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

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Future CO_2-induced climate change scenarios from Global Circulation Models (GCMs) indicate increasing air temperatures, with the greatest warming in the Arctic and Subarctic. Changes to the wind fields and precipitation patterns are also suggested. These will lead to changes in the hydrographic properties of the ocean, as well as the vertical stratification and circulation patterns. Of particular note is the expected increase in ocean temperature. Based upon the observed responses of cod to temperature variability, the expected responses of cod stocks throughout the North Atlantic to the future temperature scenarios are reviewed and discussed here. Stocks in the Celtic and Irish Seas are expected to disappear under predicted temperature changes by the year 2100, while those in the southern North Sea and Georges Bank will decline. Cod will likely spread northwards along the coasts of Greenland and Labrador, occupy larger areas of the Barents Sea, and may even extend onto some of the continental shelves of the Arctic Ocean. In addition, spawning sites will be established further north than currently. It is likely that spring migrations will occur earlier, and fall returns will be later. There is the distinct possibility that, where seasonal sea ice disappears altogether, cod will cease their migration. Individual growth rates for many of the cod stocks will increase, leading to an overall increase in the total production of Atlantic cod in the North Atlantic. These responses of cod to future climate changes are highly uncertain, however, as they will also depend on the changes to climate and oceanographic variables besides temperature, such as plankton production, the prey and predator fields, and industrial fishing.

Keywords: climate change, cod, North Atlantic, temperature.

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Introduction

Global Circulation Models (GCMs) predict significant warming around the globe under higher levels of greenhouse gases (IPCC, 2001). Although the amplitude of the warming varies according to the particular GCM used, they all show proportionately greater warming in the Subarctic and Arctic regions. Precipitation and the wind fields are expected to change also, although the uncertainty associated with these is much higher than that of temperature. These atmospheric changes will impact the ocean's water properties, circulation, and ultimately, the marine ecosystem. The increasing uncertainties involved in the progression from climate change to ocean response to ecosystem impacts have caused many to shy away from predicting possible ecosystem changes. However, politicians, fisheries managers, and, increasingly, the public are demanding predictions from scientists about the most likely outcome of such climate change. Given the implications of the predictions of GCMs, future planning must include, or at the very least, acknowledge the possibility of climate change and its ramifications. Therefore, it is paramount that, as knowledgeable scientists, we provide such information, while at the same time stressing the uncertainty of our predictions.

The approach taken in this paper is to couple current knowledge about the impact of climate variability on Atlantic cod (*Gadus morhua*) with predictions of future climate change. Cod was chosen because it is one of the most studied species in the North Atlantic, and our knowledge of its life history and its response to ocean climate variability surpasses that of most other fish species. It has a pan-Atlantic distribution (Figure 1) and inhabits waters with temperatures ranging from below −1°C to over 20°C, although

