ICES Journal of Marine Science (2011), 68(6), 1090–1104. doi:10.1093/icesjms/fsr031

Nine decades of North Sea sole and plaice distribution

Georg H. Engelhard [1]*, John K. Pinnegar [1], Laurence T. Kell [1,2], and Adriaan D. Rijnsdorp [3,4]

[1] Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft NR33 0HT, UK
[2] International Commission for the Conservation of Atlantic Tunas (ICCAT), C/Corazón de María, 8, 28002 Madrid, Spain
[3] Wageningen Institute for Marine Resources and Ecosystem Studies (IMARES), IJmuiden, The Netherlands
[4] Aquaculture and Fisheries Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands

*Corresponding Author: tel: +44 1502 527747; fax: +44 1502 513865; e-mail: georg.engelhard@cefas.co.uk.

Engelhard, G. H., Pinnegar, J. K., Kell, L. T., and Rijnsdorp, A. D. 2011. Nine decades of North Sea sole and plaice distribution. – ICES Journal of Marine Science, 68: 1090–1104.

Received 1 July 2010; accepted 13 February 2011; advance access publication 11 April 2011.

Recent studies based mainly on research survey data suggest that within the North Sea, sole *Solea solea* and plaice *Pleuronectes platessa* have exhibited distribution shifts in recent decades—on average southward for sole and northward to deeper waters for plaice. Various hypotheses may account for such shifts, including climate change effects and more intensive fishing in southern and shallower waters; but the relatively short time-span of datasets analysed so far (~3 decades) has complicated the separation of these two effects. We have made use of a unique dataset of catch and effort data for British North Sea trawlers; these cover nine decades (spanning the period 1913–2007) and are spatially detailed by ICES rectangle (0.5° latitude by 1° longitude). We quantify, for the first time, long-term distribution changes of North Sea sole and plaice over a period approaching a century, and demonstrate that the distribution shift in plaice was attributable to climate change rather than to fishing, but that both climate and fishing played a role in the distribution shift of sole. The discussion also highlights the potential impact of additional factors, including eutrophication, prey availability, and habitat modification.

Keywords: climate, depth, fishing, latitude, longitude, plaice, sole.

Introduction

Temperature is one of the primary factors, along with food availability and the provision of suitable spawning and nursery grounds, that determine fish distribution patterns, and most fish species tend to prefer a specific temperature range (Coutant, 1977; Rijnsdorp *et al.*, 2009). Consequently, shifts in long-term temperature resulting from climate change are expected to result in contractions, expansions, or shifts in fish distribution, especially near the periphery of a species' range (review: Pinnegar *et al.*, 2010). In the North Sea, a warming trend has happened over the past three decades, with a particularly steep temperature rise in 1988–1989, although there were also some relatively cold years; this has coincided with a northward shift in the distribution of many, but not all, fish species in the North Sea (Beare *et al.*, 2004; Hedger *et al.*, 2004; Perry *et al.*, 2005), sometimes by as much as 400 km. Dulvy *et al.* (2008) demonstrated, however, that there has been no net shift in the mean latitude of the fish assemblage as a whole (because some were moving north and some were moving south), but there has been a deepening and this has happened at a rate of around −3.6 m per decade (Dulvy *et al.*, 2008).

In the North Sea, plaice *Pleuronectes platessa* and sole *Solea solea* are principally caught in a mixed flatfish beam-trawl fishery. Landings of plaice by weight are approximately five times greater than those of sole; however, because sole are considerably more valuable, landings of the two species are roughly of equal value overall (Pilling *et al.*, 2008). Plaice and sole have been targeted by fishing fleets since the early nineteenth century and consequently good fishery statistics exist for these species, unlike for many others. Both species have displayed distinct distribution shifts since the 1980s. For plaice, a shift to more offshore waters has been reported (van Keeken *et al.*, 2007), at a "deepening" rate of −3.96 m per decade (Dulvy *et al.*, 2008). For sole, Perry *et al.* (2005) reported a generally southward distribution shift, i.e. opposite to the anticipated response to climate change in the northern hemisphere, assuming a latitudinal gradient of seawater temperatures, and the authors suggested that this might relate to improved environmental conditions in the southern North Sea, because of run-off from rivers (i.e. higher productivity in recent years). There has also been a concomitant shift to shallower waters, at a rate of +7.64 m per decade (Dulvy *et al.*, 2008). However, international fisheries landings data for the most recent years tentatively suggest a northward range expansion for sole (Rijnsdorp, 2010), so the relationship between distribution and climate in this warm-water species remains poorly understood and uncertain (Dulvy *et al.*, 2008).

