

Climate induced increases in species richness of marine fishes

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Abstract

Climate change has been predicted to lead to changes in local and regional species richness through species extinctions and latitudinal ranges shifts. Here, we show that species richness of fish in the North Sea, a group of ecological and socio-economical importance, has increased over a 22-year period and that this rise is related to higher water temperatures. Over eight times more fish species displayed increased distribution ranges in the North Sea (mainly small-sized species of southerly origin) compared with those whose range decreased (primarily large and northerly species). This increase in species richness can be explained from the fact that fish species richness in general decreases with latitude. This observation confirms that the interaction between large-scale biogeographical patterns and climate change may lead to increasing species richness at temperate latitudes.

Keywords: biodiversity, biogeography, climate change, extinction, fisheries, global warming, North Sea, species richness

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Introduction

The Earth's climate has warmed by approximately 0.6 °C over the past 100 years (Walther *et al.*, 2002) and temperature is expected to continue rising. Higher temperatures have a strong effect on the distribution, abundance and assemblage composition of fishes (Cushing & Dickson, 1976; Attrill & Power, 2002; Gerner *et al.*, 2004; Perry *et al.*, 2005; Kirby *et al.*, 2006), through changes in growth, survival and reproduction. Therefore, climate change has been predicted to lead to species extinctions (Thomas *et al.*, 2004) and to a poleward shifting of the latitudinal distribution ranges of species (Parmesan & Yohe, 2003; Perry *et al.*, 2005). Both these processes are likely to lead to changes in local species richness. To date, most studies of the ecological effect of climate change have concentrated on the impact at the individual species level rather than on community metrics such as species richness (but see Menéndez *et al.*, 2006; Henderson, 2007).

When species' ranges shift at the rate that is dictated by climatic warming, the composition of local communities will change in response. Communities at tempe-

rate latitudes will gain species from equatorial directions, for which the higher temperatures that were previously too cold become suitable, and lose species to pole-ward regions, for which conditions become too warm. However, if species are unable to shift their range pole ward at the rate that is necessary to stay within their preferred temperature range, species richness in the receiving area of higher latitude will decline, possibly leading to a breakdown of ecosystem functioning. This may be relevant for the integrity of ecosystems, as recent studies show that species richness has an effect on the rate and stability of ecosystem functioning, such as primary and secondary production (Hooper *et al.*, 2005) and is important for human well-being (Díaz *et al.*, 2006). Coastal marine ecosystems are globally among the most socio-economically and ecologically important habitats and changes in fish species richness may change the nature and value of commercial fisheries.

It is generally recognized that for most taxonomic groups and ecosystems, species richness decreases with latitude (Willig *et al.*, 2003) and that this is related to climate, although the causes are under debate (Clarke & Gaston, 2006). Because of this relationship, cool-temperate regions that experience warming can be expected to exhibit increases in richness, provided that all species can physically reach new suitable habitats. This

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depends on the dispersal abilities of the species and the presence and connectivity of suitable habitats. The net effect of higher temperatures on species richness in a certain region therefore depends on the number of species gained from lower latitudes vs. the number of species lost to higher latitudes. Marine fish species richness in the Atlantic Ocean decreases with latitude and correlates positively with sea surface temperature (Macpherson & Duarte, 1994; Macpherson, 2002). Increasing temperature due to climate change may, therefore, lead to a northward shift of latitudinal patterns and lead to an increase of local and regional fish species richness at temperate latitudes, because the number of species lost is lower than the number of species gained.

