Climate Change and Distribution Shifts in Marine Fishes

Allison L. Perry,[1]* Paula J. Low,[2]† Jim R. Ellis,[2] John D. Reynolds[1]*

We show that the distributions of both exploited and nonexploited North Sea fishes have responded markedly to recent increases in sea temperature, with nearly two-thirds of species shifting in mean latitude or depth or both over 25 years. For species with northerly or southerly range margins in the North Sea, half have shown boundary shifts with warming, and all but one shifted northward. Species with shifting distributions have faster life cycles and smaller body sizes than nonshifting species. Further temperature rises are likely to have profound impacts on commercial fisheries through continued shifts in distribution and alterations in community interactions.

Climate change is predicted to drive species ranges toward the poles (*1*), potentially resulting in widespread extinctions where dispersal capabilities are limited or suitable habitat is unavailable (*2*). For fishes, climate change may strongly influence distribution and abundance (*3*, *4*) through changes in growth, survival, reproduction, or responses to changes at other trophic levels (*5*, *6*). These changes may have impacts on the nature and value of commercial fisheries. Species-specific responses are likely to vary according to rates of population turnover. Fish species with more rapid turnover of generations may show the most rapid demographic responses to temperature changes, resulting in stronger distributional responses to warming. We tested for large-scale, long-term, climate-related changes in marine fish distributions and examined whether the distributions of species with fast generation times and associated life history characteristics are particularly responsive to temperature changes.

We studied the demersal (bottom-living) fish assemblage in the North Sea. This group is composed of more than 90 species with varied biogeographical origins and distribution patterns. North Sea waters have warmed by an average of 0.6°C between 1962 and 2001, based on four decadal means before 2001, and by 1.05°C from 1977 to 2001 (*7*), which correspond with our fish survey time series. Survey data were used to calculate catch per unit effort to determine centers of abundance (mean latitudes and depths) for all species and boundary latitudes for those species that have either northerly or southerly range limits in the North Sea (*7*). No species range was entirely confined to the North Sea. Measures of distribution were regressed against same-year and time-lagged bottom temperatures, and also a composite measure of temperatures, the North Atlantic Oscillation Index, the Gulf Stream Index, and the ratio of abundances of northern and southern calanoid copepod species (*7*). We also controlled for changes in abundance that may have influenced species distributions (*7*).

Centers of distribution as measured by mean latitudes shifted in relation to warming for 15 of 36 species (Table 1). These trends were shown by both commercially exploited species [such as Atlantic cod (*Gadus morhua*) and the common sole (*Solea solea*)], and by species that are not targeted by fisheries [such as scaldfish (*Arnoglossus laterna*) and snakeblenny (*Lumpenus lampretaeformis*)]. Distances moved ranged from 48 to 403 km (average distance $\bar{x} = 172.3 \pm 98.8$ km, $n = 15$ species) (Fig. 1) and most of these shifts (13 of 15) were northward (Table 1). The spatial temperature gradient of the North Sea is somewhat unusual; water temperatures become colder with increasing latitude in the southern North Sea but become slightly warmer with increasing latitudes in the north (*8*), where warm North Atlantic Current waters enter the region (*9*). This temperature pattern may explain one of the two exceptional species that moved south, the Norway pout (*Trisopterus esmarkii*). Its distribution was centered in the northern North Sea, and its southern movement brought it into cooler waters. The other exception was the common sole. We speculate that the southward shift in its distribution may have been caused by the fact that the cleanup of the Thames estuary led to its emergence as a major sole nursery ground during the study period (*10*).

Most species that showed climate-related latitudinal changes also shifted in depth, which was unsurprising because North Sea depths are roughly positively correlated with latitude (*8*). A further six species, including plaice (*Pleuronectes platessa*) and cuckoo ray (*Leucoraja*

