studies exploring drift and dispersive processes in well-known nursery areas of fish larvae (e.g. Werner *et al.*, 1996, 2001). These studies demonstrate the importance of the mesoscale variability in water density, and of the flowfield in the vicinity of frontal features. Flow convergence and divergence are particularly intensive near fronts, and fish larvae and other plankton can potentially be concentrated in the frontal zone owing to factors which direct the horizontal and vertical movements of the organism. Among these are physical factors, such as light, water turbulence, and flow, and biological factors, such as larval buoyancy, swimming performance, and availability of prey (Sclafani *et al.*, 1993).

Studies on the early life of North Sea cod carried out during the past two decades illustrate a marked correspondence between frontal features and peak abundance of cod eggs, larvae, and pelagic juveniles. Apparently, the hydrographic fronts enhance conditions for cod early life stages, as evidenced by elevated prey abundance and cod growth rates in the central section of the fronts (Munk, 1997, 2007). Hence, it is hypothesized that the oceanographic changes in the North Sea influenced the strength and spatial extension of hydrographic fronts in the area, and thereby influenced the conditions, growth, and survival of recruiting cod.

This hypothesis is investigated by inspecting hydrographic variability at major nursery grounds for cod in the North Sea. The nursery grounds are identified and demarcated from catch data of pelagic juveniles from the North Sea international 0-group gadoid surveys (Holden, 1981). Three major grounds are identified, named after the adjacent bank: Viking Bank, Ling Bank, and Great Fisher Bank. For each of these, an area of three ICES statistical rectangles is chosen as the central nursery area. From the ICES hydrographic database, bottom salinity and temperature measurements are retrieved from these areas for the months June, July, and August from the years 1965–2005. Subsequently, the average for each year and area is calculated and illustrated.

These observations of hydrography at the nursery grounds during the four decades illustrate the significant variability, a marked decline in salinity during the second half of the 1980s, and a general increase in temperature since the late 1980s. Changes in salinity and temperature resulted in a general decline in bottom-water density during the period. Comparison of observed bottom-water density and hydrographic fronts at the grounds indicate that water density could be used as a proxy for frontal performance; hence, it is likely that conditions for 0-group cod varied markedly during the investigated period. In addition, findings illustrate the likelihood of different hydrographic changes for the different subpopulations of North Sea cod.

A1.10 Spatial distribution of 0-group fish in the Barents Sea

Jan Erik Stiansen, Elena Eriksen, Geir Odd Johansen, and Randi Ingvaldsen

Capelin (*Mallotus villosus* Müller), juvenile herring (*Clupea harengus* L.), cod (*Gadus morhua* L.), and haddock (*Melanogrammus aeglefinus* L.) are commercially and ecologically important fish species in the Barents Sea, representing different biogeographic groups. All these stocks have nursing areas in the Barents Sea. However, the response of the spatial distribution of the fish larvae from climate variability is not well known. For more than 20 years, spatial data on fish larvae have been collected in August–September in the Barents Sea, together with hydrographic data. These spatial data span a period with a strong increasing temperature trend, from the cold 1960s–1970s to the very warm 1990s–2000s. The presented data are from the period 1980–1996 (Figure A16). Climatic variation is represented by time-series of spatial temperature fields based on observations, observed mean temperatures in Atlantic water masses, and modelled inflow of Atlantic water masses into the area. Fish larvae are presented as 0-group fish (age 0, ca. 0.5 years old). Geographic distributions of the 0-group are based on field observations from designated 0-group surveys. Results from the spatial analysis of variation in fish larvae distribution, as affected by climatic variation, are presented. Further, a study of temperature limits for the distribution areas is shown. Finally, the results are discussed with respect to expected future climate changes in the Barents Sea.

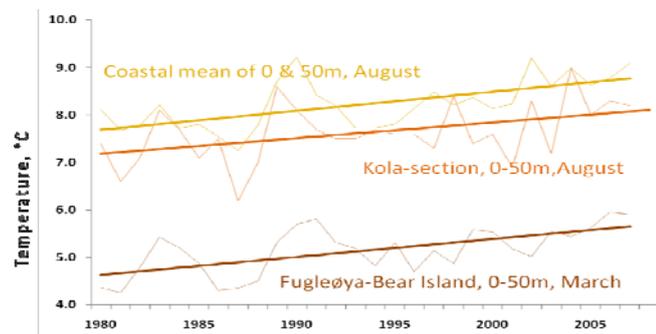


Figure A16. Temperature development in different areas of the Barents Sea.