Many animals are limited in their dispersal abilities. For example, most butterfly species cannot cross open sea or other large areas of unsuitable habitat. This can prevent a northward expansion of the ranges of individual species with increasing temperatures, resulting in a negative effect of climate change on species richness (Menéndez *et al.*, 2006). Marine fish are generally less restricted in their dispersal abilities. Many marine fishes undertake long-distance migrations (>100 km) each year (Turner *et al.*, 2002), or have pelagic larvae that are carried along by ocean currents (Shackell *et al.*, 1999). Also, the continental shelves provide a continuous band of suitable habitat in ways of the water column itself and soft bottom habitats and most temperate continental fish live in these habitats. Because of their high dispersal abilities and a continuous habitat, soft-bottom and pelagic marine fish communities are one of the groups that is most likely to face increases in species richness as a result of global warming. In the current study, we have examined large-scale and long-term climate-related changes in fish species richness in the North Sea, a soft bottom basin (average depth 90 m; area about 570 000 km²), by using a long-term (1985–2006) and large-scale (>10° of longitude and latitude) fish survey. We examined climate-induced changes in temperate fish communities, as opposed to individual species (Beare *et al.*, 2004; Perry *et al.*, 2005), at a much larger spatial scale than previous community level studies (e.g. Genner *et al.*, 2004; Henderson, 2007). This study observed the increase in species richness due to climate change that can be predicted from biogeographical patterns in species richness. The results demonstrate that climate change has not led to loss of biodiversity of North Sea fish and has a positive effect on species richness through an increase of small, southerly species.

Methods

Winter bottom temperature data were obtained from the International Council for the Exploration of the Sea

(ICES) oceanographic database for 1° × 1° boxes in the North Sea. We defined the bottom as the deepest 25% of the water column and winter as the period of January to March. Temperature data were available from 1977 up to 2003. To ensure a balanced dataset, missing data were interpolated from neighbouring 1° × 1° boxes by averaging the temperature for the four directly neighbouring cells. This interpolation was performed for just under 10% of year-box combinations.

Annual data describing fish distribution (including elasmobranchs) in the North Sea (between 51 and 62° latitude) for 1985–2006 were taken from the ICES-coordinated International Bottom Trawl Survey (IBTS) programme. Over this period, six countries annually sampled by standardized protocol more than 300 stations in the first quarter of the year (January–March), leading to a dataset with catch data of over 7000 hauls. The survey design is random stratified according to a grid of ICES rectangles (0.5° latitude; 1° longitude; approximately 56 × 56 km²). In principle, each rectangle was sampled by two different countries each year, using a standard bottom-trawl net (chalut à Grande Ouverture Verticale, GOV-trawl), a trawl that is specifically designed to sample both demersal and pelagic fish (Heessen *et al.*, 1997). It is assumed that the vast majority of species present at a station are sampled using this gear. Rough grounds were avoided in the survey to prevent gear damage, as are inshore stations, so conclusions from this study are only valid for fish communities on and over sedimentary habitats. Large pelagic species and species that primarily live on rough grounds will not have been sampled representatively. The catch was sampled to provide the total catch and length frequency for all fish species caught. Because of unpredictable circumstances such as gear failure or bad weather, the same number of stations was not sampled each year. To standardize the dataset, we randomly chose one haul per ICES rectangle per year. We chose for this option, rather than averaging the species richness by rectangle, to allow an estimate of the number of rectangles occupied by individual species per year. To avoid the introduction of temporal trends that may be related to changes in the sampled survey area over time, only rectangles that were sampled in at least 18 out of 22 years were used in our analysis. In total, 141 of the 159 fished ICES rectangles were used in the analysis. The dataset was corrected for misidentifications (Daan, 2001; ter Hofstede & Daan, 2006). Fish were identified to the lowest possible taxonomic level, which was mostly to species level. Out of the 118 taxa recorded, six taxa were multispecies groups (*Mustelus mustelus* and *Mustelus asterias*, *Alosa alosa* and *Alosa fallax*, *Salmo salar* and *Salmo trutta*, *Syngnathus rostellatus* and *Syngnathus acus* and *Syngnathus typhle*, *Ammodytes tobianus* and *Ammo-*

dytes marinus and *Gymnammodytes semisquamatus*, *Pomatoschistus minutus* and *Pomatoschistus pictus*). However, for consistency we refer to all taxa as species.