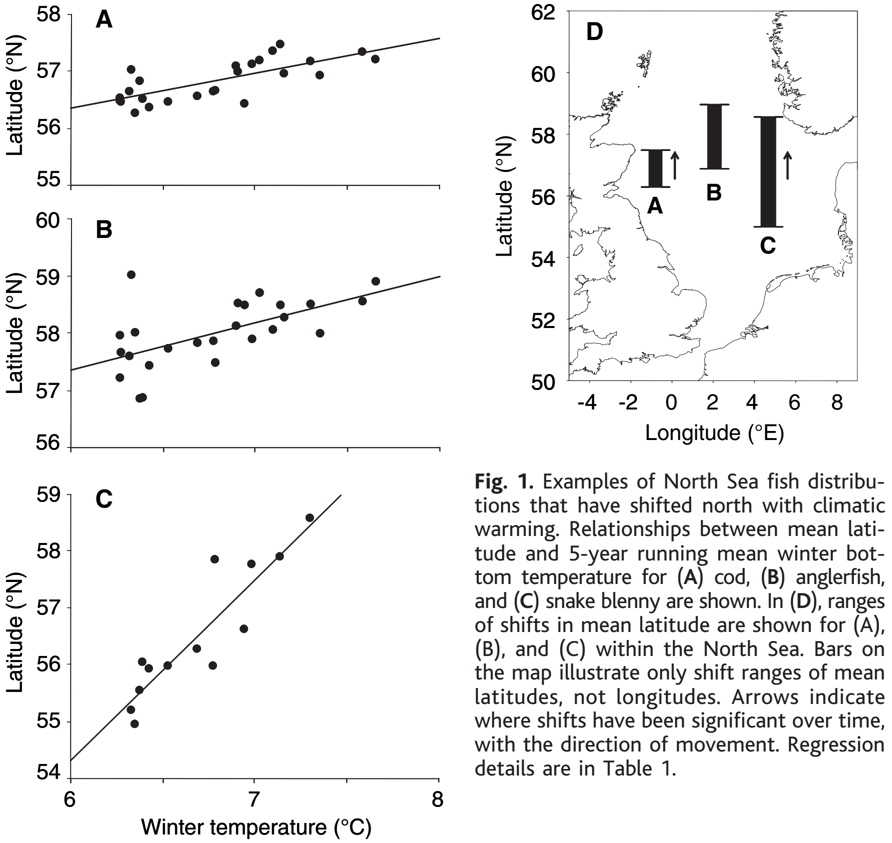

Fig. 1. Examples of North Sea fish distributions that have shifted north with climatic warming. Relationships between mean latitude and 5-year running mean winter bottom temperature for (**A**) cod, (**B**) anglerfish, and (**C**) snake blenny are shown. In (**D**), ranges of shifts in mean latitude are shown for (A), (B), and (C) within the North Sea. Bars on the map illustrate only shift ranges of mean latitudes, not longitudes. Arrows indicate where shifts have been significant over time, with the direction of movement. Regression details are in Table 1.

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[1] Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK. [2] Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK.

*To whom correspondence should be addressed. E-mail: a.perry@uea.ac.uk (A.L.P.); reynolds@uea.ac.uk (J.D.R.).

†Present address: University Marine Biological Station Millport, Isle of Cumbrae KA28 0EF, UK.

naevus), moved deeper with warming but did not change in latitude, suggesting that they may have responded to climatic variation through local movements offshore or into pockets of deeper water. Considering both latitude and depth, nearly two-thirds of species ($n = 21$ out of 36) have shown distributional responses to climatic warming (table S1).

We tested whether species boundaries have also been displaced by warming, by examining those 20 species from our data set with a southern or a northern range limit in the North Sea. The boundaries of half of these fishes moved significantly with warming (Fig. 2 and table S2). Southern boundaries shifted in 6 of 12 cases, and all shifts were northward. Four of eight northern boundaries also moved with warming. All but one of these species shifted north, despite the fact that their northern range limits lay in the relatively intensively fished southern North Sea (*11*). Shifting species again included both exploited and nonexploited fishes. Boundaries moved over distances ranging from 119 to 816 km ($\bar{x} = 304 \pm 196$ km, $n = 10$), with the highest value describing the range of movement of the southern boundary of blue whiting (*Micromesistius poutassou*), which is the target of the largest fishery in the Atlantic (*12*). In the case of bib (*Trisopterus luscus*), the northern boundary shifted by 342 km from 1978 to 2001, a trend that is supported by observations that North Sea catches of this species have been increasing (*13*).

To identify shifts that may have been driven by fishing or other nonclimatic influences, we also examined distribution changes over time. Fishing pressure could not be included explicitly in our analyses because reliable fishing effort data on a comparable spatial and temporal scale do not exist for the North Sea. However, during at least the last decade of the 25-year period of analysis, the spatial distribution of effort remained relatively constant (*11*), and total fishing effort may have declined slightly (*14*). Temporal trends in distribution suggested that fishing alone could not explain climate-related shifts; despite the general increase in temperature over the study period, warming-related shifts occurred independently of time for centers of distribution in 8 of 36 species and for range limits in 4 of 20 species (table S3). Such shifts may have reflected year-to-year environmental variability, with northward movement during warm years cancelled by southward movement during cool years. If so, long-term distribution shifts could depend strongly on future climatic variability, in addition to longer-term average conditions.

The examination of temporal trends also allowed for rough comparisons to be drawn with rates of warming-related distribution shifts in other taxa. A recent meta-analysis of climate-change impacts on natural systems estimated the mean annual rate of boundary movement for 99 species of birds, butterflies, and alpine herbs at 0.6 km northward or 0.6 m upward (*1*). From the current study, the mean rate of movement for the six fish species whose boundaries shifted in relation to both climate and time [bib, blue whiting, lesser weever

Table 1. Statistically significant multiple regressions of the effects of three measures of North Sea warming on mean latitudes of 36 demersal fishes from 1977 to 2001. PC1, first principal component from principal components analysis (PCA) of eight environmental variables (PC1 generally describes warming). Winter temp. and summer temp. indicate 5-year running mean bottom temperatures for December to March and June to September, respectively.