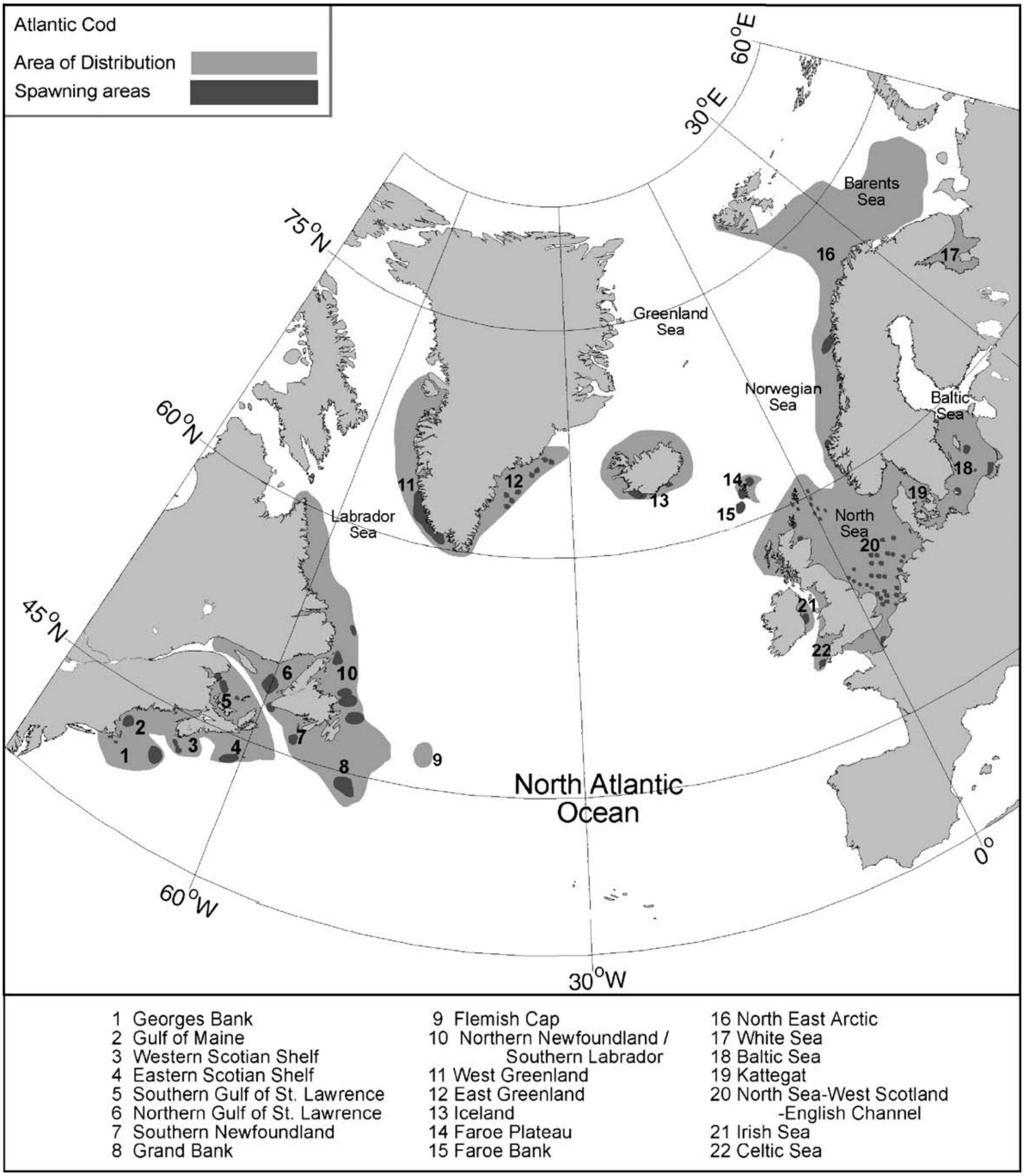

Figure 1. The present distribution of Atlantic cod.

usually they are found in waters with a temperature range of 0–12°C. Also, it is one of the most important commercial species in the North Atlantic, in spite of significant declines that have occurred in several regions during recent decades (e.g. Murawski *et al.*, 1997; O'Brien *et al.*, 2000; Astthorsson and Vilhjálmsson, 2002; Rice, 2002). Finally, the regions occupied by cod are expected to experience some of the largest anthropogenic climate changes in the world.

The focus of this paper is restricted to the impact of temperature changes on cod for two main reasons. First, the GCMs, in spite of high model-to-model differences in the amplitude of the temperature change, all predict a general warming. On the other hand, there is much greater uncertainty, even in the direction of the changes, about precipitation, freshwater discharge, and winds and, hence, general physical oceanography. Second, our understanding of the effects of temperature on cod far exceeds that of other environmental variables.

The following section reviews the effects of temperature and its variability on cod. Thereafter, I present some of the predictions from global circulation models for the areas inhabited by Atlantic cod. Finally, these two sections will be coupled to predict the response of cod to future climate change. The final section of concluding remarks includes a discussion of the uncertainties in the predictions.

Temperature effects on cod

Growth and condition

Mean bottom temperatures account for 90% of the observed (tenfold) difference in growth rates between different cod stocks in the North Atlantic, with warmer temperatures leading to faster growth rates (Brander, 1994, 1995). Temperature accounts for not only differences in growth rates between juvenile and adult cod from different stocks, but also year-to-year changes in growth rates within most cod stocks (Brander, 1995, 2003; Campana *et al.*, 1995; de Cárdenas, 1996; Clark *et al.*, 2003). Likewise, growth rates of cod larvae are temperature dependent (Otterlei *et al.*, 1999; Jordaan and Kling, 2003). Field and laboratory studies show that the temperatures at which maximum growth rates of juvenile and adult cod are size dependent (Björnsson and Steinarsson, 2002; Brander, 2003). These temperatures lie in the range 10−15°C, growth rates of larger fish peaking at lower temperatures. Reduced growth rates at the extreme ends of the temperature range are, in part, due to changes in feeding rates. Laboratory experiments by McKenzie (1934, 1938) found that adult cod ate well at temperatures within their normal tolerance range, but ceased feeding at very low (<0°C) and very high (>17°C) temperatures, even in the presence of sufficient available food.

In addition to growth, the condition of cod varies with temperature. Rätz and Lloret (2003) found a significant correlation between mean bottom temperature of the cod stock and Fulton's condition index (K) for the ten cod stocks they examined. Stocks in warmer waters were in better condition, with K rising by approximately 0.02 for every 1°C temperature increase.

Spawning and reproduction

Temperature also affects the reproductive cycle through influences on the age of maturity. Drinkwater (2002) combined the age of maturity of different cod stocks found by Hutchings and Myers (1993) with mean annual bottom temperatures from Brander (1994), and found a significant relationship between the two variables. The age of maturity decreases approximately one year for every 2°C increase in bottom temperature.

Spawning times are influenced by temperature as well. Typically, higher temperatures result in earlier cod spawning through faster gonad development, as has been observed, for example, on the northern Grand Bank (Hutchings and Myers, 1994a). However, the relationship between temperature at the spawning site and time of spawning depends on local hydrography and fish distribution. In contrast to the positive relationship between local temperatures and time of spawning found on the northern Grand Banks, years with low temperatures on St. Pierre Bank off southern Newfoundland led to earlier cod spawning (Hutchings and Myers, 1994a). These fish reside in warm offshore waters and move to St. Pierre Bank prior to spawning. In very cold years, they delay their migration to the Bank, thereby remaining in the warmer offshore waters longer, which results in faster gonad development and hence an earlier readiness to spawn.