North Sea species richness was related to the average winter temperature over the previous 5 years. To explain observed patterns, the trends in the number of rectangles occupied for each individual species was calculated as the slope of the linear regression of \log_{10} (number of rectangles occupied + 1) vs. year. We only used the trends from species where the trend was significant and residuals normally distributed (Shapiro–Wilk normality test) for further analysis. These trends were related to species life history [L_{∞} , the theoretical maximum length in growth models, a parameter that is closely related to other life-history parameters such as length at maturity, mortality rate and population growth rate (Levin *et al.*, 2006)] and reported latitudinal boundaries (Froese & Pauly, 2004). Species with known identification problems were flagged (Daan, 2001; ter Hofstede & Daan, 2006).

If the relationship between temperature and species richness was found to be stable in time, changes in temperature can be assumed to explain observed changes in species richness. If the relationship was found to be different for two periods, it means that species richness has changed at a different rate than could be predicted from temperature changes alone. The relationship between species richness and temperature was estimated in space for two time periods of 9 years (1985–1993 and 1994–2003).

Results

The average winter bottom temperature in the North Sea has increased significantly from 1977–2003 at a rate of $0.7^{\circ}\text{C decade}^{-1}$ ($R^2 = 0.43$, $F_{1,25} = 18.6$, $P = 0.0002$, Fig. 1). In the North Sea, there seems to be a marked increase in bottom temperatures from 1987 to 1988. This pattern mimics the pattern of cool temperatures from the cold winter of 1962/1963 onwards and a warming of

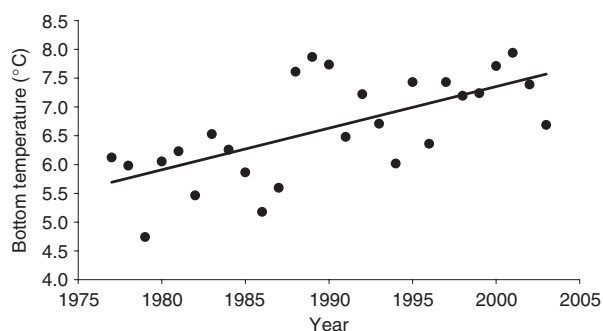


Fig. 1 Average winter bottom temperature in the North Sea 1977–2003.

regional sea-surface temperature since the 1980s that was observed in the English Channel (Hawkins *et al.*, 2003; Southward *et al.*, 2005).

The average species richness of the North Sea fish fauna has increased from 1985 to 2006, both at the scale of the ICES rectangle and for the whole North Sea (Fig. 2a and c). Species richness was significantly positively correlated to average winter bottom temperature over the previous 5 years (Fig. 2b and d). The areas with the highest winter bottom temperatures had the highest species richness throughout the studied period (Fig. 3). The slope of the relationship between water temperature and species richness remained the same throughout the examined period and there was no significant interaction between period and temperature (Fig. 3). However, as the effect of period was significant, species richness also increased over time independently of temperature.

Fish species whose distribution range expanded, contributed to the increase in local species richness. Such fish species were generally small-sized and close to their northern latitudinal boundary (i.e. southerly species), while fish that decreased their range were large species and far from their northern latitudinal boundary (Fig. 4). Distance from southerly latitude boundary did not have an effect on the distribution trend ($P > 0.05$). Over eight times more fish species displayed increased distribution ranges in the North Sea compared with those whose range decreased. Only three species showed decreased range sizes: the wolffish *Anarhichas lupus*, the spurdog *Squalus acanthias* and the ling *Molva molva*; all three large species have a high northern latitudinal boundary ($> 73^{\circ}\text{N}$). Thirty-four species displayed significant increases in distribution ranges. The five fish whose ranges expanded most were anchovy *Engraulis encrasicolus*, red mullet *Mullus surmuletus*, scaldfish *Arnoglossus laterna*, solenette *Buglossidium luteum* and lesser weever *Echiichthys vipera*. These are all small species with a northern latitudinal boundary at a relatively low latitude ($59\text{--}64^{\circ}\text{N}$, compare in Fig. 4a). As the northern latitude limit was not different for species with and without noted identification problems (ANOVA, $F_{1,90} = 0.11$, $P = 0.74$), identification problems did not bias the relationship between the trend in distribution and northern latitude limit.