Species	Common name	df	Mean latitude (°N)	SD	PC1	r^2	P	Winter temp.	r^2	P	Summer temp.	r^2	P
Agonus cataphractus	Pogge	22	54.67	0.90									
Anarhichus lupus	Atlantic wolffish	21	58.14	0.46									
Argentina spp.	Argentines	24	59.59	0.30									
Arnoglossus laterna	Scaldfish	15	54.17	0.31				0.456	0.43	0.006			
Buglossidium luteum	Solenette	23	54.14	0.28									
Callionymus lyra	Dragonet	23	55.40	0.65	0.265	0.16	0.049	0.937	0.34	0.002			
Echiichthys vipera	Lesser weever	24	53.30	0.13				0.191	0.39	0.001			
Eutrigla gurnardus	Grey gurnard	23	56.13	0.35	0.194	0.30	0.006	0.651	0.61	<0.001	0.402	0.17	0.040
Gadiculus argenteus	Silvery pout	23	59.83	0.41									
Gadus morhua	Atlantic cod	23	56.81	0.34	0.256	0.58	<0.001	0.534	0.38†	<0.001	0.578	0.33†	<0.001
Glyptocephalus cynoglossus	Witch	24	58.22	0.42									
Hippoglossoides platessoides	Long rough dab	24	57.62	0.21				0.304	0.40	0.001			
Lepidorhombus boscii	Fourspot megrim	24	60.51	0.37									
Leucoraja naevus	Cuckoo ray	19	58.06	0.57									
Limanda limanda	Dab	24	55.86	0.13				0.180	0.35†	0.001			
Lophius piscatorius	Anglerfish	23	57.99	0.58	0.254	0.19	0.032	0.818	0.37	0.001			
Lumpenus lampretaeformis	Snake blenny	12	56.52	1.15				3.174	0.81	<0.001			
Melanogrammus aeglefinus	Haddock	24	57.91	0.16									
Merlangius merlangus	Whiting	23	56.57	0.15	0.066	0.19	0.034						
Merluccius merluccius	Hake	24	58.84	0.59									
Micromesistius poutassou	Blue whiting	21	60.13	0.48									
Microstomus kitt	Lemon sole	24	57.06	0.24									
Molva molva	Ling	24	59.26	0.74									
Myxine glutinosa	Hagfish	11	57.51	0.62									
Pleuronectes platessa	Plaice	24	55.52	0.18									
Pollachius virens	Saithe	24	59.44	0.20									
Psetta maxima	Turbot	13	54.73	0.31									
Rhinonemus cimbrius	Four-bearded rockling	22	56.05	0.68	0.419	0.40	0.001	1.147	0.53	<0.001	0.950	0.28	0.008
Scyliorhinus canicula	Small-spotted catshark	20	58.34	0.89									
Sebastes spp.	Redfish	18	59.89	0.49									
Solea solea	Common sole	13	53.68	0.66				–0.941	0.38	0.020	–0.963	0.34	0.028
Squalus acanthias	Spurdog	19	56.29	0.68									
Trigla lucerna	Tub gurnard	19	53.89	0.50									
Trisopterus esmarkii	Norway pout	23	58.59	0.26	–0.190	0.52	<0.001	–0.304	0.25	0.010	–0.429	0.37	0.001
Trisopterus luscus	Bib	9	53.29	0.51				0.489*	0.45	0.035			
Trisopterus minutus	Poor cod	23	55.63	0.66	0.334	0.26	0.012	0.877	0.33	0.003	0.753	0.18	0.035

*A relationship with annual mean summer or winter temperature. †To identify the proportion of variance in distribution accounted for by warming, r^2 and P describe the squared semi-partial correlation coefficient, where abundance was also a significant predictor of distribution.

(*Echiichthys vipera*), Norway pout, scaldfish, and witch (*Glyptocephalus cynoglossus*)] was 2.2 km per year. It is perhaps unsurprising that the rate of shift might be higher for marine fishes than for alpine herbs and butterflies, given that marine fish may generally face fewer constraints on movement. However, if such a difference is indicative of more widespread trends in marine fishes, climate change could pose a greater threat to fish populations that are constrained by their dispersal capabilities or habitat requirements.

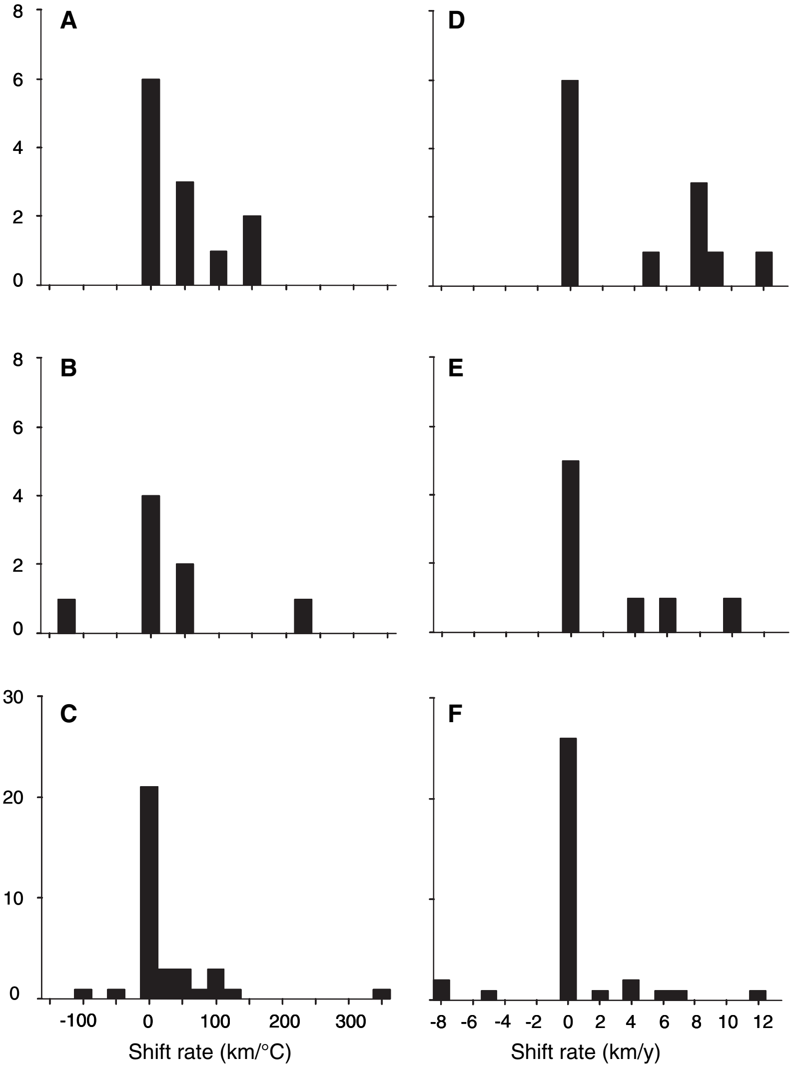

Fig. 2. Frequency distributions of fish species shift rates in relation to warming and time. (**A**) Rates of shift for northerly species' (southern) boundaries with climate. (**B**) Southerly species' (northern) boundaries with climate. (**C**) All species' mean latitudes with climate. (**D**) Northerly species'(southern) boundaries over time. (**E**) Southerly species' (northern) boundaries over time. (**F**) All species' mean latitudes over time. Rates for shifting species are slopes from regressions.