The results show that the distributional area of 0-group cod has increased (Figure A17) and underwent an increasing eastward mean displacement during the warming period (Figure A18).

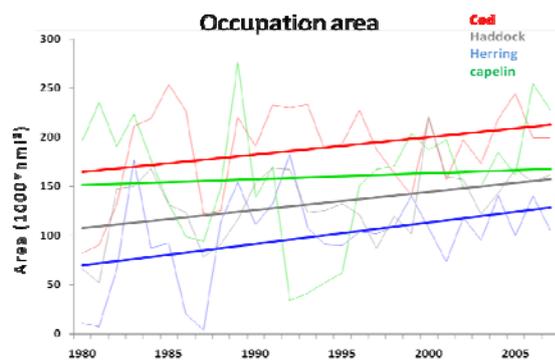


Figure A17. Occupation area of 0-group fish in the Barents Sea.

Also interesting is the work undertaken in the ICES Arctic Fisheries Working Group with multiple regression models (Figure A19).

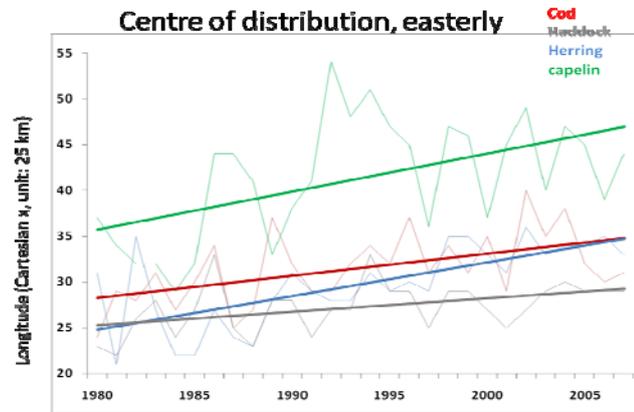


Figure A18. Development of centre of gravity of 0-group fish in the Barents Sea.

All these approaches have the possibility to provide quantitative projections into the future and may, therefore, be useful when evaluating the effect of human-induced climate-change scenarios for subsequent decades. However, the results of the spatial development are still new and need to consider density-dependence and trophic interactions in order to be trustworthy before being used for projections. This work is being carried out for the Barents Sea by the Norwegian FishExChange Project (2007–2010). FishExChange aims to provide possible future distributions of the main fish species in the Barents Sea, as well as possible effects on fisheries and socio-economics. An important component of the project is the development of an equal area (25 x 25 km) grid on which datasets covering the entire ecosystem can be interpolated.