Discussion

Sea surface temperatures can deviate greatly from sea bottom temperatures. Therefore, in contrast to some earlier studies (e.g. Beare *et al.*, 2004, one dataset in Genner *et al.*, 2004), in this study we related species richness of fish to bottom temperature rather than to surface temperature. The average winter bottom tem-

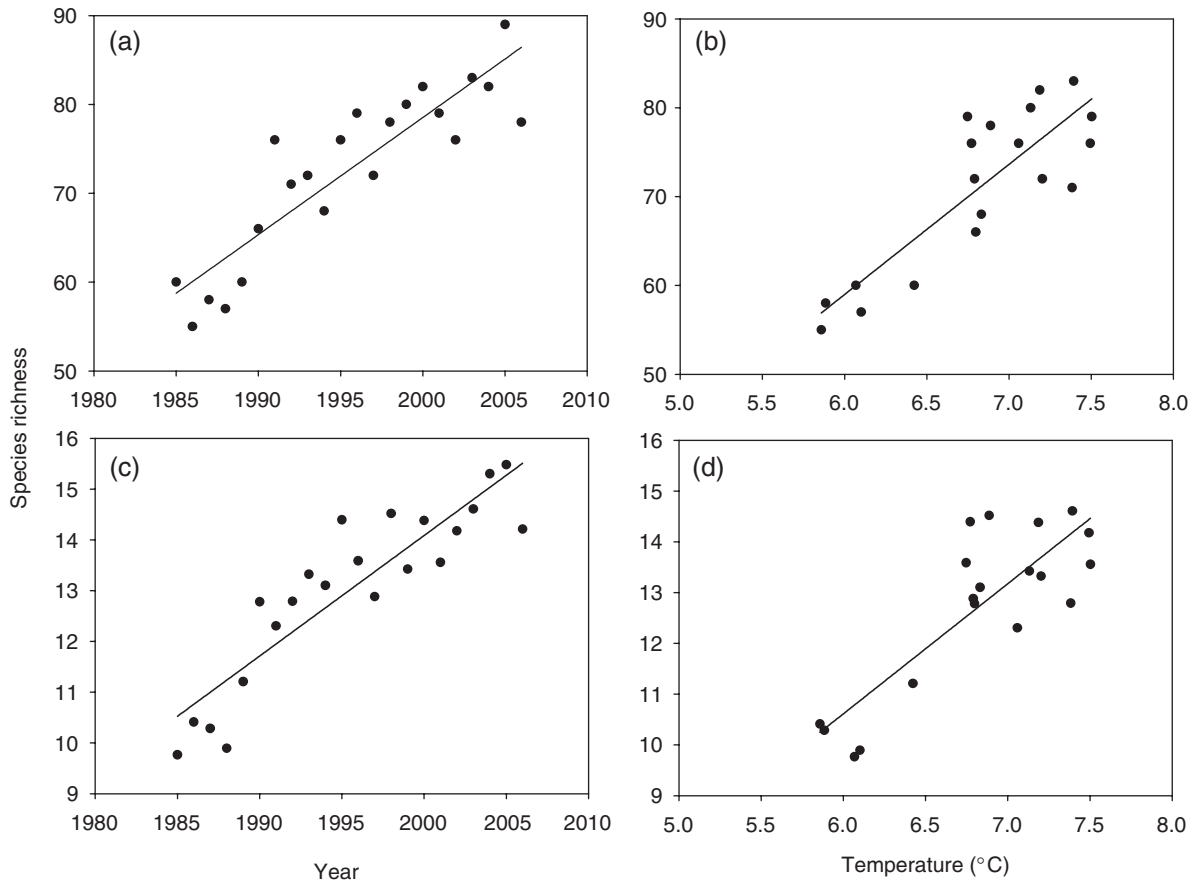


Fig. 2 Change in North Sea fish species richness over time and with temperature. (a) Total number of species recorded per year ($R^2 = 0.80$, $F_{1,20} = 77.7$, $P < 0.001$). (b) Total number of species recorded vs. average temperature over the previous 5 years ($R^2 = 0.72$, $F_{1,17} = 44.8$, $P < 0.001$). (c) Average number of species recorded per rectangle ($R^2 = 0.81$, $F_{1,20} = 82.7$, $P < 0.001$). (d) Average number of species recorded per rectangle vs. average temperature over the previous 5 years ($R^2 = 0.70$, $F_{1,17} = 39.8$, $P < 0.001$) (source: IBTS – data from ICES DATRAS). IBTS, International Bottom Trawl Survey.

