Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas

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Summary

1. Climate change impacts have been observed on individual species and species subsets; however, it remains to be seen whether there are systematic, coherent assemblage-wide responses to climate change that could be used as a representative indicator of changing biological state.

2. European shelf seas are warming faster than the adjacent land masses and faster than the global average. We explore the year-by-year distributional response of North Sea bottom-dwelling (demersal) fishes to temperature change over the 25 years from 1980 to 2004. The centres of latitudinal and depth distributions of 28 fishes were estimated from species-abundance–location data collected on an annual fish monitoring survey.

3. Individual species responses were aggregated into 19 assemblages reflecting physiology (thermal preference and range), ecology (body size and abundance-occupancy patterns), biogeography (northern, southern and presence of range boundaries), and susceptibility to human impact (fishery target, bycatch and non-target species).

4. North Sea winter bottom temperature has increased by 1·6 °C over 25 years, with a 1 °C increase in 1988–1989 alone. During this period, the whole demersal fish assemblage deepened by ~3·6 m decade^{-1} and the deepening was coherent for most assemblages.

5. The latitudinal response to warming was heterogeneous, and reflects (i) a northward shift in the mean latitude of abundant, widespread thermal specialists, and (ii) the southward shift of relatively small, abundant southerly species with limited occupancy and a northern range boundary in the North Sea.

6. *Synthesis and applications.* The deepening of North Sea bottom-dwelling fishes in response to climate change is the marine analogue of the upward movement of terrestrial species to higher altitudes. The assemblage-level depth responses, and both latitudinal responses, covary with temperature and environmental variability in a manner diagnostic of a climate change impact. The deepening of the demersal fish assemblage in response to temperature could be used as a biotic indicator of the effects of climate change in the North Sea and other semi-enclosed seas.

Key-words: climate change, habitat loss, invasive species, life-history trait, North Sea, regime shift, thermal preference

Introduction

Climate change affects demography, geographic distribution and phenology of populations and species. Demographic effects are manifest as changes in recruitment, growth and survival (O'Brien *et al*. 2000; Pörtner & Knust 2007), dis-tributional shifts as movements towards the poles or higher altitudes (Walther *et al*. 2002; Parmesan & Yohe 2003), and phenological effects as advances in the timing of spring-related events by > 2·3 days decade^{-1}, with earlier flowering, egg-laying, plankton blooms and fish migrations creating potential for mismatching between and predator and prey populations (Crick & Sparks 1999; Sims *et al*. 2001; Parmesan & Yohe 2003; Edwards & Richardson 2004). Climate change-induced habitat loss and changing species distributions are

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predicted to result in species extinctions on land and population extinctions in the sea (Thomas *et al.* 2004; Drinkwater 2005). There is an increasing need to summarize the ecological complexity of climate impacts using biological indicators to inform managers, policymakers and society (EEA 2004; MCCIP 2006).

Climate variability and longer-term change (hereafter called climate change) have led to marked changes in North East Atlantic conditions over the last century (Cushing 1982; Stenseth *et al.* 2005). Sea surface temperatures of North Atlantic and UK coastal waters have warmed by 0·2–0·6 °C decade^{-1} over the past 30 years. These seas are warming faster than the adjacent land and faster than the global average (MacKenzie & Schiedek 2007). Within the North East Atlantic region, warming was fastest in the English Channel, North Sea and Baltic Sea (ICES 2006a; Joyce 2006; Marsh & Kent 2006; Sherman *et al.* 2007). Some marked changes in North Sea fish distributions have been attributed to climate change: two-thirds of North Sea fishes have shifted mean latitude or depth. Fishes with a northern distributional boundary in the North Sea have shifted northwards and southern boundary species have retracted northwards at rates up to three times faster than terrestrial species (Perry *et al.* 2005). Exotic fishes with southerly biogeographic affinities are becoming established in the North Sea, including; anchovy *Engraulis encrasicolus* L., red mullet *Mullus surmuletus* L., sardine *Sardina pilchardus*, Walbaum 1792, John Dory *Zeus faber*, L. and snake pipefish *Entelurus aequoreus*, L. (Beare *et al.* 2004; ICES 2006b; Kirby, Johns & Lindley 2006; Enghoff, MacKenzie & Nielsen 2007).

A key question is whether the individual responses of species are context-specific phenomena or whether they are symptomatic of a more systematic change in the North Sea ecosystem resulting from climate change. If such an ecosystem-scale change can be detected, this could underpin the development of a biotic indicator of climate change impacts. There is a wide range of desirable indicator properties, including specificity to a single pressure, sensitivity or strength of response, the lag in response and the spatial and taxonomic representativeness of the indicator (Rice & Rochet 2005). Here we summarize the effects of climate change on the demersal fish assemblage and develop an indicator that is taxonomically representative of a wide range of fish species.

We search for an assemblage-wide biotic indicator of climate change in the North Sea ecosystem by comparing the distribution changes of fish species and assemblages to temperature and climate change over the past 25 years. For each year, we calculated the distance moved north or south and the deepening and shallowing of each fish species or assemblage relative to the long-term average. Species distributional responses were aggregated into non-mutually exclusive assemblages reflecting differences in physiology, ecology, biogeographic origin and human impact. We demonstrate a coherent deepening of fish species in response to climate change and two distinct latitudinal responses to climate change: a northward shift in mean latitude and southward extension of minimum latitude.

Methods

We used the North Sea English groundfish survey data to assess changes in the geographic distribution of 28 demersal fish species. The English Groundfish Survey (EGFS) samples a grid of trawl stations typically covering up to 84 statistical rectangles (between 51·75 to 61·75° N latitude) and has been fished annually throughout the North Sea as part of the International Council for the Exploration of the Sea (ICES) international bottom trawl survey in autumn (August–October). All fishes caught were identified and measured. Catch rates were raised to number of individuals caught per 60-min tow (for more details see Maxwell & Jennings 2005).

Species were included if they were reliably identified throughout the time period and effectively sampled by the net (Sparholt 1990; Knijn *et al.* 1993; Maxwell & Jennings 2005; Dulvy *et al.* 2006). Pelagic fish were excluded because of the likelihood that they were captured in the water column during net shooting or hauling. The 28 species retained for analysis were representative of the breadth of morphology, life histories, ecology and taxonomic diversity of the bottom-dwelling fishes sampled by the survey (Table 1) and represent most of the numerical abundance and biomass of the demersal fish assemblage (Jennings *et al.* 2002). The Latin names for all study species are presented in Table 1; hereafter, only common names will be used.

Species were categorized into a number of assemblages based on their thermal physiology, ecology, biogeography and exploitation status (Table 1). These assemblages are not mutually exclusive and each species appears in one or more assemblage categorization. This approach allows the identification of those traits most related to the climate change response with greater statistical power afforded by combining data from more than one species (Maxwell & Jennings 2005).

The autumn thermal preference of each fish species was described using: (i) the most preferred temperature, and (ii) the range of the preferred temperatures (for details see Supplementary Appendix S1). The preferred temperatures of fishes were bimodally distributed: species preferring temperatures below 15·5 °C were classified as relatively cold-tolerant and those preferring temperatures above that level as warm-tolerant. Most species (n = 21) had narrow thermal ranges spanning less than 4 °C; a few species had slightly wider thermal ranges, such as dab, sole, solenette, lesser weaver, bib, plaice, four-bearded rockling and hake (Table 1).