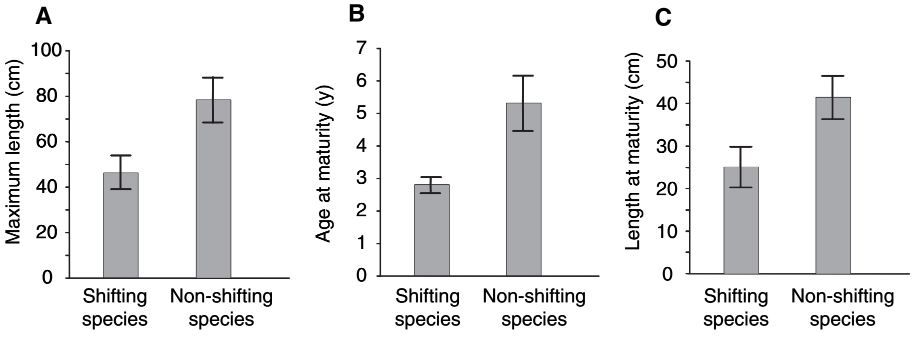

Fig. 3. Differences in life-history traits between shifting (n = 15) and nonshifting (n = 21) species with respect to centers of distribution (mean latitudes). (**A**) Maximum body size [$t = -2.41$, degrees of freedom (df) = 34, P = 0.02]. (**B**) Age at maturity ($t = -2.86$, df = 27, P = 0.01). (**C**) Length at maturity ($t = -2.29$, df = 29, P = 0.03). Means are shown with standard errors.

If the differences in rates of movement among the taxa documented here result from differential rates of population turnover, we would expect species with life history traits associated with fast population growth to have responded most strongly to climate change. To test this prediction, we compared life history traits between shifting and nonshifting species (*7*). As predicted, shifting species tend to have faster life histories than do nonshifting species, with significantly smaller body sizes, faster maturation, and smaller sizes at maturity (Fig. 3). Body growth rates did not differ significantly between shifting and nonshifting species (P = 0.19). These relationships therefore provide a starting point for predicting species' responses to future climate change. These predictions could be refined, through detailed studies of the relative sensitivities of different life history stages, to uncover the specific mechanisms driving the patterns.

Our study shows that climate change is having detectable impacts on marine fish distributions, and observed rates of boundary movement with warming indicate that future distribution shifts could be pronounced. Mean annual surface temperatures in the North Sea are predicted to increase by 0.5 to 1.0°C by 2020, 1.0 to 2.5°C by 2050, and 1.5 to 4.0°C by 2080 (*15*). We used the midpoints of these temperature ranges as the basis for a rough approximation, which suggested that two types of commercial fishes, blue whiting and redfishes (*Sebastes* spp.), may retract completely from the North Sea by 2050, and by 2080, bib may extend its range northward to encompass the entire region. Such changes will clearly also depend on the responses of their predators and prey to increases in bottom temperature and on the availability of suitable habitat.

These findings may have important impacts on fisheries. For example, species with slower life histories are already more vulnerable to overexploitation (*16–18*) and may also be less able to compensate for warming through rapid demographic responses. A further concern is that differential rates of shift could result in altered spatial overlap among species, thereby disrupting interactions and also potentially compounding the decoupling effects of climate-driven changes in phenology (*19*). Previous work off the eastern United States has shown that fishes with the most temperature-sensitive distributions included key prey species of nonshifting predators (*20*). Such changes could have unpredictable effects in an ecosystem already under heavy anthropogenic pressure.

References and Notes

1. C. Parmesan, G. Yohe, *Nature* **421**, 37 (2003).
2. C. D. Thomas *et al.*, *Nature* **427**, 145 (2004).
3. C. M. Wood, D. G. McDonald, Eds., *Global Warming: Implications for Freshwater and Marine Fish* (Cambridge Univ. Press, Cambridge, 1997).
4. K. Brander *et al.*, *Int. Counc. Explor. Sea Mar. Sci. Symp.* **219**, 261 (2003).
5. G. Beaugrand, K. M. Brander, J. A. Lindley, S. Souissi, P. C. Reid, *Nature* **426**, 661 (2003).
6. G. Beaugrand, P. C. Reid, F. Ibañez, J. A. Lindley, M. Edwards, *Science* **296**, 1692 (2002).
7. Materials and methods are available as supporting material on *Science* Online.
8. R. J. Knijn, T. W. Boon, H. J. L. Heessen, J. F. G. Hislop, *Atlas of North Sea Fishes* [International Council for the Exploration of the Sea (ICES) Cooperative Research Report 194, ICES, Copenhagen, 1993].
9. A. N. Strahler, A. H. Strahler, *Physical Geography: Science and Systems of the Human Environment* (Wiley, New York, 1997).
10. R. M. Thomas, in *A Rehabilitated Estuarine Ecosystem: The Environment and Ecology of the Thames Estuary*, M. J. Attrill, Ed. (Kluwer, Dordrecht, Netherlands, 1998), pp. 115–139.
11. S. Jennings *et al.*, *Fish. Res.* **40**, 125 (1999).
12. ICES Advisory Committee on Fishery Management (ACFM), *Report of the Northern Pelagic and Blue Whiting Fisheries Working Group* (ICES CM 2004/ACFM:24, ICES, Copenhagen, 2004).
13. S. I. Rogers, J. R. Ellis, *Int. Counc. Explor. Sea J. Mar. Sci.* **57**, 866 (2000).
14. N. Daan, H. Gislason, J. Pope, J. Rice, *Changes in the North Sea Fish Community: Evidence of Indirect Effects of Fishing*? (ICES CM N:10, ICES, Copenhagen, 2003).
15. U.K. Climate Impacts Programme, *UKCIP02 Scenarios Gateway—Maps Gateway*; available at www.ukcip.org.uk/scenarios/marine/marine.html.
16. N. K. Dulvy, Y. Sadovy, J. D. Reynolds, *Fish Fish.* **4**, 25 (2003).
17. S. Jennings, J. D. Reynolds, S. C. Mills, *Proc. R. Soc. London Ser. B* **265**, 333 (1998).
18. J. D. Reynolds, S. Jennings, N. K. Dulvy, in *Conservation of Exploited Species*, J. D. Reynolds, G. M. Mace, K. H. Redford, J. G. Robinson, Eds. (Cambridge Univ. Press, Cambridge, 2001), pp. 145–168.
19. M. Edwards, A. J. Richardson, *Nature* **430**, 881 (2004).
20. S. A. Murawski, *Trans. Am. Fish. Soc.* **122**, 647 (1993).