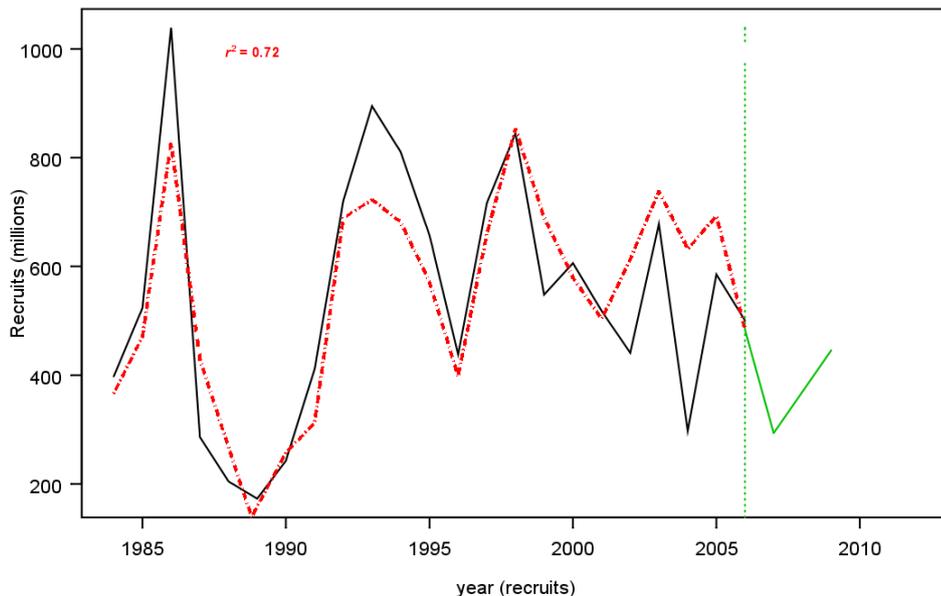


Figure A19. Example of multiple regression model for the number of recruits of Northeast Arctic cod. The black line is the number of recruits at age 3 from virtual population analysis (VPA) using data for 1985–2005; the red line is the number of recruits at age 3 estimated by the Stiansen *et al.* (2005) model. The correlation between the observed and estimated recruits is $r^2=0.72$, and the green line is the number of recruits at age 3 for 2006–2009 forecasted by the model.

A1.11 Comments on coherence of cod stock dynamics in the Northwest Atlantic Ocean

Brian J. Rothschild

This extended abstract is based on the paper “Coherence of Atlantic cod stock dynamics in the Northwest Atlantic Ocean” (Rothschild, 2007). The figures and some material are taken directly from the paper.

There are nominally 11 stocks of cod in the Northwest Atlantic, designated by the following North Atlantic Fisheries Organization divisions and subdivisions: 3NO, 3M, 3Ps, 2J3KL, 4RS3Pn, 4TVn, 5Z, 5Y, 4VsW1, 4X, and 4VNMO. The location of these stocks is shown in Figure A20. Most studies of these stocks refer to individual stocks or stock groups. Sinclair (1996), however, reviewed the few studies that considered the stocks as an ensemble. This paper extends Sinclair’s work.

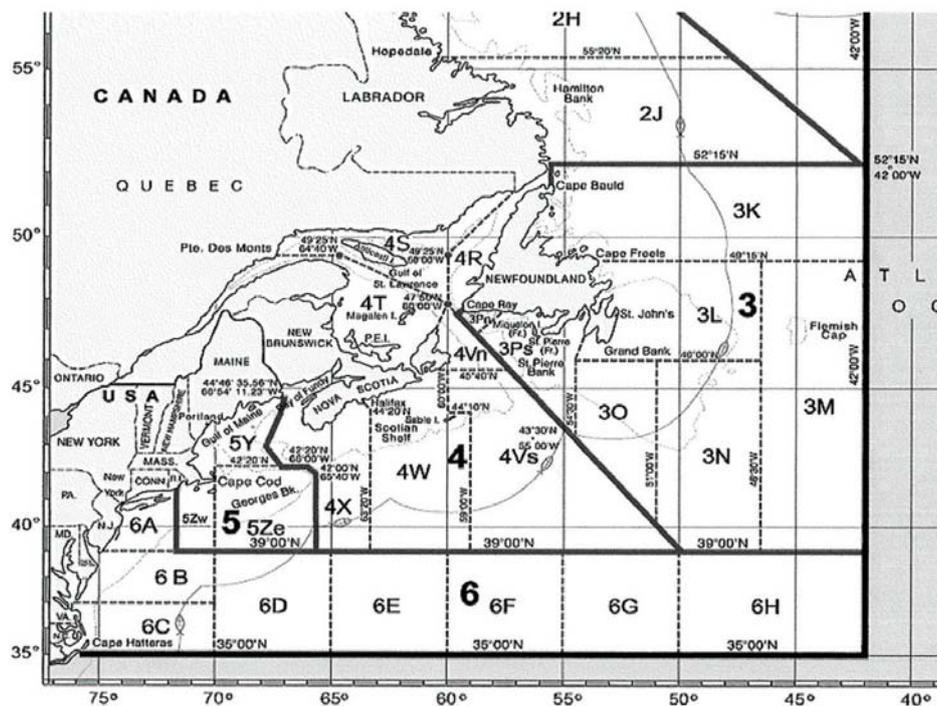


Figure A20. Areas associated with nominal Atlantic cod stocks in the Northwest Atlantic, as defined by the North Atlantic Fisheries Organization.

Shelton *et al.* (2006) provided estimates for the spawning-stock biomass (SSB) for the 11 stocks. Here, the reported SSB statistics were normalized in standard deviation units and plotted in Figure A21. There is a remarkable temporal coherence in the SSB values for the 11 stocks (Figure A21). Essentially, the stocks were relatively abundant in the 1960s, declined to very low levels in the mid-1970s, increased to peak abundance in the mid-1980s, and then reached unprecedented low values in the early 1990s. The declines in the separate stocks have been widely attributed to overfishing. However, the temporal coherence in stock abundance suggests that (i) all stocks would have to be exposed to the same intensity of fishing; (ii) the stocks are truly not separate stocks; or (iii) if the stocks are separate, then all stocks experienced the same coherent sub-basin-scale environmental forcing.