We used body size as a proxy measure of ecological performance. Body size is a good descriptor of life history and demography and also of production, consumption and metabolism (Reynolds *et al.* 2005; Jennings, De Oliveira & Warr 2007). Large-bodied species were defined as the 18 species with a maximum length ≥ 60 cm (Table 1). Species with numerical abundance lower than (or greater than) median numerical abundance were categorized as less abundant or abundant, respectively. The spatial extent of occurrence was measured as the mean number of ICES statistical rectangles occupied, and less common (or widespread) species had less than (or greater than) the median number of rectangles.

The biogeographic affinities [boreal (northern) and Lusitanian (southern)] of each species were derived from the scientific literature (Wheeler 1969; Yang 1982). Exploitation status was based on stock assessment reports and regional atlases, and species were categorized as 'target', 'bycatch' and subject to some fishing mortality and 'non-target'.

Species' geographic distributions were summarized using the centre of distribution estimated as the mean latitude weighted by the natural log of the mean abundance (survey catch) in each statistical rectangle (Rindorf & Lewy 2006). We used four measures of geographic distribution: the mean latitude, minimum latitude, maximum latitude and mean depth. Change in distribution was standardized by calculating

Table 1. Demersal North Sea fish species surveyed by the English Groundfish Survey, body size (cm), biogeographic affinity and thermal characteristics (°C), exploitation status, categorical numerical abundance and spatial occupancy and presence of a northern or southern range boundary. Thermal classification: W, warm thermal preference; C, cold thermal preference; g, generalist with broader thermal range; s, specialist with narrow thermal range. Numerical abundance: LA, less abundant; A, abundant. Spatial occupancy: LC, less common; W, widespread

Common name	Latin binomial	Body size	Biogeographic affinity	Mean temperature	Temperature range	Thermal classification	Exploitation status	Abundance category	Spatial occupancy category	Range boundary
Pogge	*Agonus cataphractus* L.	20	Boreal	15·4	3·9	Cs	Non-target	LA	LC	N
Wolffish	*Anarhichas lupus* L.	125	Boreal	13·4	2·4	Cs	Bycatch	LA	W	S
Scaldfish	*Arnoglossus laterna* (Walbaum, 1792)	25	Lusitanian	16·4	3·2	Ws	Non-target	LA	LC	N
Solenette	*Buglossidium luteum* (Risso, 1810)	13	Lusitanian	16·4	4·5	Wg	Non-target	A	LC	N
Grey gurnard	*Eutrigla gurnardus* L.	45	Lusitanian	17·0	3·6	Ws	Bycatch	A	W	–
Cod	*Gadus morhua* L.	132	Boreal	13·8	2·3	Cs	Target	A	W	–
Witch	*Glyptocephalus cynoglossus* L.	60	Boreal	13·3	3·3	Cs	Bycatch	LA	W	S
Long rough dab	*Hippoglossoides platessoides* (Fabricius, 1780)	30	Boreal	13·8	2·4	Cs	Bycatch	A	W	–
Megrim	*Lepidorhombus whiffiagonis* (Walbaum, 1792)	61	Lusitanian	13·3	2·7	Cs	Bycatch	LA	LC	S
Dab	*Limanda limanda* L.	42	Boreal	17·0	4·5	Wg	Bycatch	A	W	S
Angler	*Lophius piscatorius* L.	75	Lusitanian	13·4	2·2	Cs	Target	LA	W	S
Haddock	*Melanogrammus aeglefinus* L.	76	Boreal	13·7	2·4	Cs	Target	A	W	–
Whiting	*Merlangius merlangus* L.	45	Lusitanian	13·2	3·2	Cs	Target	A	W	S
Hake	*Merluccius merluccius* L.	110	Lusitanian	13·8	5·8	Cg	Target	LA	W	S
Lemon sole	*Microstomus kitt* (Walbaum, 1792)	60	Boreal	15·2	2·3	Cs	Target	A	W	S
Ling	*Molva molva* L.	200	Boreal	13·1	2·1	Cs	Target	LA	LC	–
Plaice	*Pleuronectes platessa* L.	95	Lusitanian	17·0	4·4	Wg	Target	A	W	–
Saithe	*Pollachius virens* L.	130	Boreal	13·4	2·7	Cs	Target	A	W	S
Cuckoo ray	*Leucoraja naevus* (Müller & Henle, 1841)	70	Lusitanian	12·6	1·8	Cs	Bycatch	LA	LC	S
Starry ray	*Amblyraja radiata* (Donovan, 1808)	60	Boreal	13·7	2·4	Cs	Non-target	A	W	–
Four-beard rockling	*Rhinonemus cimbrius* L.	41	Boreal	13·9	4·6	Cg	Non-target	LA	LC	S
Lesser spotted dogfish	*Scyliorhinus canicula* L.	75	Lusitanian	12·4	2·1	Cs	Bycatch	LA	LC	S
Sole	*Solea solea* L.	60	Lusitanian	17·2	4·8	Wg	Target	LA	LC	S
Spurdog	*Squalus acanthias* L.	105	Atlantic	15·0	2·5	Cs	Bycatch	LA	W	–
Lesser weaver	*Trachinus vipera* (Cuvier, 1829)	15	Lusitanian	17·2	4·5	Wg	Non-target	A	W	S
Norway pout	*Trisopterus esmarki* (Nilsson, 1855)	25	Boreal	13·6	3·2	Cs	Target	A	W	S
Bib	*Trisopterus luscus* L.	46	Lusitanian	17·6	4·4	Wg	Non-target	LA	LC	N
Poor cod	*Trisopterus minutus* L.	40	Lusitanian	16·6	3·5	Ws	Non-target	A	W	N

anomalies of the departure from the mean over the 25-year study period. Latitude anomalies were converted from degrees to kilometres. Positive latitude anomalies represent northward change in species' centre of distribution, whereas positive depth anomalies represent shallowing. Assemblage-scale distribution measures were calculated from the average of geographic anomalies across component species. All relationships between geographic response and time or a climate variable were tested using robust regression (Venables & Ripley 2002).

A systematically changing survey distribution could confound the detection of climate-related geographic shifts. The number of survey stations has varied over time particularly during 1980–1984, but since then a relatively constant grid of > 70 stations have been surveyed each year. In spite of the changing number of stations in the early period, mean depth and mean latitude of the stations has remained stable and the interannual variation in survey distribution explained relatively little interannual variance in fish distributions, except for the redfish *Sebastes viviparus* Krøyer, 1845 which was excluded from the analysis.