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Supporting Online Material

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Materials and Methods
Tables S1 to S4
References

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Supporting Online Material

Materials and Methods

Data

Annual data describing demersal fish distribution and abundance in the North Sea (between 51-62° latitude) from 1977-2001 were taken from the English Groundfish Survey (EGFS) programme. Species were included in analyses if they were caught at a minimum of five stations each year, during at least ten years. Blue whiting (*Micromesistius poutassou*), although not considered a demersal fish, was retained in the dataset because the EGFS is considered to sample this species effectively in the North Sea. In accordance with EGFS records, redfishes (*Sebastes* spp.) were combined, as were argentines (*Argentina silus* and *A. sphyraena*). Abundance-weighted mean annual latitudes and depths were derived for each species. For fishes with northern or southern range limits in the North Sea, abundance-weighted annual boundary latitudes were also calculated, based on the three most extreme stations of occurrence in each year.

Bottom temperature data were obtained from the International Council for the Exploration of the Sea, for 1° x 1° boxes in the North Sea. Annual means and five-year running means (to allow for potential lagged effects) were calculated for winter (the four coldest months, December-March) and summer (the four warmest months, June-September). Data on the winter North Atlantic Oscillation Index (NAOI) (the normalised sea level pressure difference between Gibraltar and Reykjavik, Iceland), which is associated with changes in fish abundance, growth, and productivity (*S1, S2*) were from Jones *et al*. (*S3*), with updated values provided by the Climatic Research Unit, University of East Anglia (*S4*). Gulf Stream Index (GSI) data (measuring the relative extent of the northern wall of the Gulf Stream along the east coast of North

America) were obtained from the Plymouth Marine Laboratory (*S5*). Average annual abundances of the calanoid copepod species *Calanus helgolandicus* and *C. finmarchicus* (which are major food sources for many juvenile fish) (*S6*), were provided by the Sir Alister Hardy Foundation for Ocean Science.

Life history parameter estimates were compiled from the primary literature, FishBase (*S7*), and regional fish guides (*S8, S9*). Growth rates and maximum lengths were described as K and L_∞ from the von Bertalanffy growth equation, $L_t = L_\infty(1 - e^{-K(t-t_0)})$ (where L_t is length at age t, L_∞ is the asymptotic length at which growth rate is theoretically zero, K is the rate of growth towards this asymptote, and t_0 is the age at which length would theoretically have been zero (*S10*)). Maximum observed length (L_{max}) was included, because it was available for more species than L_∞, and serves as a useful surrogate for L_∞, (*S11*). We also used mean age and length at maturity (T_{mat}, and L_{mat}) for 50% of the population. For parameter estimates and references, see Table S4. Values were used for North Sea populations where possible, and otherwise were selected for the closest available region. Means were calculated where sex-specific values were reported or multiple estimates were available, and mean values were also used for the combined redfish and argentine species.

Statistical analyses

In order to assess the direct effects of warming on species distributions, winter and summer temperatures (same-year and five-year running means) and abundance were entered into multiple regressions for each species, using (a) mean latitude (b) mean depth and, where applicable, (c) boundary latitude as dependent variables. Where significant models included both abundance and environmental predictors, semi-partial correlation coefficients were examined to determine the relative influence of warming.

We also examined less direct effects of warming on distributions, through multiple regressions in which we again controlled for changes in abundance and regressed the distribution variables against composite variables of warming rather than temperatures. These new variables were the first and second factors from a Principal Components Analysis of eight environmental variables that generally described warming (winter temperature, five-year running mean winter temperature, summer temperature, five-year running mean summer temperature, NAOI, NAOI with a 1-year lag, GSI, and the ratio of *C. helgolandicus* abundance: *C. finmarchicus* abundance) and were correlated with the position of species centres and boundaries. The first principal component (PC1) explained 47% of the variance in these variables, and generally described warming. PC2 accounted for a further 18% of the variance. Finally, we used simple linear regression to examine changes in mean latitudes and boundary latitudes over time.

We tested for life history differences between species whose mean latitudes shifted and did not shift in relation to warming. Small sample sizes limited the use of phylogenetically paired comparisons, although life history differences lay in the expected direction for 6 of 9 pairs.

The effects of using mean values for life history parameters estimates for redfishes and argentines were checked by redoing analyses using values for individual species from each group, and by excluding these groups altogether. None of these variations altered our findings.

Table S1 Statistically significant multiple regressions of the effects of 3 measures of North Sea warming on mean depths of 36 demersal fishes, 1977-2001. PC1, first Principal Component from PCA of eight environmental variables (PC1 generally describes warming). Winter and summer temp., 5-year running mean bottom temperatures for Dec-Mar and Jun-Sep, except where ^{a} indicates a relationship with annual mean summer or winter temperature. Where abundance was also a significant predictor of distribion, ^{s} denotes that r^2 and P describe the squared semi-partial correlation coefficient (to identify the proportion of variance in distribution accounted for by warming).