Miller *et al.* (1995) found that temperature accounts for 52% and 70% of the seasonal variance of egg and larval size-at-hatch, respectively, for Atlantic cod on the Scotian Shelf, with size decreasing as temperature increases in the range 2−14°C. Cod egg incubation times are also temperature dependent. Page and Frank (1989) found that they varied from 8 to 42 days at 14 and 1°C, respectively, for Atlantic cod on the Scotian Shelf. Thus, eggs in colder water are more vulnerable to predation owing to longer stage duration and may, therefore, experience lower survival.

Distribution and migration

Temperature is one of the primary factors, together with food availability and suitable spawning grounds, in determining the large-scale distribution pattern of fish and shellfish, including cod. Because most fish species or stocks tend to prefer a specific temperature range (Coutant, 1977; Scott, 1982), an expansion or contraction of the distribution range of species often coincides with long-term changes in temperature. These changes are most evident near the northern or southern boundaries of the species range; warming results in a distributional shift northward, and cooling draws species southwards for both warm- and cold-water species (Rose, 2005).

Several studies have indicated significant distributional changes in cod. One of the best documented was off west Greenland in response to the large-scale, North Atlantic-wide warming during the 1920s and 1930s (Rogers, 1985; Johannessen *et al.*, 2004). As the water warmed, cod gradually spread from southern Greenland up to Disko Island, a distance of approximately 1200 km, in less than 20 years (Jensen and Hansen, 1931; Hansen, 1949). Cod inhabited these waters until the 1970s when they all but disappeared, parallelling a decline in water temperature (Hovgard and Buch, 1990). Similar northward movements of cod occurred elsewhere in the northern North Atlantic. For example, cod spawning off Iceland prior to the warming was primarily restricted to the southern shelf regions. However, as the waters warmed around Iceland, cod spawning spread to the north shelf areas, thereby surrounding the island (Sæmundsson, 1934; Vilhjálmsson, 1997). With the dramatic cooling around Iceland in the 1960s, cod spawning largely ceased in the north and returned to the pattern observed prior to the warming. In the Barents Sea, cod appeared in large quantities on Bear Island Bank in response to the warming of the early 20th century, resulting in the re-establishment of a cod fishery there after an absence of almost 40 years (Blacker, 1957). Cod also penetrated farther east to Novaya Zemlya and north off West Svalbard, during the 1920s (Beverton and Lee, 1965).

During the warm period of the early 1990s in the Barents Sea, there was a general eastward movement of age 3 cod (Ottersen *et al.*, 1998), consistent with the response observed in the 1920s and 1930s. However, there was also an increase in the population abundance during the 1990s, so the relative importance of the environment vs. population size relationship in causing this distributional shift is unknown. On the opposite side of the Atlantic over the continental shelf off Labrador to the Grand Banks, the cold waters of the late 1980s and early 1990s were suggested as the cause of a southward shift in cod distribution (deYoung and Rose, 1993; Rose *et al.*, 1994, 2000; Taggart *et al.*, 1994; Atkinson *et al.*, 1997; Drinkwater, 2002). This occurred at the same time as the dramatic decline in the abundance of the cod, and some researchers suggested that the apparent shift in cod distribution was caused by spatial fisheries patterns, i.e. northern populations being fished out earlier than populations farther south (Hutchings and Myers, 1994b; Hutchings, 1996; Myers *et al.*, 1996). However, a physical southward movement of cod is supported by analysis of blood chemistry, in particular, the amount of antifreeze levels in the blood (Rose *et al.*, 2000), genetics (Ruzzante *et al.*, 2001), and the southward movement of many other commercial and non-commercial species (Gomes *et al.*, 1995; Drinkwater, 2002).

Abundance and recruitment

Recruitment levels of individual cod stocks frequently have been associated with variations in temperature during the first year of life (e.g. Hermann *et al.*, 1965; Sutcliffe *et al.*, 1977; Sætersdal and Loeng, 1987). The strength, and even the sign, of the relationship between temperature and cod recruitment varied between stocks, however. A comparative analysis of the temperature-recruitment relationship for many of the cod stocks in the North Atlantic by Planque and Frédou (1999) provided insight into the reasons for the variability in the relationships (Figure 2). They found that the sign of the relationship between sea surface temperature (SST) and recruitment was generally positive for cold-water stocks (adults which inhabit bottom temperatures $\leq 6°C$) and negative for warm-water stocks (adults which inhabit bottom temperatures $\geq 9°C$). Stocks in the mid-range of bottom temperatures (7–8°C) tended to have little or no relationship between SST and recruitment.

In a study of North Sea cod under climate change, Clark *et al.* (2003) estimated a 30% decrease in recruitment in response to a 0.25°C increase in temperature. They further noted that continuation of current fishing levels in combination with expected temperature increases would lead to a faster rate of decline in the North Sea stock than if temperature changes were not considered.