Long-term environmental data were provided by ICES (www.ices.dk). For the time series analysis, bottom temperatures (from the lower half of the water column) were averaged for winter (January–March) for 80 $0.5° \times 1°$ ICES statistical rectangles (there were insufficient replicate stations (< 15 rectangles) to perform an equivalent analysis for the summer period). Southern North Sea salinity data are collected from near-surface waters by ferries travelling between Harwich and Rotterdam at weekly intervals at approximately 52° N (Joyce 2006). The data were averaged by month and a winter mean taken for January–March. The North Atlantic Oscillation Index (NAOI) is the normalized sea level pressure difference between Gibraltar and Iceland. An annual index was calculated by averaging the winter (December–February) values and the data were sourced from www.cru.uea.ac.uk/cru/data/nao.htm (Jones, Jonsson & Wheeler 1997). The Gulf Stream Index (GSI) is a measure of the latitudinal height of the north wall of the Atlantic Gulf Stream and was sourced from web.pml.ac.uk/gulfstream/inetdat.htm (Taylor & Stephens 1980). GSI is not directly linked to North Sea conditions but is an indicator of regional North Atlantic climate. A composite index of North East Atlantic climate change was calculated as the first principal component axis of the 5-year running averages of five variables (winter bottom temperature, NAO, GSI, salinity and inflow). We used right-aligned 5-year running means calculated from the current year and the four previous years to approximate a fish's lifetime environmental experience. North Atlantic Current inflow into the North Sea is linked to regional climate variability, local biological productivity and fish recruitment success (Reid *et al.* 2003; Pingree 2005; ICES 2006a). Monthly predictions of net inflow across a section between Shetland and Orkney were derived from runs of a coupled physical, chemical and biological model system (NORWECOM) (Skogen *et al.* 1995). Water transport was measured in Sverdrups ($10^6 m^3 s^{-1}$) and increasing negative values represent greater southward inflow of Atlantic water. A demersal exploitation rate was calculated for each year between 1980 and 2003 as the catch-weighted sum of demersal fish fishing mortalities, as estimated in ICES North Sea stock assessments, for cod, haddock, saithe, whiting, plaice, and sole (Daan *et al.* 2005).

Results

CLIMATE CHANGE IN THE NORTH EAST ATLANTIC AND NORTH SEA

The North Atlantic Oscillation and the Gulf Stream indices have increased, peaking in 1995 with strong negative values in 1985 and 1996 (Fig. 1a,b). North Sea winter bottom temperatures have risen by 1·6 °C over 25 years, a 1 °C increase occurred in 1988–1989 alone (Fig. 1c). The mean annual temperature increase was 0·07 °C (± 0·02 SE; $F_{1,23} = 10.9$, $P = 0.003$). The warming bottom temperatures coincided with a long-term shift towards a positive NAO phase, a northward shift in the Gulf Stream and stronger Atlantic inflow into the northern North Sea (NAO: $r = -0.81$, $P < 0.0001$; GSI: $r = -0.76$, $P < 0.0001$: Fig. 1a,b). The inflow of Atlantic water into the North Sea also increased, peaking in 1990 followed by a slight weakening (Fig. 1d). Correspondingly, salinity in the southern North Sea was lower than average in the early 1980s and greater around 1990, coinciding with the peak inflow of saline Atlantic water (Fig. 1e). The first and second principal component axis capture 73% and 14%, respectively, of the variation in the 5-year running means of these five climate variables. The first axis score (dotted line) represents a longer-term trend in climate becoming negative by 1990, reaching a minimum in 1995 before rising to near zero in 2000 and stabilising thereafter (Fig. 1f). The second axis (solid line) represents shorter-term climate variability and was negative in the mid-1980s and mid-1990s and positive in the early 1990s and around 2000 (Fig. 1f).

DEEPENING RESPONSE OF INDIVIDUAL FISH SPECIES OVER TIME

Most species have deepened over time with 11 deepening significantly (at $P < 0.01$; Fig. 2). On average, the 22 deepening species have deepened by ~5·5 m decade^{-1} (range: 0·6–14 m decade^{-1}). Coldwater species, like megrim and anglerfish, are deepening fastest with warm-water species shallowing over time (Figs 3 and 5; for Latin names see Table 1). Sole and bib are southerly warm-water species and have been shallowing at rates of 7·6 m and 6 m decade^{-1}, respectively (Fig. 3). Similar to the deepening pattern, these shallowing trends are also consistent with climate change and belie an initial deepening in the cool period around 1985 and subsequent shallowing in the warmer period around the mid- to late 1990s (Fig. 3).

DEEPENING RESPONSE OF FISH ASSEMBLAGES OVER TIME

Overall, the 28-species North Sea demersal fish assemblage has deepened significantly at a rate of ~3·6 m decade^{-1} ($F_{1,23} = 18.4$, $P < 0.0002$; Fig. 4a). The mean depth varied from year to year but tracks temperature over the longer time-scale; the assemblage was shallowest in the cool mid-1980s and deepest during the peak warming in the mid-1990s and shallows slightly thereafter (Fig. 4a).