perature in the North Sea has increased $0.7\text{ }^{\circ}\text{C decade}^{-1}$, which is more than 10 times the global average temperature increase of $0.06\text{ }^{\circ}\text{C decade}^{-1}$ (Walther *et al.*, 2002). Recorded bottom temperature increase was also faster than the recorded and predicted temperature increase of surface waters of $0.15\text{ }^{\circ}\text{C decade}^{-1}$ for the North Sea (Sheppard, 2004). However, bottom temperatures increased at a similar rate to the most recent estimates of sea surface temperatures in the North Sea since 1985 (MacKenzie & Schiedek, 2007). Short-term and local climatic variations are likely to change temperatures at faster rates than global climate change, but nevertheless, this discrepancy raises the question why North Sea bottom temperature has increased as fast as observed. Answering this question would require detailed analysis of changes in oceanographic patterns which is beyond the scope of this paper.

The species richness of the North Sea fish fauna (including elasmobranchs) has increased from 1985

to 2006, a period when bottom temperature rose significantly. There are several observations that support the hypothesis that this rise in species richness was related to increasing water temperatures. (1) Species richness was significantly positively correlated to average bottom temperature over the previous 5 years. (2) Species richness also correlated to bottom temperature in space and the slope of this relationship was stable over time. (3) The distribution range of many species expanded and the species with the highest expansion were species where their northern latitude boundary was close to the North Sea (= southerly species). (4) The distribution range of only a few species was reduced and these were species which have their northern latitude boundary far north of the North Sea (= northerly species). All four observations confirm the prediction from macroecological patterns of fish species richness (Macpherson, 2002) that increasing temperature results in to a northward shift of latitudinal

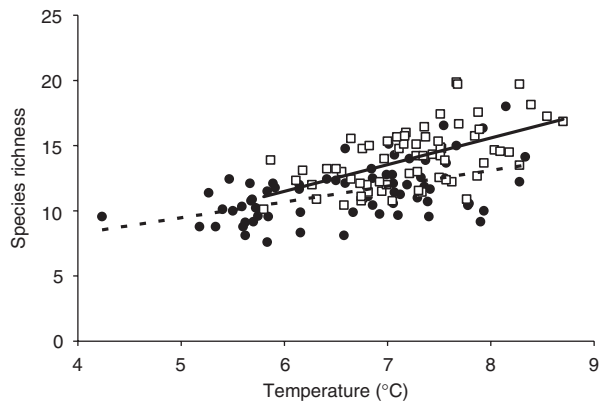


Fig. 3 Average species richness per ICES rectangle vs. temperature for two time period (GLM – temperature $F_{1,130} = 89.2$, $P < 0.001$, period $F_{1,130} = 22.8$, $P < 0.001$, interaction temperature–period $F_{1,130} = 3.5$, $P = 0.063$). Closed circles and dashed line: 1985–1994, open squares and solid line: 1995–2003 (source: IBTS – data from ICES DATRAS). IBTS, International Bottom Trawl Survey; ICES, International Council for the Exploration of the Sea.

patterns and lead to an increase of local fish species richness at temperate latitudes, because the number of species lost is lower than the number of species gained. Similarly, Henderson (2007) predicted that a 2 °C temperature rise would result in about a 10% increase in species richness in the Bristol Channel, England, and these additional species would be presently more southerly distributed species.