Climate scenarios

To quantitatively analyse the response of each of the cod stocks to anthropogenic warming, we need coupled atmosphere–ocean regional models to determine the extent of the warming. Because these are not yet available, I have chosen to use the IPCC (2001) multi-model scenarios for an indication of the rise in temperature that can be expected in the waters occupied by cod. Figure 3 shows the expected air temperature changes by 2100 in North Atlantic regions occupied by cod, based on the model results. Similar changes are expected in the upper layer ocean temperatures (Loeng *et al.*, in press). Examination of the temperature variability in the regions occupied by cod suggests that the amplitude of temperature anomalies change little with depth, over the depth ranges where cod are found (K. Drinkwater, unpublished data). Therefore, I have assumed that these temperature changes are at least an indication of what will be experienced by cod stocks inhabiting the continental shelves. Most cod are caught between 50 and 400 m, although they certainly are not restricted to these depths.

The mean temperature change by the year 2100 ranges from a minimum of 2–3°C to upwards of 6°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. The uncertainties in the rise in temperature for most areas, however, are comparable to the means (IPCC, 2001).

Cod stock responses to warming temperatures

What will be the impact on the cod stocks throughout the North Atlantic given the above temperature scenarios? Because the predicted temperature changes are based on GCMs and not on regional models, they can only be considered as a rough guide. My approach is, therefore, largely qualitative and considers the general response to progressive temperature changes in terms of distribution, growth, maturity, and recruitment.

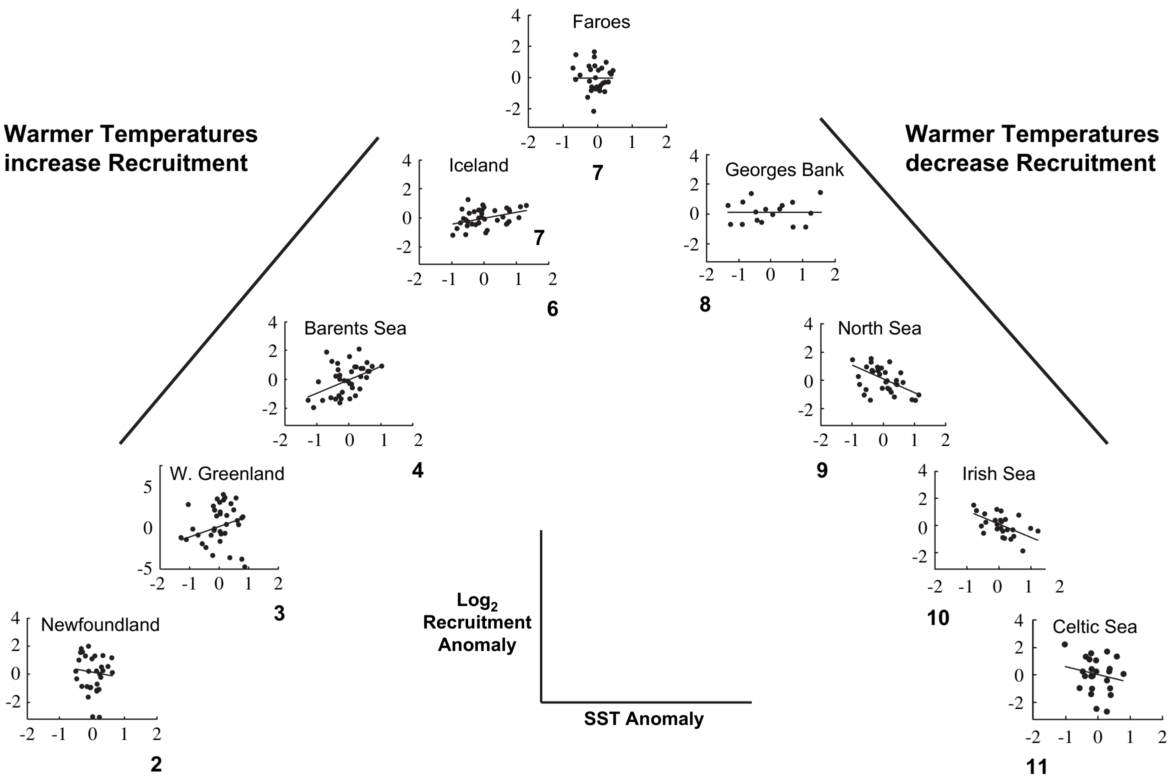

Figure 2. The relationship between the $\log_2$ of the recruitment anomaly and sea surface temperature (SST) anomaly in °C for various cod stocks. The large axis in the bottom centre of the diagram shows the axis legends for all of the plots. The numerical value at the bottom of each plot represents the mean annual bottom temperatures for the stocks. Note that stocks are plotted with bottom temperature increasing to the right. For the cold-water stocks, the SST-recruitment relationship is generally positive while for the warm-water stocks it is negative. There is no relationship in the mid-temperature range. Modified from Planque and Frédou (1999).