Species	Common name	df	Mean depth (m)	SD	PC1	r^2	P	Winter temp.	r^2	P	Summer temp.	r^2	P
Agonus cataphractus	Pogge	22	46.7	6.6									
Anarhichus lupus	Atlantic wolffish	21	103.0	8.0									
Argentina spp.	Argentines	24	138.1	7.6									
Arnoglossus laterna	Scaldfish	15	35.5	4.3							4.153^a	0.34	0.017
Buglossidium luteum	Solenette	22	33.8	3.9	2.170	0.32	0.005	2.765^a	0.25	0.012	5.461	0.28	0.007
Callionymus lyra	Dragonet	23	55.7	12.4	6.882	0.31	0.005	17.768	0.35	0.002	13.973	0.16	0.049
Echiichthys vipera	Lesser weever	24	33.2	2.9							3.300	0.18	0.034
Eutrigla gurnardus	Grey gurnard	23	62.6	6.5	4.223	0.42	0.001	10.534	0.47	<0.001	10.809	0.36	0.001
Gadiculus argenteus	Silvery pout	23	160.1	9.1									
Gadus morhua	Atlantic cod	23	81.7	7.9	5.5024	0.33^s	<0.001	9.692	0.22^s	0.001	13.465	0.31^s	<0.001
Glyptocephalus cynoglossus	Witch	24	120.5	10.3									
Hippoglossoides platessoides	Long rough dab	23	97.5	4.4	2.293	0.28	0.009	5.951	0.35	0.002	6.014	0.27	0.008
Lepidorhombus boscii	Fourspot megrim	24	148.3	9.8									
Leucoraja naevus	Cuckoo ray	19	81.2	14.6				19.986	0.36	0.005			
Limanda limanda	Dab	23	58.8	3.5	2.033	0.34	0.003	3.621	0.20	0.024	5.811	0.39	0.001
Lophius piscatorius	Anglerfish	23	99.4	10.5	5.841	0.28	0.009	14.049	0.34	0.002			
Lumpenus lampretaeformis	Snake blenny	12	101.1	21.3				61.100	0.87	<0.001			
Melanogrammus aeglefinus	Haddock	24	98.5	3.5				3.999	0.24	0.013			
Merlangius merlangus	Whiting	24	76.4	4.5									
Merluccius merluccius	Hake	24	121.1	13.8									
Micromesistius poutassou	Blue whiting	20	165.0	14.0	7.889	0.33	0.007	12.645^a	0.40	0.002			
Microstomus kitt	Lemon sole	24	80.7	4.5									
Molva molva	Ling	24	129.3	16.3									
Myxine glutinosa	Hagfish	11	113.5	12.6									
Pleuronectes platessa	Plaice	23	53.1	3.5	1.92	0.31	0.005	3.348	0.17	0.041	5.427	0.33	0.003
Pollachius virens	Saithe	24	143.3	7.1									
Psetta maxima	Turbot	13	43.7	6.6									
Rhinonemus cimbrius	Four-bearded rockling	22	91.4	13.1	6.058	0.22	0.024	16.790	0.31	0.005			
Scyliorhinus canicula	Small-spotted catshark	20	83.8	9.9									
Sebastes spp.	Redfish	18	137.9	17.1	8.201	0.27	0.024	15.044^a	0.39	0.004			
Solea solea	Common sole	13	37.5	6.7									
Squalus acanthias	Spurdog	19	69.8	11.8									
Trigla lucerna	Tub gurnard	19	33.12	2.3									
Trisopterus esmarkii	Norway pout	23	118.0	4.3	-1.922	0.20	0.029						
Trisopterus luscus	Bib	9	39.5	6.5									
Trisopterus minutus	Poor cod	23	67.1	8.6	4.126	0.23	0.018	11.246	0.33	0.003			

Table S2 Statistically significant multiple regressions of the effects of 3 measures of North Sea warming on boundary latitudes of 20 demersal fishes, 1977-2001. PC1, first Principal Component from PCA of 8 environmental variables (PC1 generally describes warming). Winter and summer temp., 5-year running mean bottom temperatures for Dec-Mar and Jun-Sep, except where ^{a} indicates a relationship with annual mean summer or winter temperature. Where abundance was also a significant predictor of distribution, ^{s} denotes that r^2 and *P* describe the squared semi-partial correlation coefficient (to identify the proportion of variance in distribution accounted for by warming).

Species	Common name	df	Boundary latitude (°N)	SD	PC1	r^2	*P*	Winter temp.	r^2	*P*	Summer temp.	r^2	*P*
Northerly species													
Anarhichus lupus	Atlantic wolffish	21	56.18	0.77									
Gadiculus argenteus	Silvery pout	23	58.50	0.59									
Glyptocephalus cynoglossus	Witch	23	55.70	0.74	0.293	0.15^{s}	0.012	0.706	0.17^{s}	0.01	0.893	0.18^{s}	0.007
Hippoglossoides platessoides	Long rough dab	23	54.11	0.28	0.138	0.24	0.016	0.545	0.60^{s}	<0.001			
Lepidorhombus boscii	Fourspot megrim	24	59.01	1.00									
Leucoraja naevus	Cuckoo ray	19	56.80	0.38									
Melanogrammus aeglefinus	Haddock	23	53.96	0.49	0.267	0.28^{s}	0.006	0.379^{a}	0.29	0.008			
Micromesistius poutassou	Blue whiting	20	57.67	1.72	0.923	0.29	0.011	1.452^{a}	0.34	0.005			
Molva molva	Ling	23	56.41	1.00									
Pollachius virens	Saithe	24	56.89	0.88									
Sebastes spp.	Redfish	18	58.46	0.83							1.391	0.38	0.005
Trisopterus esmarkii	Norway pout	24	54.85	0.51				0.359^{a}	0.23	0.015			
Southerly species													
Agonus cataphractus	Pogge	22	57.47	1.07									
Arnoglossus laterna	Scaldfish	15	54.91	0.61				0.542	0.11	0.029			
Buglossidium luteum	Solenette	23	55.25	0.53									
Echiichthys vipera	Lesser weever	23	54.70	0.37	0.162	0.19	0.035	0.500	0.30	0.004			
Psetta maxima	Turbot	13	55.97	0.92									
Solea solea	Common sole	13	54.91	0.78									
Trigla lucerna	Tub gurnard	19	55.23	0.85							-1.084	0.24	0.029
Trisopterus luscus	Bib	8	54.23	0.73	0.549	0.88	<0.001	0.997	0.55	0.015	2.026	0.82	<0.001