The increasing species richness with increasing temperature is unlike observed trends for British butterflies, where species richness did not increase because climatically suitable habitats were not colonized by southern species, relating to their limited dispersal capabilities and the patchy distribution of their habitat (Menéndez *et al.*, 2006). This suggests that the high dispersal rates of marine fish in areas of continuous habitat result in rapid responses of fish communities to climate change. In fact, species richness increased more than predicted by temperature alone (Fig. 3), which indicates that other factors besides climate may contribute to the increase in species richness. A possible factor is improvement of identification accuracy of the fish species during the surveys, but more likely is an increase in small species due to a release from predation by large commercial fish given the overexploitation of these larger species (Jennings & Blanchard, 2004). There is no theoretical basis to predict the effect of fishing on species richness (Rochet & Trenkel, 2003), but nevertheless, the reduction in abundance of target species and the possible increase in abundance of nontarget species due to release from competition and predation are likely to have effects on

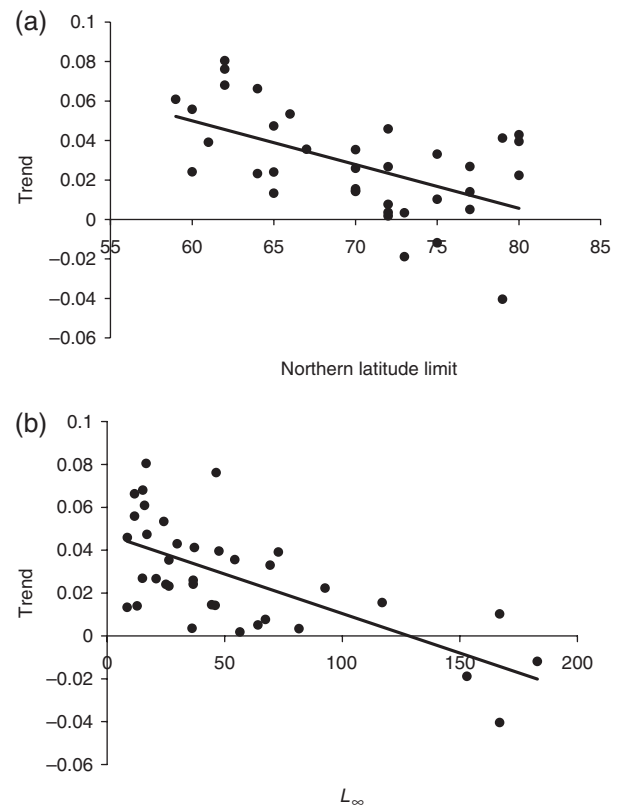


Fig. 4 Effect of (a) latitude limit and (b) life-history on distribution trends of fish species in the North Sea ($R^2 = 0.53$, latitude limit: $F_{1,34} = 6.2$, $P < 0.017$, L_{∞} : $F_{1,34} = 32.8$, $P < 0.0001$).

local species richness. Water quality in many estuarine systems that empty into the North Sea, such as the Scheldt, Rhine and Thames, has also significantly improved during the study period, and may have contributed to increasing species numbers, in particular in the southern North Sea (Attrill, 1998). Another explanation is that the northward shift of southerly species occurred faster than the northward shift of northerly species, because of a lag between a change in environmental conditions and local extinction of species. For example, this can happen when reproduction is inhibited by temperature changes, but the adult populations takes several years to die out. This builds up an ‘extinction debt’ in that warming may impose future extinctions as some species eventually disappear in response to the unsuitable climatic conditions (Malcolm *et al.*, 2002). The existence of an extinction debt cannot be identified using the current dataset.

Changes in the fish assemblage have been related to temperature changes in this paper. The temperature regime in the North Sea is affected by the North Atlantic Oscillation (NAO), and several previous studies observed correlations between the NAO – index and

responses at various levels of marine communities during the period 1985–2003 (e.g. Attrill & Power, 2002; Beaugrand & Reid, 2003; Henderson, 2007) Reid *et al.* (2001) describe a regime shift in hydrodynamics, phyto- and zooplankton, and fish in the North Sea in 1987–1988, which was correlated to a shift in the NAO. That regime shift is obvious in our bottom temperature dataset (see Fig. 1), but no sudden change in species richness was observed at that time. The observed changes in the fish assemblage of the North Sea are, therefore, likely to reflect long-term increases in temperature, as well as cyclical changes in other variables that are related to the NAO index.