Abundance and recruitment

To predict the abundance response of current cod stocks to future warming, I have relied heavily upon the following. First, cod stocks are not observed much above annual mean bottom temperatures of 12°C (Dutil and Brander, 2003). The reason for this is unclear. It may be that the metabolic costs are too high or that cod cannot compete successfully with other species at such warm temperatures. Surface temperatures are generally much higher than bottom temperatures, so another possibility is that the eggs and larvae cannot survive in such warm waters. Regardless of the cause, I assume that this relationship will continue in the future. Thus, if bottom temperatures warm beyond 12°C, I assume that cod will disappear, either through moving into colder waters or because of high mortality.

Second, the temperature-recruitment relationships found by Planque and Frédou (1999) were converted into a change in recruitment per unit change in SST and plotted against the mean annual bottom temperature of the stock (Sundby, 2000) (Figure 4). Note that the SST-recruitment relationship for northern cod in Figure 4 is positive, while that estimated by Planque and Frédou (1999) was slightly negative (Figure 2). Planque and Frédou (1999) used SSTs from an extensive region off Newfoundland and Labrador and noted the large uncertainty in the estimates of the temperature variability in this region. Their results for northern cod also conflicted with the positive relationship between temperature and recruitment for this same stock found by deYoung and Rose (1993). As a result, I recalculated the relationship using a more representative temperature time-series than the one used by Planque and Frédou (1999). A continuous monitoring site exists off eastern Newfoundland (known as Station 27), which has been shown to represent low-frequency temperature variability through southern Labrador, the northeast Newfoundland shelf, and the Grand Banks (Petrie *et al.*, 1992). These areas constitute the geographical range of the northern cod. Using Station 27 data, a positive relationship between recruitment and temperature was found and is consistent with the results of deYoung and Rose (1993).

Figure 4 suggests that at bottom temperatures <5°C, recruitment increases with increasing SST, and at bottom temperatures >8.5°C, recruitment decreases. At bottom temperatures between these two values, there is little

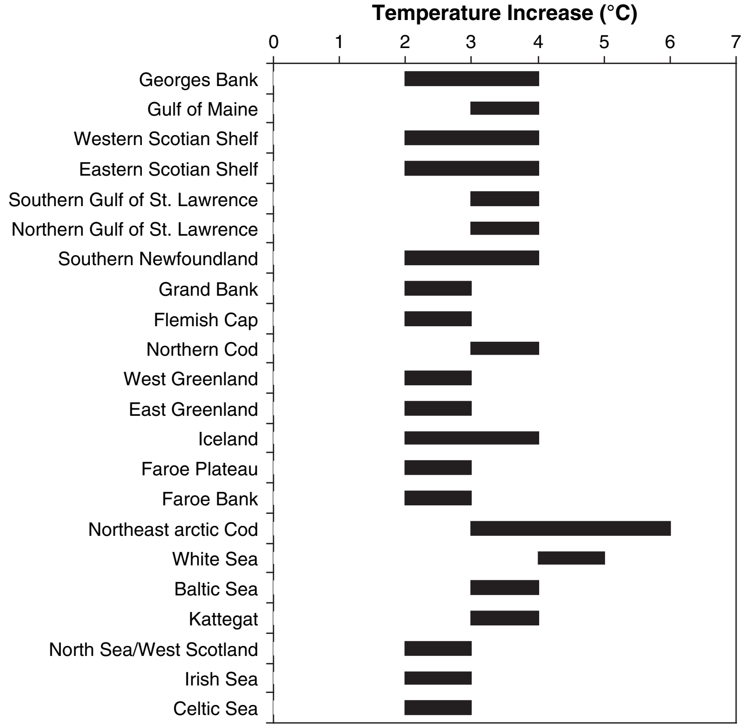

Figure 3. The anticipated range of the increase in the annual mean temperatures by the year 2100 in the continental shelf waters occupied by cod for different stocks, based on the multi-model results published by the IPCC (2001). The location of the cod stocks is given in Figure 1. Note, Northern cod is stock 10 in Figure 1.

change in recruitment with changes in SST. 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 of approximately 8 °C and there is currently no relation between SSTs and recruitment (Planque and Frédou, 1999) (Figure 2). However, if mean bottom temperatures increased by just 1 °C, then based upon Figure 4, it would be expected that recruitment would become temperature dependent, resulting in decreasing recruitment based on warmer SSTs. If higher SSTs were to continue, this would tend to reduce the stock further. Next, I consider what would happen to each of the stocks for uniform mean temperature increases of 1–4 °C (Figure 5).