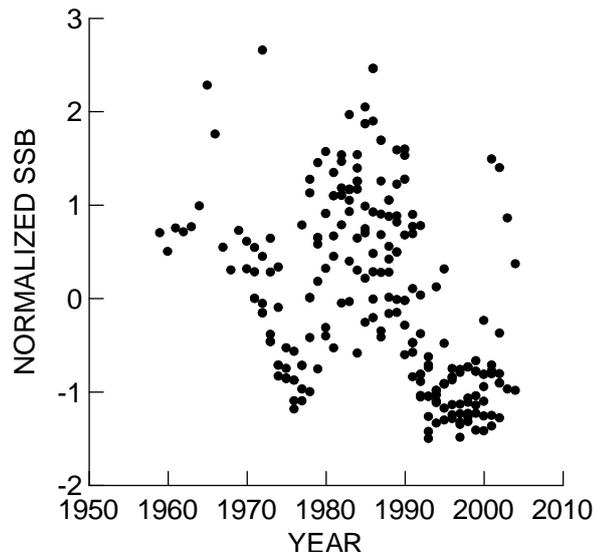


Figure A21. Normalized spawning-stock biomass (SSB). The ordinate is in standard deviation units. Note the depression in 1975, the peak in 1985, and the general decline after 1985.

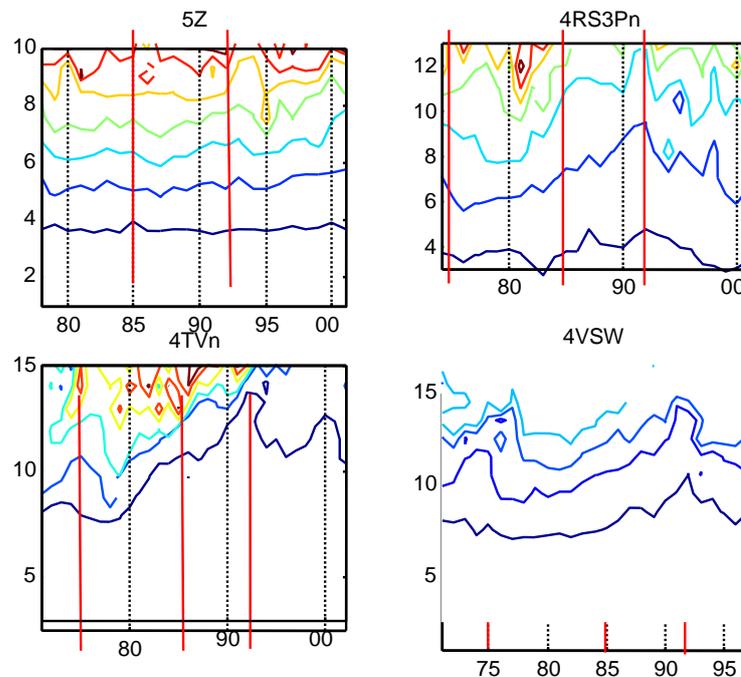


Figure A22. Weight-at-age contours for four stocks of Atlantic cod (see Figure A20 for stock codes). The y -axis is age, the x -axis is year, and the contoured z -axis is weight. An upward movement in a contour indicates a reduction in weight-at-age. The vertical red bars mark the 1975 and 1992 minima and the 1985 maximum in spawning-stock biomass. As early data are lacking for the 5Z stock, the year scale is different. Contour intervals are in 2 kg units, except for the 4RS3Pn stock, which is in 1 kg units.

A variety of evidence can be brought to bear on the causal basis for the dynamic changes in cod stocks. The evidence primarily involves (i) the weight-at-age; and (ii) the interrelated dynamics of SSB, fishing mortality (F), and recruitment (R). With regard to weight-at-age, there is evidence of dramatic changes for stocks where data were readily available. A striking example of a decline in the weight-at-age is shown in Figure A22 for the 4TVn cod stock in the Gulf of St Lawrence. At the beginning of the time-series, in the early 1970s, a 7-year-old cod weighed 2 kg; by the early 1990s, a 12-year-old cod weighed 2 kg. There was an almost constant decline in weight-at-age

over a 20-year period. The decline in weight-at-age might have been expected as a density-dependent response to the increasing population up to 1985, but the continuing decline, along with the decline in abundance after 1985, surely signalled a major change in the productivity of the ecosystem, or at least changes in the energy flow through the ecosystem.