An increase in species richness as a result of climate change can only be expected in ecosystems where species richness decreases with latitude. In the case of benthic and pelagic fish in the Atlantic Ocean, species richness seems to decrease at higher latitude, except for a plateau between 35°N and 15°S (Macpherson, 2002). In this tropical zone, climate warming can therefore not lead to an increase in species richness, and is likely to lead to a decrease in species richness. This also means that the increase in species richness at temperate latitudes cannot continue indefinitely with future increases in temperature. Therefore, we hypothesize that species richness will react positively to global warming only at temperate or higher latitudes, and if suitable habitats at different latitudes are well connected. When habitats are patchy and poorly connected (e.g. for poor dispersers such as butterflies and island populations), climate change is likely to always have a negative effect.

On average, fish species are smaller at lower latitudes (Macpherson & Duarte, 1994) and therefore a decrease in the size of fish species can be expected if climate change causes a northward shift of fish communities. The North Sea has been heavily exploited over the last century, and as a decrease in fish size has also been predicted and observed as an effect of exploitation by commercial fisheries (Rochet & Trenkel, 2003; Jennings & Blanchard, 2004), the observed increase in small species is at least partly due to fishing pressure and can probably be explained only to some extent by climate change. Exploitation pressure could not be included in our analysis because reliable fishing effort data was not available on a comparable spatial and temporal scale for the North Sea. Nevertheless, bottom trawling effort seems relatively stable from 1985 to 1995 and the spatial distribution of bottom trawling effort did change little over this period (Jennings *et al.*, 1999).

Published sources and anecdotal evidence suggest that large southern species such as conger eel, sea bass and tuna species are increasing around Britain (Henderson, 2007). Such species are often not sampled effectively with the fishing gear that is used in the IBTS,

either because their habitats are not sampled to avoid gear damage (e.g. conger eels and sea bass on reefs) or because the species are pelagic and fast swimming (e.g. tuna species). Our conclusion that average species size decreases with increasing temperature, therefore, applies to small pelagic and benthic open habitat species, and not necessarily to reef dwelling species such as sea bass, conger eel and wrasse nor for open water predators such as tunas.

Spatial patterns in bottom temperature in the shallow North Sea are rather different in summer and winter. In winter, relatively warm oceanic water enters the North Sea from the north and to a lesser extent from the south from the English Channel. This results in the highest bottom temperatures in the north and extreme south-west, and cold water in the central and south-eastern North Sea (Otto *et al.*, 1990). In summer, the deeper northern North Sea is thermally stratified and coldest, while the southern North Sea is warmest. If spatial patterns in species richness remain constant throughout the year, the relationship between species richness and temperature in space would be opposite in summer and winter, which would make it very difficult to interpret spatial patterns in species richness. If the relationship between species richness and temperature remains constant throughout the year, significant changes in the spatial patterns of species richness would need to occur through the year. The relatively warm water in the north-western North Sea during winter is likely to result in some southern fish species entering the North Sea around the northern tip of Scotland, rather than through the Strait of Dover. This colonization pattern has been observed for horse mackerel *Trachurus trachurus* after the 1987–1988 regime shift (Reid *et al.*, 2001).

We would like to emphasize that an increase in species richness due to climate change may have negative ecological and socio-economic effects. The observed replacement of large species by small species will have an effect on energy flow through the food web and, therefore, change the dynamics of the ecosystem. Socio-economically, all three species that decreased their range in the North Sea are commercial important species, while only one of the five most increasing species (*M. surmuletus*) and less than half of all 34 species that expanded their range are of commercial value in the North Sea. Therefore, a shift from large species to more, smaller species due to climate change is likely to decrease the value of fisheries. Southward (1980) already mentioned that climatic warming is likely to have a negative effect on fisheries in a paper discussing changes in fish in the English Channel during warming in the 1950s.

The results presented show that species richness increases in reaction to fast climatic warming on a part

of the temperate European continental shelf (i.e. the North Sea which is one of the world's most important ecological and socio-economical habitats). These results show that marine fish, a group with high potential dispersal rates in a well-connected habitat, exhibit the increase in species richness with climatic warming that can be expected from large scale biogeographical patterns in species richness. This provides new insights towards a better understanding of the potential large-scale consequences of climate change.

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