The deepening response over time was consistent across all but one assemblage and significant for 14 out of 19, at $P < 0.01$ (Fig. 5a). The average rate of deepening for these assemblages was 4·3 m decade^{-1} (range: 3–6 m decade^{-1}). Those assemblages not exhibiting a significant depth response are comprised of species that are warm-tolerant, small-bodied, less common with relatively low occupancy, have a northern range boundary in the North Sea and are unexploited; these species include scaldfish, solenette and bib (Table 1).
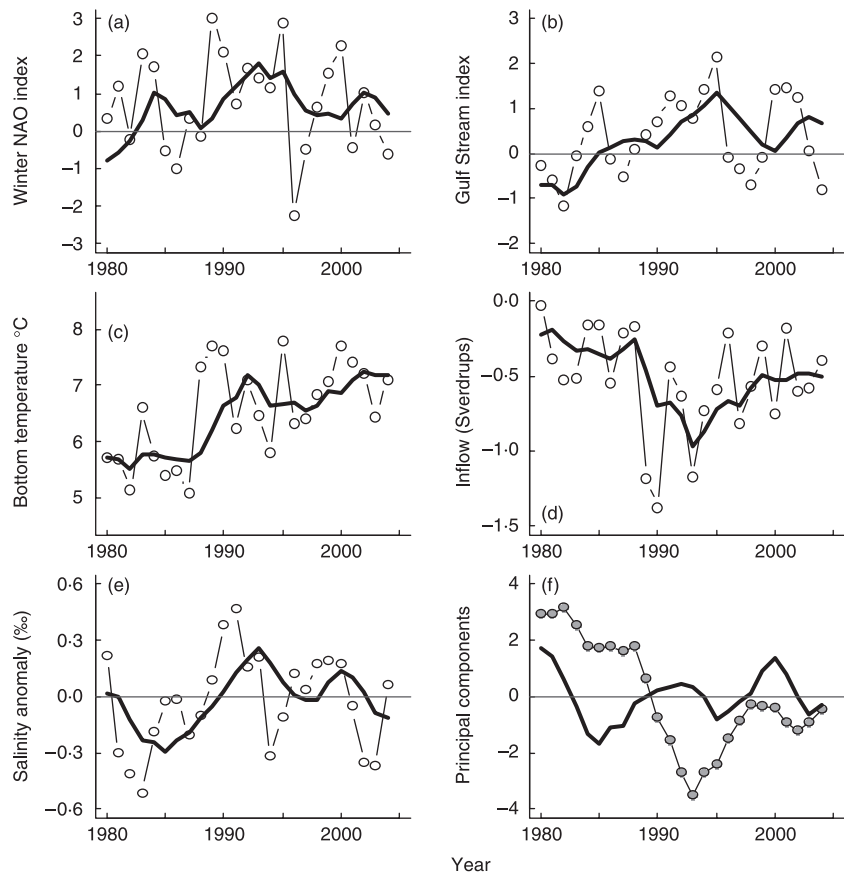
Fig. 1. Physical climate indices from the North Sea and North East Atlantic spanning 1980–2004; (a) North Atlantic Oscillation Index (December–February), (b) Gulf Stream Index, positive values represent northward displacement of the Gulf Stream wall, (c) mean winter bottom temperature (January–March), (d) net inflow between Orkney and Shetland, (e) southern North Sea salinity anomaly, and (f) the principal component axes (first axis, grey points; second axis, bold line) of the 5-year running mean of these five climate indices. Annual values are represented by the connected points with the 5-year right-aligned running mean represented by the bold line.
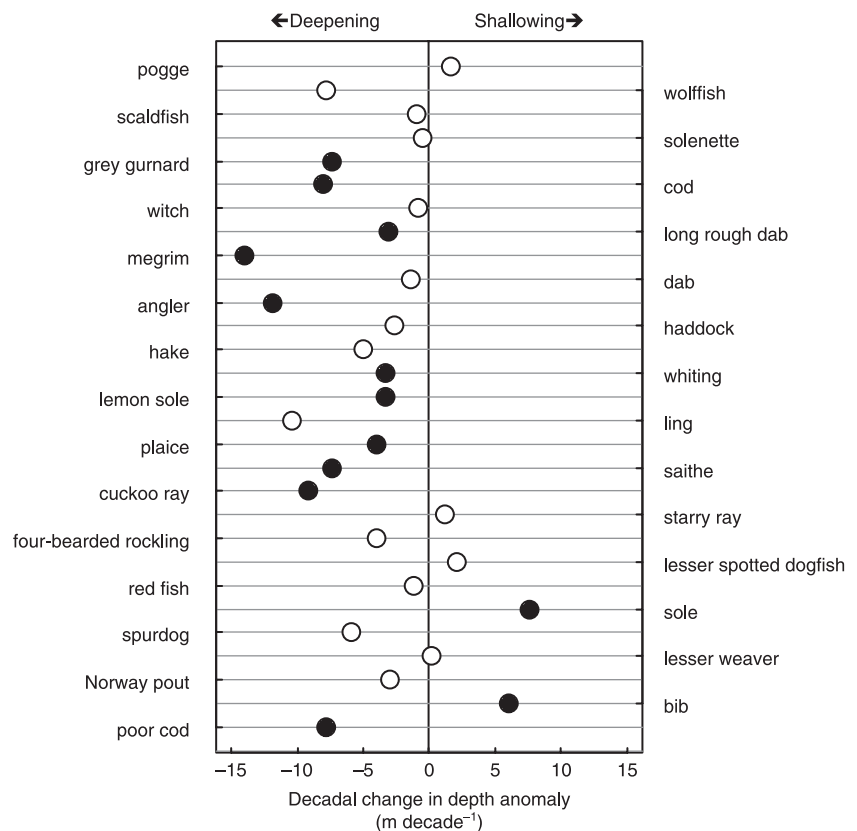
Fig. 2. Trend in depth anomaly of individual fishes over time (m decade^{-1}). Solid points are significant at $P < 0.01$.
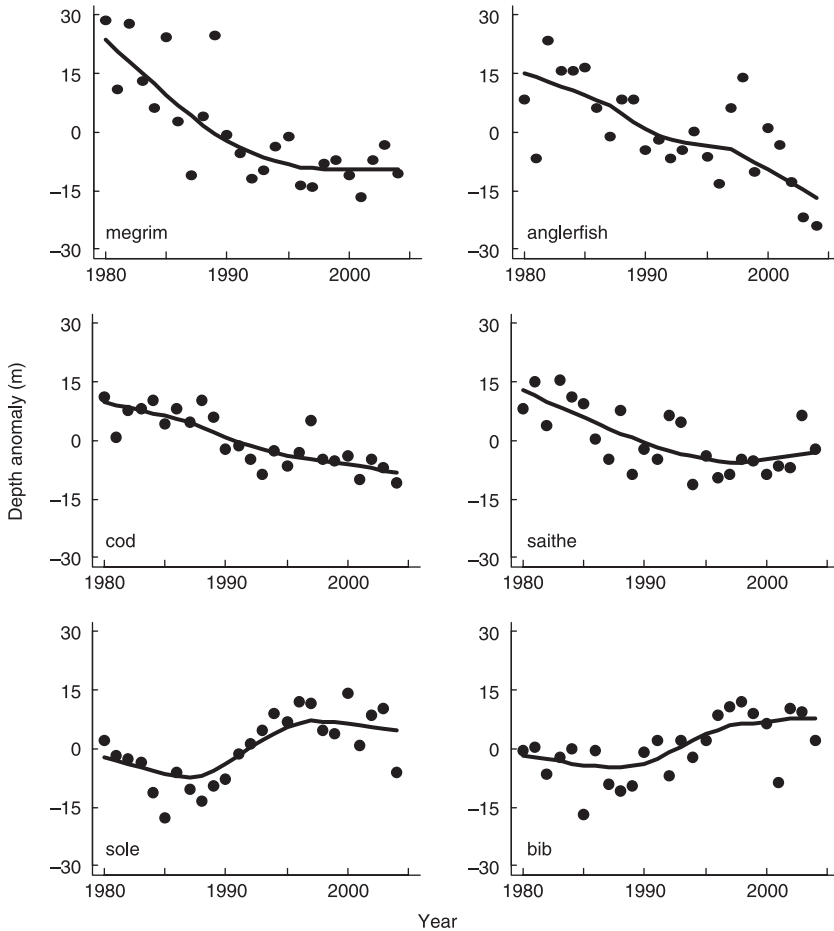
Fig. 3. Deepening of four coldwater boreal fishes and shallowing of two warmwater southern fishes over time. The trend line is a loess smoother (span = 0·75).
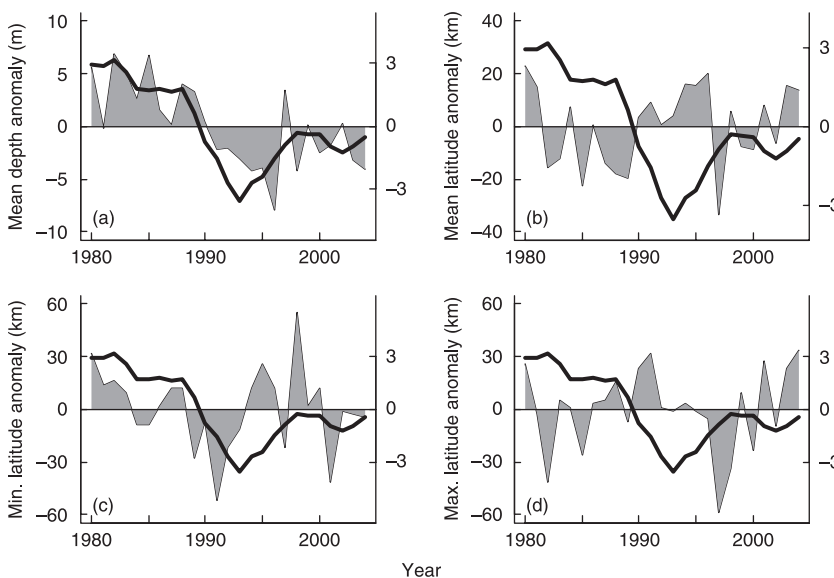

Fig. 4. Annual variation in geographic response of the North Sea demersal fish assemblage. Anomalies of (a) mean depth, (b) mean latitude, (c) minimum latitude and (d) maximum latitude. Positive anomalies indicate shallower (panel a) or northerly distribution (panels b–d), and negative anomalies representing deepening or a more southerly distribution. Only the mean depth anomaly exhibits a significant trend over time (*P* < 0·001). The solid line is the 5-year running mean of the first principal component axis representing climate change (see Fig. 1f).