With a sustained 1 °C change, several of the southern cod stocks become stressed. I predict that the cod stocks in the Celtic Sea and the English Channel would eventually disappear as waters warm above 12 °C, as is likely (Figure 3). Stocks in the Irish Sea, the southern North Sea, and Georges Bank would decline owing to decreasing recruitment with increasing temperatures. On the other hand, cold-water stocks, such as most of those off eastern Canada, and off Greenland, in the Barents Sea, and the Kara Sea would benefit from increased recruitment owing to the warmer waters. The recruitment levels of the remaining stocks would not change appreciably. As the temperature increased to 2 °C above current values, it is expected that the Irish Sea stock would disappear. The Georges Bank and North Sea stocks would continue to decline, and the stocks in the Kattegat, off West Scotland, and 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 see any change

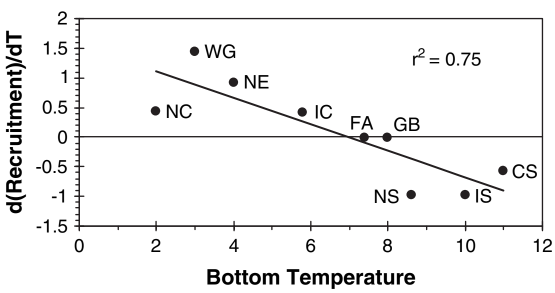

Figure 4. The rate of change in recruitment per unit change in sea surface temperature as a function of bottom temperature (°C) for various cod stocks. (NC = Northern Cod, WG = West Greenland, NE = Northeast Arctic Cod, IC = Iceland, FA = Faroes, GB = Georges Bank, NS = North Sea, IS = Irish Sea, and CS = Celtic Sea).

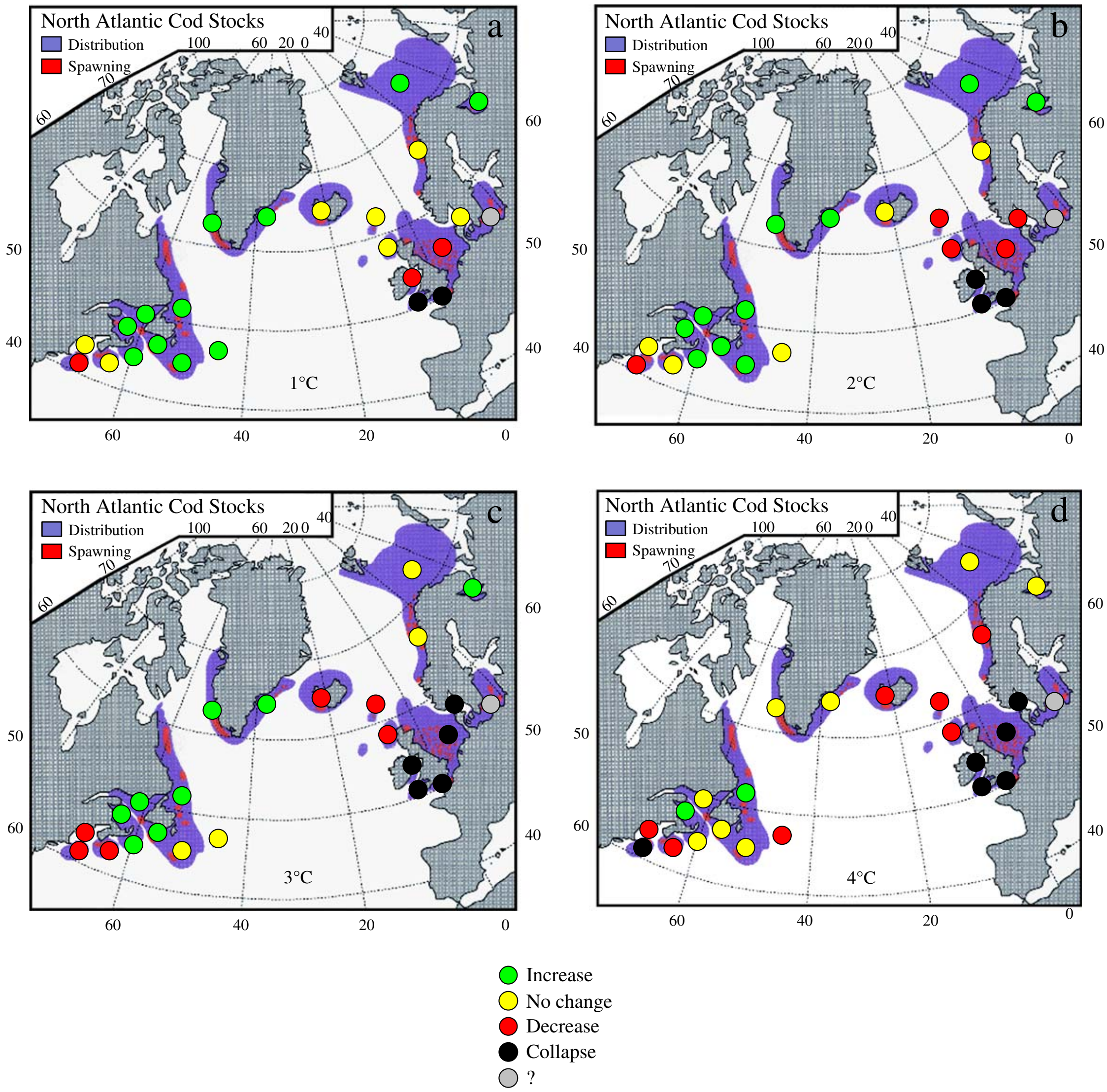

Figure 5. Expected changes in the abundance of the cod stocks with a temperature increase of (a) 1 °C, (b) 2 °C, (c) 3 °C, and (d) 4 °C above current levels.