Table S3 Statistically significant linear regressions between time and (i) boundary latitudes; and (ii) mean latitudes of North Sea demersal fishes, 1977-2001. *Latitude shifted south with warming. Arrows indicate where abundance has increased or decreased significantly over time. See Table 1 and Table S2 for full species lists and relationships between distributions and warming.

Species	Common name	df	Latitude (°N)	SD	Year coefficient	r^2	P	Latitude related to warming?	Abundance trend over time
(i) Boundary Latitudes									
Northerly species									
Anarhichas lupus	Atlantic wolffish	21	56.18	0.77	0.079	0.48	<0.001	No	↓
Glyptocephalus cynoglossus	Witch	24	55.73	0.73	0.068	0.46	<0.001	Yes	
Lepidorhombus boscii	Fourspot megrim	24	59.01	1.00	0.076	0.32	0.003	No	
Micromesistius poutassou	Blue whiting	21	57.71	1.69	0.111	0.27	0.014	Yes	
Molva molva	Ling	23	56.41	1.00	0.068	0.24	0.015	No	
Trisopterus esmarkii	Norway pout	24	54.85	0.51	0.041	0.35	0.002	Yes	↑
Southerly species									
Arnoglossus laterna	Scaldfish	15	54.91	0.61	0.052	0.32	0.022	Yes	
Echiichthys vipera	Lesser weever	24	54.72	0.39	0.035	0.43	<0.001	Yes	↑
Trisopterus luscus	Bib	9	54.43	0.94	0.093	0.80	0.001	Yes	
(ii) Mean latitudes									
Agonus cataphractus	Pogge	22	54.67	0.90	-0.074	0.37	0.002	No	
Callionymus lyra	Dragonet	24	55.44	0.69	0.063	0.45	<0.001	Yes	
Eutrigla gurnardus	Grey gurnard	24	56.15	0.36	0.036	0.54	<0.001	Yes	↑
Gadus morhua	Atlantic cod	24	56.84	0.36	0.035	0.53	<0.001	Yes	↓
Lepidorhombus boscii	Fourspot megrim	24	60.51	0.37	0.021	0.17	0.041	No	
Lumpenus lampretaeformis	Snake blenny	12	56.52	1.15	0.107	0.63	0.001	Yes	
Rhinonemus cimbrius	Four-bearded rockling	24	56.07	0.67	0.055	0.36	0.002	Yes	
Scyliorhinus canicula	Small-spotted catshark	20	58.34	0.89	-0.077	0.35	0.004	No	↑
Solea solea	Common sole	13	53.72	0.66	-0.049	0.36	0.024	Yes*	
Trisopterus esmarkii	Norway pout	24	58.59	0.26	-0.019	0.29	0.005	Yes*	↑

Table S4 Life history parameter estimates for 36 North Sea demersal fish species. L_∞, asymptotic (maximum) length; K, growth rate from the von Bertalanffy equation; L_{max}, maximum recorded length; T_{mat}, age at which 50% of the population are mature; L_{mat}, length at which 50% of the population are mature.

Species	Common Name	L_∞ (cm)	L_{max} (cm)	K (y^{-1})	T_{mat} (y)	L_{mat} (cm)	References
Agonus cataphractus	Pogge	15	20	0.475	.	.	*S8, S12, S13*
Anarhichas lupus	Atlantic wolffish	162.5	125	0.0435	6.5	55	*S8, S14*
Arnoglossus laterna	Scaldfish	15	25	0.936	.	6.8	*S8, S15, S16*
Buglossidium luteum	Solenette	10.75	12.5	0.573	3	7	*S8, S15, S17*
Callionymus lyra	Dragonet	23	25	0.47	2.5	13	*S8, S18*
Echiichthys vipera	Lesser weever	.	17	.	.	.	*S19*
Eutrigla gurnardus	Grey gurnard	46	45	0.16	3	23	*S8, S20*
Gadiculus argenteus	Silvery pout	15.5	15	0.693	.	.	*S8, S21*
Gadus morhua	Atlantic cod	123.1	131.8	0.23	3.8	69.7	*S11, S22*
Glyptocephalus cynoglossus	Witch	44	60	0.2	4.5	29	*S20*
Hippoglossoides platessoides	Long rough dab	25	30	0.34	2.6	15	*S7, S20*
Lepidorhombus boscii	Fourspot megrim	50	35	0.155	1.5	.	*S7, S23, S24*
Leucoraja naevus	Cuckoo ray	92	70	0.11	9	59	*S8, S20*
Limanda limanda	Dab	27	40	0.26	2.3	13	*S8, S20*
Lophius piscatorius	Anglerfish	106	74.6	0.18	4.5	61	*S11, S20*
Lumpenus lampretaeformis	Snake blenny	.	50	.	3	20	*S8*
Melanogrammus aeglefinus	Haddock	68.3	75.5	0.19	2.5	33.5	*S22*
Merlangius merlangus	Whiting	42.4	44.9	0.32	1.5	20.2	*S11, S22*
Merluccius merluccius	Hake	105	135	0.184	6.75	51.75	*S8, S25*
Micromesistius poutassou	Blue whiting	37.1	34	0.23	2.3	25.1	*S7, S22*
Microstomus kitt	Lemon sole	37	60	0.42	4	27	*S8, S20, S26*
Molva molva	Ling	183	200	0.118	6.5	90	*S8, S27*
Myxine glutinosa	Hagfish	.	80	.	.	25	*S8*
Pleuronectes platessa	Plaice	54.5	95	0.11	2.5	26.6	*S8, S22*
Pollachius virens	Saithe	177.1	130	0.07	4.6	55.4	*S8, S22*
Psetta maxima	Turbot	69.6	100	0.2497	4.5	49	*S8, S15, S17, S28*
Rhinonemus cimbrius	Four-bearded rockling	36	40	0.2	3	25	*S8, S20*
Scyliorhinus canicula	Small-spotted catshark	88	100	0.2	5	58	*S8, S20*
Sebastes marinus	Redfish	74.4	100	0.0615	11	35	*S8, S29*
Sebastes viviparus	Norway haddock	36	35	0.07	20	12.5	*S8, S20*
Solea solea	Common sole	45.3	60	0.363	4	29	*S8, S15*
Squalus acanthias	Spurdog	90	105	0.15	6.5	67	*S8, S20*
Trigla lucerna	Tub gurnard	68.15	75	0.1524	.	.	*S8, S30, S31*
Trisopterus esmarkii	Norway pout	23	25	0.52	2.3	19	*S8, S22*
Trisopterus luscus	Bib	42.35	46	0.211	2	22.5	*S17, S32*
Trisopterus minutus	Poor cod	20	40	0.51	2	15	*S8, S20*