LATITUDINAL RESPONSE OF FISH ASSEMBLAGES OVER TIME

In contrast to the relatively coherent deepening, the demersal fish assemblage exhibited heterogeneous latitudinal range changes with no overall trend north or south (Fig. 4b–d). Mean latitude, and to a lesser degree maximum latitude, was more southerly in the cool 1980s and farther north during the warmer 1990s (Fig. 4b,d). Minimum latitude was more northerly in the early cooler years, moving southward in the warmer years before retracting northward in the late 1990s (Fig. 4c).

Two broad geographic responses to climate change patterns are discernable: (i) a northward shift both in mean latitude
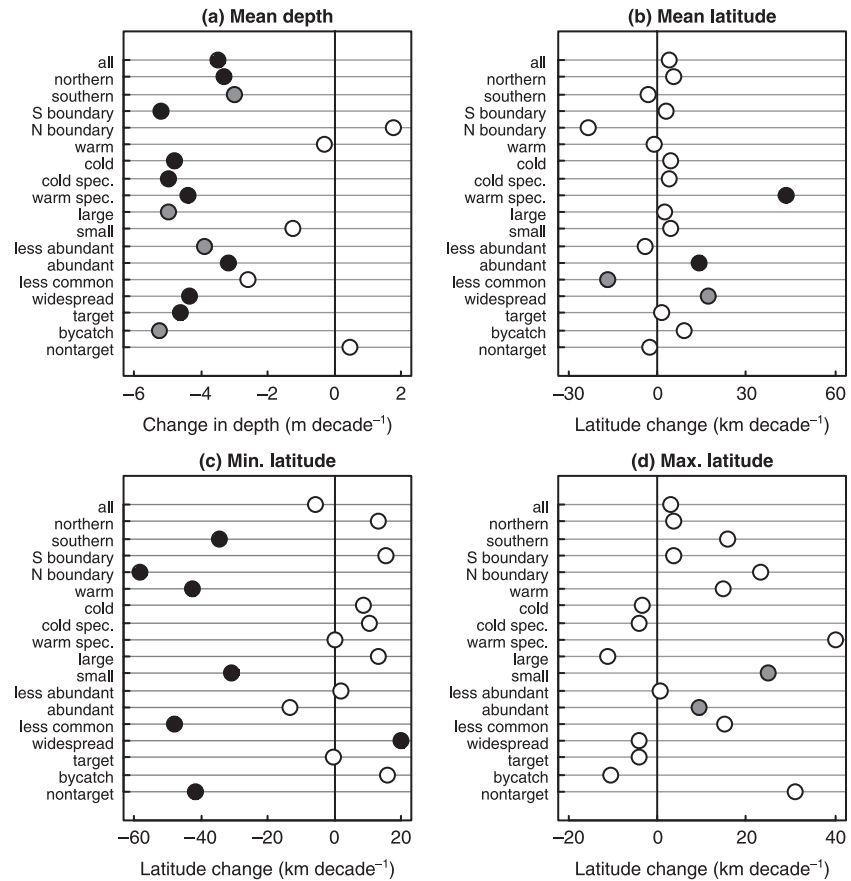
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Fig. 5. Trend in geographic response of different demersal fish assemblages over time; (a) mean depth, (b) mean latitude, (c) mean minimum latitude and (d) mean maximum latitude. Black and grey points indicate statistical significance at $P \leq 0.001$ and $P \leq 0.01$ respectively. The *x*-axis represents the direction and strength of geographic response over time – the slope of a regression of distribution measure on year. Positive values indicate shallower (panel a) or northerly distribution (panels b–d), with negative anomalies representing deepening or a more southerly distribution.

and maximum latitude, and (ii) a mixed or southward shift in minimum latitude. The northward shift in mean latitude over time was exhibited by assemblages comprised of abundant, widespread, warm-tolerant species with narrow thermal ranges, such as grey gurnard and poor cod (Fig. 5b). Some assemblages did not deepen and instead revealed a southward shift of the minimum latitude. These assemblages were comprised of unexploited, warm-tolerant, small-bodied, abundant, less common, low-occupancy species, with a northern range boundary in the North Sea, such as scaldfish, solenette and bib.

SENSITIVITY OF THE DEPTH AND LATITUDE RESPONSE TO TEMPERATURE, CLIMATE AND EXPLOITATION

Depth and latitude anomalies responded most significantly to 5-year running means of winter bottom temperature while accounting for year effect (Fig. 6) and composite climate index when aggregated at the assemblage-level. This pattern only holds when smoothed by running means and holds best for the 5-year running mean; the zero-lagged data did not yield significant relationships. The deepening of the whole North Sea fish assemblage was related to winter bottom temperature and composite climate index: the assemblage was relatively shallow in cooler years and deeper in warmer years (winter bottom temperature 5-year running means: $F_{1,23} = 25.9$, $P < 0.001$; PCA 1 of 5-year running means:

$F_{1,23} = 24.4$, $P < 0.001$). All 19 assemblages deepened with warmer climate at a rate of 2–7 m °C^{-1} and the mean and maximum latitudes of most assemblages moved northward with warming climate at a rate of 10–70 km °C^{-1}. However, the minimum latitude moved southward with warming climate by up to 80 km °C^{-1} for many assemblages, except for the northward movement of the minimum latitude of warm-specialist species at a rate of 40 km °C^{-1}.

Demersal exploitation rate explained relatively little variance in the interannual variation of geographic distribution of the demersal fish assemblage. When all combinations of three explanatory variables (composite climate index or bottom temperature, year and exploitation rate) are considered together, only bottom temperature or climate index significantly explain most variance in depth anomaly of the demersal fish assemblage (Appendix S2, Supplementary material). This pattern also holds for assemblages of target or bycatch species.

Discussion

We present evidence for a coherent deepening of the North Sea fish assemblage in response to climate change. The rate of deepening of the whole assemblage was 3·6 m decade^{-1} and for individual species ranges up to 10 m decade^{-1}. This rate of deepening is analogous and comparable to upward altitudinal response of terrestrial organisms, which averages 6·1 m decade^{-1} (Parmesan & Yohe 2003). Before considering the
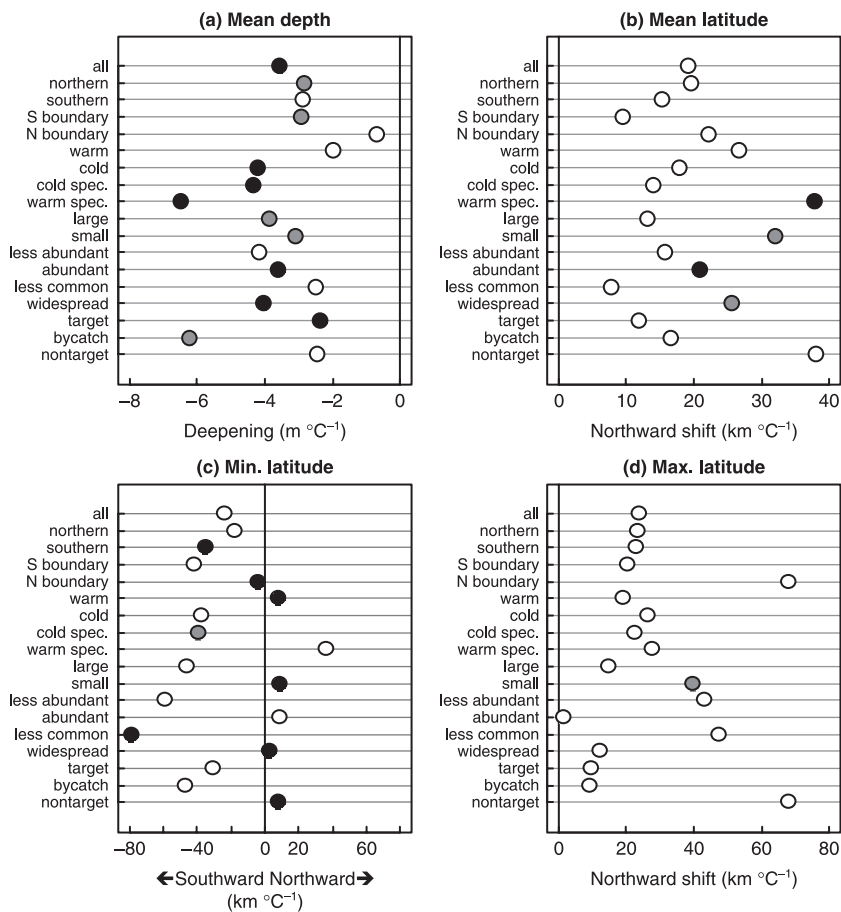
Fig. 6. Temperature sensitivity of the geographic response of fish assemblages measured as the (a) deepening in metres per degree of warming averaged over the current and previous 4 years (m °C⁻¹) or (b–d) range shift in kilometres moved per degree of warming (km °C⁻¹). Negative values represent a southward shift in response to warming and positive values a northward shift. Solid points indicate statistical significance of the overall model at $P < 0.001$ and grey points $P < 0.01$.