With regard to the dynamics of SSB and F , normalized SSB and F is plotted in Figure A23. The abundance of the ensemble of cod stocks began to decline (1985–1990) before fishing mortality reached high levels; in other words, Figure A23 could be interpreted as a decrease in cod causing the increase in fishing mortality. Therefore, the general interpretation is that environmental factors were the primary cause of the post-1960s coherent fluctuations in cod abundance. The decline in average weight began in the early 1980s and could be related to the increase in cod abundance at that time. However, the continuing decline in average weight as the stock declined precipitously after 1985 signalled major changes in the ecosystem structure supporting cod and other stocks. These changes were undoubtedly related to a major change in the forage structure of the Northwest Atlantic. This is speculation, but there are a number of more-or-less local studies that support the contention. Unfortunately, there is no overview of a sub-basin-scale change in forage structure.

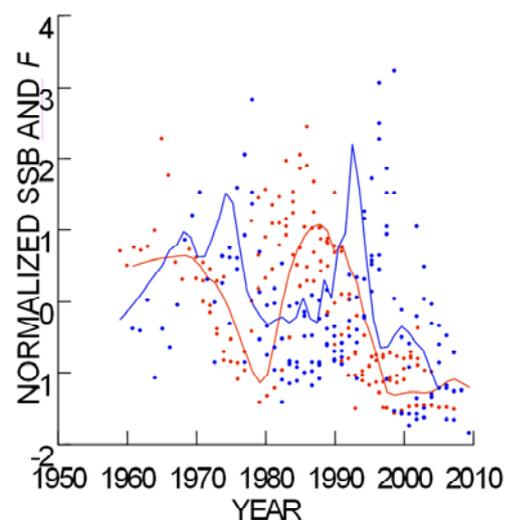


Figure A23. Ensemble of normalized spawning-stock biomass (SSB = red circles) and fishing mortality (F = blue circles) data from nominal stocks 3NO, 4TVn, 4VsW, 4X, and 5Z (see Figure A20). LOWESS smoothers (tension = 0.1) are fit through the data (red and blue lines).

Contributing to the puzzle is a possible climate effect, which is the occurrence of the great salinity anomaly in the Northwest Atlantic in 1972, the early 1980s, and the early 1990s. It could be reasoned that the anomalies reduced production and resulted in changes to the forage that affected cod abundance. These anomalies are significant from a climate point of view because increased run-off from the Canadian archipelago, coupled with the anomalies, would enhance the freshwater storage during the extensive ice years.

Although fishing did not seem to cause the coherent variations in cod, it is apparent that it played an important role in the sense that, as the stock declined, nominal fishing effort remained relatively constant whereas fishing mortality increased substantially, accentuating the decline.

List of acronyms and abbreviations

AMO	Atlantic Multidecadal Oscillation
CC	carrying capacity
CCC	ICES/GLOBEC programme on Cod and Climate Change
DePreSys	Decadal Climate Prediction System
EBFM	ecosystem-based fishery management
ENM	ecological-niche model
GCM	global circulation model
GLOBEC	Global Ocean Ecosystem Dynamics
IBM	individual-based model
IPCC	Intergovernmental Panel on Climate Change
LGM	last glacial maximum
MAR(1) model	first-order multivariate autoregressive model
NAO	North Atlantic Oscillation
NoAssim	a hindcast set which is identical to DePreSys but does not assimilate the observed state of the atmosphere or ocean
NPZD	nutrient–phytoplankton–zooplankton–detritus
RCM	regional climate model
SR	stock–recruitment
SSB	spawning-stock biomass
SST	sea surface temperature
STOCOBAR	STOck dynamics of COd in the BARents Sea
TAC	total allowable catch
THC	thermohaline circulation
VPA	virtual population analysis
WKCFCC	Workshop on Cod and Future Climate Change
WKEFA	Workshop on Integration of Environmental Information into Fisheries Management Strategies and Advice

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