in recruitment. At a temperature increase of 3 °C, we could expect to see the disappearance of the Kattegat and North Sea stocks. The southernmost stocks in the western Atlantic (Georges Bank, the Gulf of Maine, and the Browns Bank/Bay of Fundy) would all 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 of 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. If there were a 4 °C temperature change, the Georges Bank stock is likely to disappear. The Norwegian coastal cod stocks would begin to see declining recruitment along with the Flemish Cap stock. The recruitment of the eastern Scotian Shelf, northern Gulf of St. Lawrence, southern Newfoundland, Greenland, and 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. It should be noted that even small changes in the recruitment rates, either positive or negative, could lead to potentially large increases or decreases, respectively, in the abundance of the individual cod stocks.

Range extension

It is quite clear that, with future warming, there will be a northward migration of cod similar to the response observed during the warm periods in the 20th century. But how far north could they go? Cod can be expected to occupy the entire Labrador Shelf as they did during the warm period of the 1950s and 1960s and, perhaps, extend farther north along the Baffin Island Shelf. They would also be expected to occupy the West Greenland coast north of Disko Island as in the 1930s to the 1960s, as well as the east Greenland coast as far north as the Denmark Strait. They will increase their numbers off northern Iceland and, in the Barents Sea, will spread east to Nova Zemlya and north as the Polar Front moves northeastwards. They will also spread northwards along western Svalbard. All of these range extensions have been observed in the past and so would not be surprising. Could the cod extend further into the high Arctic? This is possible, if the regions were free of ice in at least the summer period, as the coupled GCMs predict. Thus, cod may extend to the northern Kara Sea, if only to migrate there in summer. The critical conditions are whether they would have sufficient food and access to warm enough winter temperatures. Currently, several stocks occupy cold waters in summer, but migrate into warmer waters in winter (Gulf of St. Lawrence, Newfoundland/Labrador, Barents Sea, etc.). Since cod are believed to feed little in the winter, inhabiting warmer water at this time, when the metabolic costs would be higher, does not seem to be in their best interests. It is likely, however, that the warmer water may be required for gonadal development. If indeed this is the case, and based on current stocks requiring a minimum of approximately 4°C in winter, the question of how far cod might be able to penetrate into the Arctic might depend on their ability to migrate into such warm waters during winter.

Additional changes

In addition to the possible disappearance and decline in the southern stocks, an increased abundance of the northern stocks, and a northward range extension, we might also expect other changes. These are likely to include changes in migration times for stocks undertaking annual movements from their over-wintering grounds to their summer feeding and spawning areas. The feeding period would be extended since cod would be expected to arrive earlier to their summer feeding grounds and leave later. For example, for the southern Gulf of St. Lawrence stock, the migration onto the summer grounds is triggered by the disappearance of sea ice (Sinclair and Currie, 1994). Under future warming, less ice should mean an earlier migration into the southern Gulf from the over-wintering area in the Laurentian Channel. In areas where the seasonal ice cover will disappear altogether, there might not be a need to migrate at all. This would depend on sufficient winter temperatures for gonadal growth and sufficient prey as discussed above.

For regions where mean bottom temperature does not exceed 12°C, cod production usually increases with temperature (Dutil and Brander, 2003). Coupled with anticipated distributions of the northward extensions, the overall production of Atlantic cod should, therefore, increase, even with the potential disappearance of some of the southern stocks. Also, I might have overestimated the negative effect on those southern stocks, since the warming is generally estimated to be less for the southern regions than the maximum 4°C scenario I used (Figure 5). In addition, warming in northern regions could exceed 4°C, which would lead to even higher production rates. The increase in production would be caused by improved growth rates, better condition fish, and higher recruitment. Also, since mortality is generally linked to growth rates, survival of young fish should increase with the higher growth rates if predator−prey relationships remain unchanged.

Spawning locations should extend northwards, as was observed during the warming of the 1920s and 1930s. This pattern was observed in Iceland where spawning expanded to the northern side of the island where previously it was primarily limited to the south coast (Vilhjálmsson, 1997). Also, along the coast of Norway, proportional spawning increased in the north and decreased in the south during the same period (Sundby and Nakken, 2005). With higher temperatures, gonadal development is quicker, resulting in earlier spawning. With the faster growth rates, the age of maturity is likely to decrease, meaning that more of the population will be sexually mature, which in turn should add to the increased production.