indicator properties of the deepening of the demersal fish assemblage, we consider these three questions: (i) What is the ecological significance of deepening fishes? (ii) Why is the deepening response more coherent than the latitudinal response? (iii) Are changes in fish distribution largely a consequence of fisheries exploitation?

The ecological significance of upward-shifting alpine fauna is readily apparent. These species face shrinking habitats and greater likelihood of extinction (Grabherr, Gottfried & Pauli 1994). However, the ecological significance of the deepening of the North Sea bottom-dwelling fishes is less clear. The ecological consequences may be more critical for geographically-restricted species that cannot deepen or shift to remain within their preferred temperature range in response to climate change. One such species, the eelpout *Zoarces viviparous*, L. 1758, has declined due to rapid warming in the shallow enclosed Wadden Sea (Pörtner & Knust 2007). For many coastal and offshore fishes, however, the geographic barriers to the shift of fishes toward thermally optimal habitats in deeper northerly waters are less apparent. However, the comparatively smaller area of deeper habitats > 80 m, in the North Sea suggests that deeper-dwelling shelf species (e.g. megrim) are more likely to be limited by habitat availability.

The deepening response was more coherent than the heterogeneous latitudinal response. The weak latitudinal response arises because it is a composite of two opposing latitudinal responses displayed by two ecologically distinct components of the demersal fish assemblage. The climate-driven northward shift in mean latitude of widespread abundant species has already been well-documented, along with some southward-shifting exceptions (Perry *et al.* 2005). We examine these exceptions further and find the southward shift of warm-tolerant southern species is consistent with the effects of (i) winter inflows of warm water into the northeastern North Sea in winter (Norway pout), and (ii) the warming and increasing availability of shallow winter habitats in the southern North Sea (e.g. sole, solenette and scaldfish). The southerly shifts in fish distributions may result from the peculiarities of winter hydrography in the North Sea (Holliday & Reid 2001; Perry *et al.* 2005). In winter, the Scottish east coast and central southern North Sea temperatures are comparable and relatively warm (~5–6 °C), and the coldest areas are found in the shallow coastal waters, particularly in the southeast (Fig. 2b). The relatively warm winter temperatures in the northwestern North Sea are apparent during positive NAO phases which result in stronger inflow of warmer North Atlantic Current waters (Edwards *et al.* 2002; Pingree 2005). Consequently, the main route into the North Sea for southern warm-tolerant species can be via the Shetland–Orkney gap as well as the English Channel. Indeed, many warm-water species first appear in the northwestern North Sea before expanding southward, such as the John Dory and snake pipefish which invaded earlier this decade (Ehrich & Stransky 2001; ICES 2006b, p. 82; Kirby *et al.* 2006; Harris *et al.* 2007).
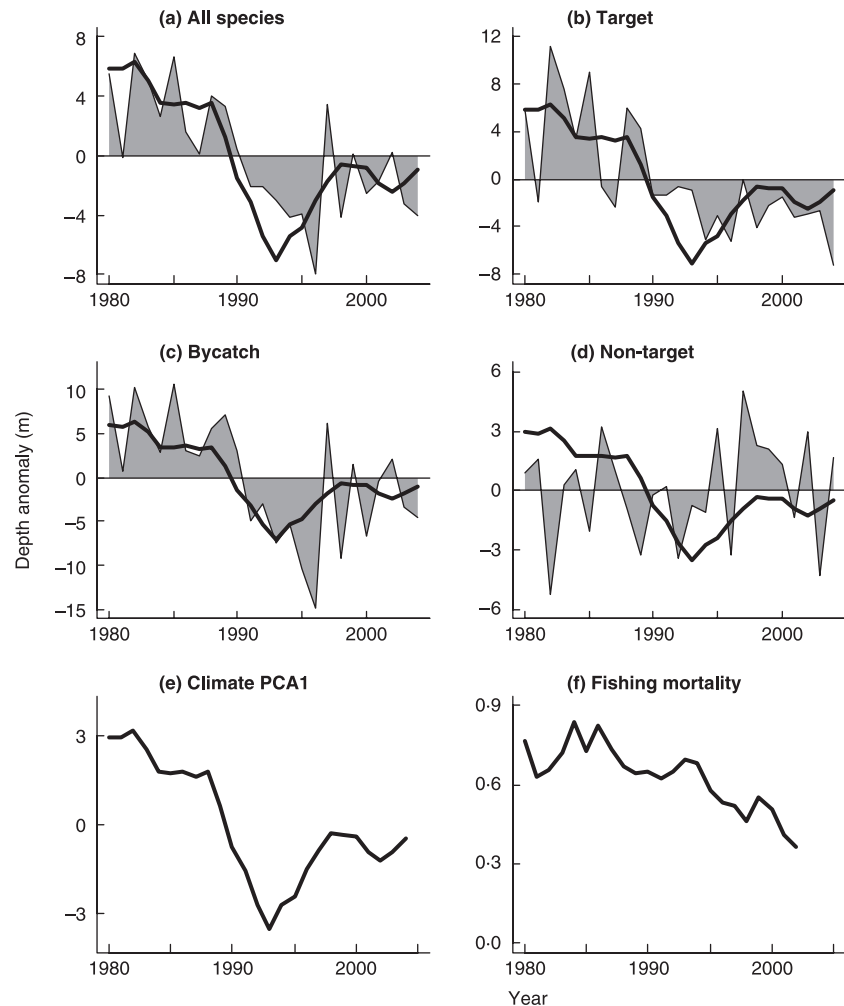
Fig. 7. Exploitation, climate and depth change of (a) all, (b) target, (c) bycatch, and (d) non-target demersal fishes, (e) a composite climate index and (f) a demersal exploitation index. (a–d) The solid line is the 5-year running mean of the first principal component axis representing climate change (e). Positive values indicate shallower distribution with negative anomalies representing deepening.