References

S1. M. J. Attrill, M. Power, *Nature* **417**, 275 (2002).
S2. G. Ottersen *et al*., *Oecologia* **128**, 1 (2001).
S3. P. D. Jones, T. Jónsson, D. Wheeler, *Int. J. Climatol.* **17**, 1433 (1997).
S4. T. Osborn, *North Atlantic Oscillation* (www.cru.uea.ac.uk/~timo/projpages/nao_update.htm, 2002).
S5. A. H. Taylor, *Latitude of the Gulf Stream* (www.pml.ac.uk/gulfstream, 2002).
S6. L. S. Parsons, W. H. Lear, *Prog. Oceanogr.* **49**, 167 (2001).
S7. R. Froese, D. Pauly, *FishBase* (www.fishbase.org, 2002).
S8. B. J. Muus, J. G. Nielson, *Sea Fish* (Scandinavian Fishing Year Book, Hedehusene, Denmark, 1999).
S9. P. J. Miller, M. J. Loates, *Fish of Britain and Europe* (Harper Collins, London, 1997).
S10. R. J. H. Beverton, S. J. Holt, *On the Dynamics of Exploited Fish Populations* (Ministry of Agriculture, Fisheries and Food, London, 1957).
S11. N. H. Denney, S. Jennings, J. D. Reynolds, *Proc. R. Soc. London Ser. B* **269**, 2229 (2002).
S12. S. Le Gall, *Vie milieu* **20A**, 153 (1969).
S13. E. Ehrenbaum, *Eier und Larven von Fischen. Nordisches Plankton* (Lipsius & Tischer, Kiel, 1905).
S14. G. Beese, R. Kändler, *Ber. Deut. Wiss. Komm.* **20**, 21 (1969).
S15. C. Déniel, *J. Fish Biol.* **37**, 149 (1990).
S16. O. Giovanardi, C. Piccinetti, "Biology and fishery of the scaldfish *Arnoglossus laterna* (Walbaum 1792) in the Adriatic Sea" (FAO Fish. Rep. 290, FAO, Rome, 1983).
S17. R. J. Knijn, T. W. Boon, H. J. L Heessen, J. F. G. Hislop, "Atlas of North Sea Fishes" (ICES Coop. Res. Rep. 194, ICES, Copenhagen, 1993).
S18. H. W. van der Veer *et al*., *Neth. J. Sea Res.* **26**, 139 (1990).
S19. E. Tortonese, in *Checklist of the fishes of the north-eastern Atlantic and of the Mediterranean (CLOFNAM)*, J. C. Hureau, T. Monod, Eds., vol II, (UNESCO, Paris, 1986), pp. 951-954 .
S20. S. Jennings, S. P. R. Greenstreet, J. D. Reynolds, *J. Anim. Ecol.* **68**, 617 (1999).
S21. R. Letaconnoux, *Bull.Inst. Océanogr.* **913** (1947).
S22. S. Jennings, J. D. Reynolds, S. C. Mills, *Proc. R. Soc. London Ser. B* **265**, 333 (1998).
S23. R. Castilho, M. T. Dinis, K. Erzini, *Fish. Res*. **16**, 339 (1993).
S24. J. R. Fuertes, *Invest. Pesq*. **42**, 241 (1978).
S25. G. Belloc, *Rev. Trav. Inst. Pêch. Marit.* **2**, 231 (1929).
S26. B. B. Rae, *The Lemon Sole* (Fishing News, London, 1965).
S27. G. Joenoes, *Ber. Deut. Wiss. Komm.***16**, 129 (1961).
S28. T. Mengi, *Ber. Deut. Wiss. Komm.* **7**, 119 (1963).
S29. V. I. Travin, *Dok. Akad. Nauk. SSSR* **77**, 741 (1951).
S30. J. Collignon, *Bull. Inst. Pêch. Maroc* **16**, 3 (1968).
S31. C. Papaconstantinou, *et al*., "Investigations on the abundance and distribution of demersal stocks of primary importance in the Thermatikos Gulf and the Thracian Sea (Hellas)" (Tech. Rep., North Aegean Sea Series 4., National Centre for Marine Research, Athens, 1994).
S32. U. Labarta, M.J. Ferreiro, "Age and growth of the Galician coast pouting (*Trisopterus luscus* L.). Preliminary data." (ICES C.M. G:65, ICES, Copenhagen, 1982).