Concluding remarks

Anthropogenic warming is projected to lead to increased air and sea temperatures globally and proportionately higher increases in the Arctic and Subarctic regions (IPCC, 2001). Indeed, much recent evidence indicates that dramatic warming is already occurring (ACIA, 2004). This includes rising air and sea temperatures, melting glaciers, decreasing sea ice and shrinking permafrost. These changes in the climate and physical oceanography are producing responses in the marine ecosystem and will continue to do so in the future if the warming continues. I have outlined some of the changes that I believe are likely to occur to Atlantic cod in the North Atlantic in response to increased warming, based on the current understanding of the effects of temperature variability on cod. The responses include the disappearance of some of the southern cod stocks currently occupying the warmest waters, an extension in distribution northwards, perhaps including the area beyond the Barents Sea farther into the Arctic, and likely establishment of newer spawning sites in the north. There should be earlier migrations from the over-wintering grounds and, in areas where ice disappears, migration could end altogether. Spawning would likely occur earlier with faster gonadal development, and the average age of maturity is expected to decrease. There will be higher growth rates and fish in better condition in most of the regions, which will lead to an overall higher production of Atlantic cod.

These projections have been made ignoring other important human impacts, such as industrial fishing or unanticipated ecosystem reorganization. We know that fishing has played and will continue to play a strong and, in some cases, a dominant role in fish abundance, distribution, and growth. It is argued that fishing has played a major role in the collapse of the northern cod stocks (Hutchings and Myers, 1994b; Hutchings, 1996), as well as the decline in other Northwest Atlantic cod stocks (Sinclair and Murawski, 1997) and North Sea cod (Cook *et al.*, 1997). However, it is clear that both fishing and climate interact so that both have contributed to some of the recent declines (Drinkwater, 2002; Clark *et al.*, 2003). Thus, projections made in this paper will be highly dependent on the reaction of the fishing industry. The disappearance of the southern stocks will occur more rapidly than climate warming would suggest if fishing intensity continues at its current rate (e.g. Clark *et al.*, 2003). If these stocks are to be preserved, fishing pressure must ease as warming increases. Even with a relaxation of fishing pressure, climate changes may still be enough to cause the stocks to disappear. The prediction that cod will move northwards along the Labrador coast is, in part, based on a healthy cod stock to the south. In spite of the fisheries moratorium on northern cod, as well as on the eastern Scotian Shelf cod stock for more than ten years, these stocks have not returned or recovered. Recent work on the latter region indicates that major ecosystem changes have occurred with the increase of pelagics, the displacement of the large demersals with smaller ones, and a general decline in the overall community condition index (Choi *et al.*, 2004). These changes coincided with decreases in temperature and with major changes in the fisheries. Regardless of the cause, large-scale ecosystem changes may explain, in spite of the moratorium, why the cod have not shown signs of recovery. This emphasizes that future changes to cod will also depend on the changes to other parts of the ecosystem. This will include changes in the primary and secondary production in the North Atlantic and, more specifically, to the food base for larval, juvenile, and adult cod. The former includes *Calanus finmarchicus*, arguably the most important food item for cod (Sundby, 2000), although several cod stocks feed on other zooplankton. It is of interest that, in some cases, the appearance of *C. finmarchicus* had negative effects on cod recruitment (Gaard, 1999; Drinkwater *et al.*, 2000). If fishing reduces current cod stocks to minimal levels, there may not be enough cod remaining to expand and drive the increased production in response to increasing temperature, certainly not to the extent that could potentially occur, given reduced fishing. Also, the expanding and increasing cod production may be reduced quickly through increased quotas or TACs, thereby limiting the overall production increase and the extent of the geographic expansion.

I have only considered changes in ocean temperatures associated with local atmospheric heating. Temperature may also change substantially owing to variations in the circulation patterns, as well as in the strength of the mixing and stratification, and these, in turn, could affect biological components of the ecosystem important to cod. I have not dealt with these latter properties because of the much higher uncertainty in variables such as wind and precipitation.

Finally, it is important to note that the response to temperature change is not, in most cases, a direct response, but rather an indirect response to changes in prey or predators. For example, Beaugrand *et al.* (2003) showed that, in the Northeast Atlantic, one of the consequences of climate variability is a distributional and abundance shift between the northern zooplankton species *C. finmarchicus* and the more southern species *C. helgolandicus*. As temperature warms, the boundary between the two species moves north and, where their distributions overlap, the latter becomes relatively more important. The spring-spawning *C. finmarchicus* is an important prey of cod larvae, while *C. helgolandicus* spawns in the autumn and does not constitute an important component of the diet of larval cod. Thus, Beaugrand *et al.* (2003) hypothesized that the reason cod do not do well under warm conditions in southern regions of the Northeast Atlantic is because of lesser recruitment owing to lack of *C. finmarchicus*. Also, during the intense warming of the northern North Atlantic in the 1920s and 1930s when cod spread northwards off west and east Greenland, Iceland, and into the Barents Sea, this is considered to be a result of increased phytoplankton and zooplankton production in response to the warming (Drinkwater, in press).

While the predictions presented herein remain highly uncertain, I believe that they are a reasonable first approximation based on past observations and expect Atlantic cod will respond in accordance with anticipated warming of the sea. However, with the rapid increase in modelling capabilities, the development of coupled regional models, and improved understanding of the physics, the biology, and the effects of fishing, it is to be hoped that, in the near future, the public, the politicians, and the fisheries managers can look forward to better and more quantitative predictions of responses to global change, of not only Atlantic cod but other fish species and the ecosystem as a whole.

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