Southern North Sea species were previously excluded from large areas of shallow inshore habitat in winter because these waters cool down to ~1 °C (Anonymous 1981). For example, sole overwinter in deeper warmer waters before returning to the shallows in spring (Henderson & Seaby 2005). There is anecdotal evidence that sole are arriving inshore earlier due to the rapidly warming seas (R. Millner, personal communication). We hypothesize that the southward shift of smaller, warm-tolerant southern species is due to increased warming and availability of shallow inshore habitat in winter and spring, although small species may have also benefited from the overexploitation of their predators (Daan *et al.* 2005). To summarize, the contrasting latitudinal responses of two ecologically distinct groups of fishes are consistent with climate change and the hydrographic conditions in the North Sea, and combining both results in an overall lack of latitudinal response.

A key question is whether the distribution changes of demersal fishes are a consequence of fisheries exploitation. Two lines of evidence suggest fisheries exploitation may contribute to changing fish abundance and distribution. First, exploitation influences the age structure, abundance and occupancy of target populations which might change their responsiveness to climate warming (Fisher & Frank 2004;

Rindorf & Lewy 2006). Secondly, some coldwater species, such as Atlantic cod, are now relatively rare, yet were previously abundant in comparably warm stages such as the Stone Age (Atlantic period, 7000–3900 BC) and the latter part of the medieval warm period (*c.* 1200 AD) (Bolle *et al.* 2004; Enghoff *et al.* 2007). This suggests fisheries exploitation may be more important than warm temperature in determining the abundance of such species (Enghoff *et al.* 2007).

Understanding the relative contribution of fishing and climate change in determining North Sea fish dynamics has been the 'holy grail' of the European fisheries science community. The spatial pattern of fishing may change fish distributions in a manner similar to that expected from climate change. Fishing effort, particularly by beam trawls, has been greater in the southern North Sea compared to the northern part (Jennings *et al.* 2000). If a species was comprised of several subpopulations across its geographic range, then those in the more heavily fished areas would be depleted more than those in the less heavily fished areas, and this might be seen as having an effect on the range of the species. Ideally, any biotic indicator would respond specifically to a single driver or pressure (e.g. climate change) and be less specific and responsive to other pressures, (e.g. exploitation or eutrophication) (Rice & Rochet 2005). The climate response of the depth anomaly is

relatively independent of fishing mortality and consistent across assemblages of species exposed to different levels of fishing mortality (Fig. 7). The lack of depth response of non-target species reflects the ecology and spatial pattern of winter warming of the North Sea rather than the absence of exploitation per se. These non-target southern North Sea species are responding differently to climate change by expanding southward. While there is little doubt that fisheries exploitation has had major effects, particularly on the abundance of fish populations, this analysis suggests that the depth response of the assemblage is highly specific to climate change.

The deepening response of the demersal fish assemblage to temperature could be used as one indicator of the biological effects of climate change in the North Sea and other semi-enclosed seas. The deepening response has a number of useful indicator properties, including high temperature sensitivity and high specificity to climate change (rather than to fishing). These indicators are readily measurable using routinely collected survey data, have high taxonomic representation of changes in the demersal fish assemblage of the North Sea ecosystem, and can be readily communicated to non-specialist audiences. However, the responsiveness of the depth (or latitude) indicator to temperature is relatively low, reflecting conditions in the current and preceding 4 years more strongly than in the present season or year. This is not surprising given the multiple direct and indirect pathways through which climate and environment influence population and assemblage dynamics and community turnover times (Salen-Picard *et al.* 2002; Blanchard *et al.* 2005; Rindorf & Lewy 2006). The lagged response suggests that the depth and latitude indicators are best suited for medium-term surveillance of the ecological effects of climate. We suggest that a latitude indicator may be more appropriate for north–south- oriented shelf seas (e.g. Iberian Peninsula or Bay of Biscay), and a depth indicator may be more suited to semi-enclosed seas (e.g. Mediterranean or Baltic Seas).

Acknowledgements

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Thermal preferences of North Sea demersal fishes

Appendix S2. The effect of bottom temperature, year, and exploitation on the depth anomaly of the combined North Sea demersal fish assemblage

Fig. S1. The probability distribution of bottom temperatures encountered by the English Groundfish Survey in autumn from 1980–2004.

Fig. S2. Autumn thermal profiles of (a, b) saithe and (c, d) scaldfish.

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Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas

Nicholas K. Dulvy, Stuart I. Rogers, Simon Jennings, Vanessa Stelzenmüller, Stephen R. Dye and Hein R. Skjoldal

SUPPLEMENTARY MATERIAL

Appendix 1. Thermal preferences of North Sea demersal fishes

If all thermal habitats available to bottom dwelling fishes were sampled in a representative manner then thermal preference of a species could be described by calculating the mean and variance of the temperature at the locations occupied by that species. There are two limitations of this approach; (i) it assumes the trawl survey encompasses and adequately describes the thermal structure of the entire habitat of North Sea fishes, and (ii) it overlooks information about the thermal properties of the sites not occupied by a species.

One approach is to use the frequency with which different temperatures were sampled across the survey grid to generate a probability distribution function. This can be used as a null expectation, against which the probability distribution function of the actual temperatures occupied by a fish species can be compared. Thermal *preference* may be inferred if the probability of occurrence at a given temperature is greater than expected from the thermal distribution of the survey sites. If the thermal distribution of the fish is similar to the thermal distribution of the survey then the thermal preference cannot be inferred, because the possibility that the thermal distribution of that species may solely be a function of the survey distribution cannot be ruled out. This might arise if the survey is sampling only a small proportion of the geographic and thermal range of the species.

Thermal preferences were calculated from bottom temperatures taken on all English Ground Fish Survey hauls from the 17 years including 1983-1998 and 2000. The distribution of temperatures sampled over this part of the survey ranged from $10.84 - 22.13^{\circ}C$ is not normally distributed: the survey encounters cooler water more often than warmer water. Across the survey grid there is a relatively low probability that cool water $<12^{\circ}C$ and that warm water $>18^{\circ}C$ are sampled (Fig. S1). The northerly-distributed saithe has a greater than expected probability of occurrence in cool water between 12-$15^{\circ}C$ and a lower than expected probability of occurrence above 15 $^{\circ}C$ (Fig. S2a). The southerly-distributed scaldfish has zero probability of occurrence in temperatures below $13^{\circ}C$ and a greater than expected probability of occurrence between 15-21$^{\circ}C$ (Fig. S2c).

A better way to visualise thermal preference is to subtract the survey probability distribution function from the fish pdf and plot the departures from the null expectation (Fig. S2b & d). Positive y-axis values represent thermal preference, however negative values cannot be interpreted as avoidance. We

summarised the thermal preference of each species using the most preferred temperature (at the peak) and the range of preferred temperatures (10th and 90th quantiles).
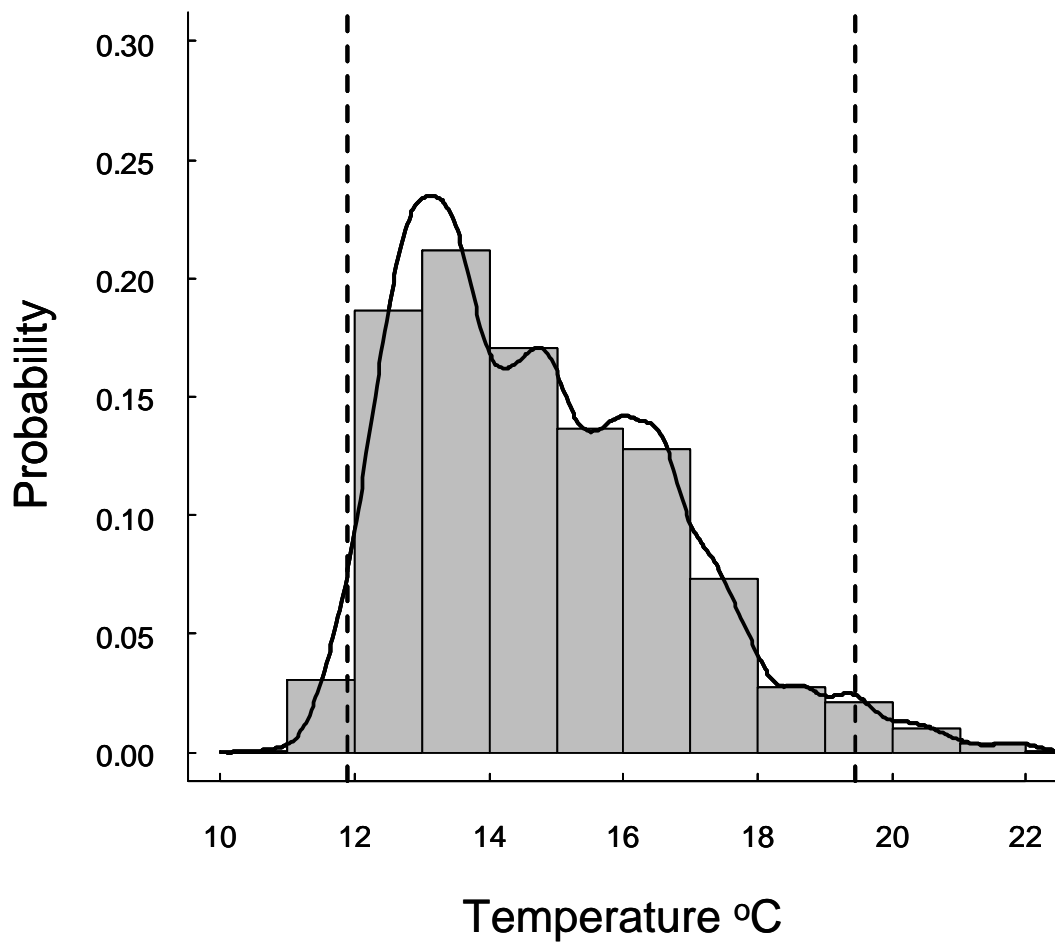

Fig. S1. The probability distribution of bottom temperatures encountered by the English Groundfish Survey in autumn from 1980-2004. The mean autumn temperature during this survey is 14.4oC and the dashed lines represent the upper and lower 95% confidence interval 11.88-19.46oC. The histogram bars represent a 1 degree bin size whereas the line is the actual continuous probability distribution.
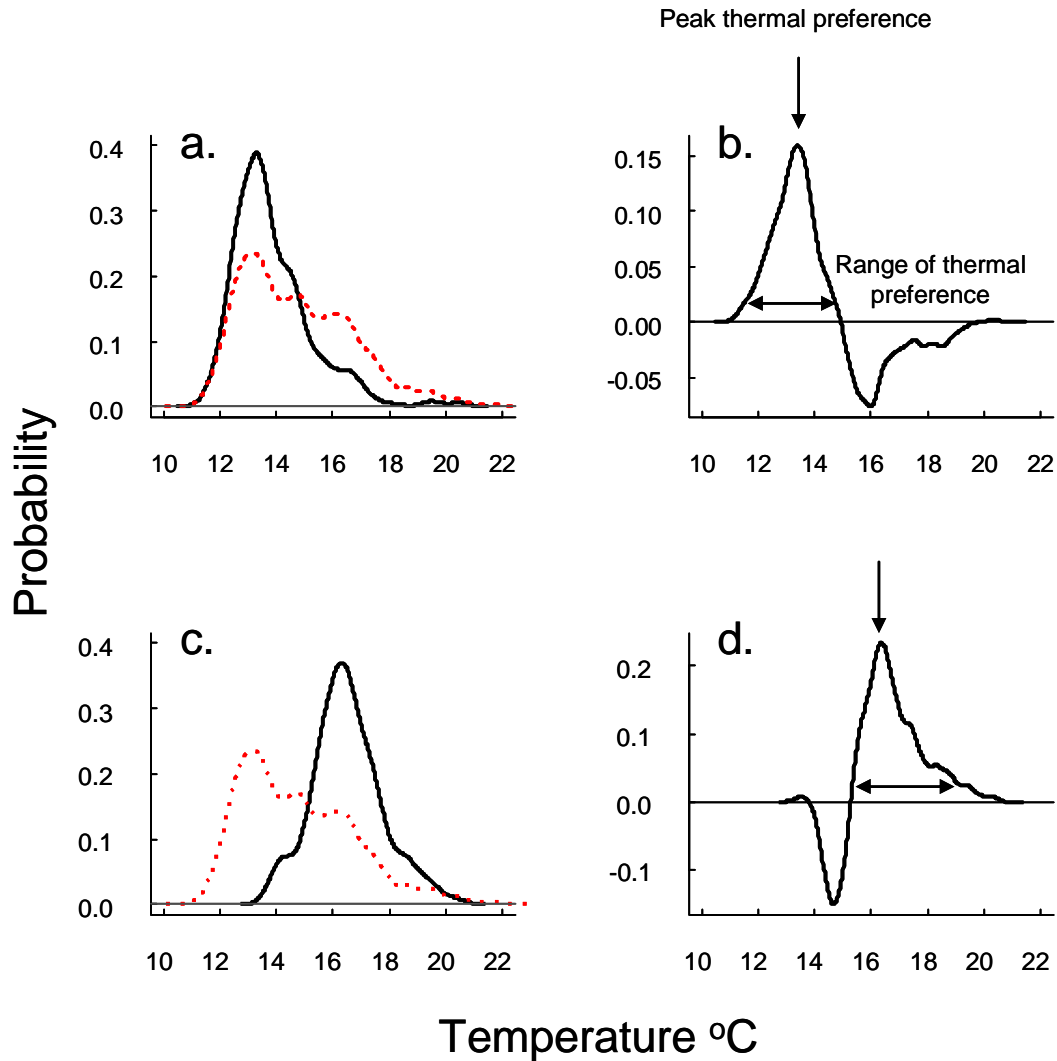
Fig. S2. Autumn thermal profiles of (a,b) saithe and (c,d) scaldfish. (a,c) The probability of occurrence of each species (black line) and the probability of surveying a particular temperature (red dashed line) across the range of temperatures sampled. (b,d) Thermal preference was calculated by subtracting the survey temperature pdf from the species temperature pdf.

Table S1. The effect of bottom temperature, year, and exploitation on the depth anomaly of the combined North Sea demersal fish assemblage with (a) winter bottom temperature or (b) climate index and year and exploitation rate as explanatory variables. Note this result still holds when the order of entry is reversed.

	Degrees of Freedom	Sum of Squares	F value	P value
(a) bottom temperature	1	155.9	17.52	0.0005
Year	1	2.1	0.2333	0.63
Exploitation index	1	6.2	0.7009	0.41
Residual	19	169.1		

Adjusted $R^2 = 0.41$, $F_{3,19} = 6.15$, $P = 0.0042$

(b) Climate Index	1	188.6	25.5859	0.00007
Year	1	4.2	0.5724	0.4586
Exploitation index	1	0.5	0.0608	0.8079
Residual	19	140.1		

Adjusted $R^2 = 0.51$, $F_{3,19} = 8.74$, $P = 0.0007$