Most studies on North Sea fish distribution have so far been based on fishery-independent survey data from government institutes and have been limited to the most recent three to four decades (Hedger *et al.*, 2004; Perry *et al.*, 2005; Hiddink and ter Hofstede, 2008), because of scarcity or absence of older, consistently collected survey data with reasonable spatial coverage. Over this period (1970–2010), however, sea temperatures in the North Sea generally have increased in the south and at the same time fishing pressure has been consistently higher in the southern part than farther north (Jennings *et al.*, 1999). This makes it particularly hard to disentangle the potential effects of climate change and fishing pressure on distribution shifts (and these hypotheses are not mutually exclusive), because a greater rate of fishery-induced depletion in the southern North Sea than the north would look like an apparent "northward" shift, as might be anticipated to have happened under climate change. This difficulty in interpretation has motivated the current study based on a unique dataset of British commercial catch per unit effort (cpue) records spanning a far longer time-span—the past nine decades—covering both warming and cooling periods and including periods of contrasting levels of fishing effort.

Here we quantify, for the first time, long-term distribution changes of North Sea sole and plaice over a period approaching a century. We interpret the findings in the light of climate change and long-term changes in fishing pressure. We test the hypotheses that:

1. Long-term shifts in sole and plaice distribution are better explained by climate variables than by indices of fishing pressure.
2. Longer time-series of fish distribution data offer greater insight into likely mechanisms/influences than shorter time-series derived from fishery-independent surveys.
3. Data from commercial fisheries can yield useful insight into the long-term implications of climate change.

Methods

For the period 1913–1980, data were obtained from "statistical charts" (catalogued in Engelhard, 2005) that were produced by the UK Ministry of Agriculture, Fisheries and Food [MAFF; now the UK Department for Environment, Food and Rural Affairs (Defra)]. These display fishing effort (hours fished) and fish landings by British otter trawlers (either steam- or motor-driven) for each ICES rectangle (0.5° latitude by 1° longitude) in the North Sea. These data record all fish that were landed by the otter trawl fleet into England and Wales (1913, 1968–1980) or into England, Scotland, and Wales (1920–1967). For the period 1968–2007, data on otter trawler landings into Scotland were obtained from the Fisheries Management Database of Marine Scotland (cf. Greenstreet *et al.*, 1999). For 1982–2007, data on otter trawl landings into England and Wales were obtained from the Fisheries Activity Database of Defra/Cefas.

Over the time-span examined, important improvements have happened in the flatfish catching power, or technical efficiency, of otter trawlers (Wimpenny, 1953; Robinson, 2000), although a recent long-term analysis suggested that plaice fishing power of motor otter trawlers around the Millennium was not markedly higher than that of steam otter trawlers of the 1920s (but an order of magnitude lower than in beam trawlers; Engelhard, 2008). Our aim was not to analyse temporal changes in absolute cpue values, but rather to look at trends in spatial distribution of catches. We therefore normalized the cpue values in any given year (divided by the annual mean), to overcome the confusing effect of an increase in fishing power. We assumed that relative cpue by the commercial fleet gives an appropriate indication of the spatial distribution of the species, but acknowledge that potential bias might arise from uneven spatial distribution of effort by more or less powerful vessels within the North Sea. By decade, cpue values were calculated by rectangle for a large area encompassing most of the North Sea (shaded in Figure 1).

As an approach to quantify long-term changes in population distribution, we calculated the "centres of gravity" of the latitudinal, longitudinal, and depth distributions of the two species (as in Heino *et al.*, 2003; see also Rindorf and Lewy, 2006). This analysis was based on an area within the North Sea that included only those rectangles with cpue data for the most years in the time-series (see the polygon line in Figure 1). Within this polygon, the latitudinal (or longitudinal) centre of gravity of distribution in a given year was calculated as the average of the latitudes (or longitudes) of all rectangle centres, weighted by the cpue value in each rectangle. Weighted standard deviations and standard errors of the weighted mean latitudes were calculated (Bevington, 1969). The centres of gravity of depth distributions were calculated analogously and, given that both flatfish species are bottom-dwellers, based on the mean sea depth in any given rectangle.

We examined sole and plaice distribution in relation to (i) climate variables and (ii) fishing pressure. As a broad-scale climate indicator, the North Atlantic Oscillation (NAO) winter index (December of the previous year to March of the focal year) for 1913–2007 was taken from Jones *et al.* (1997), with

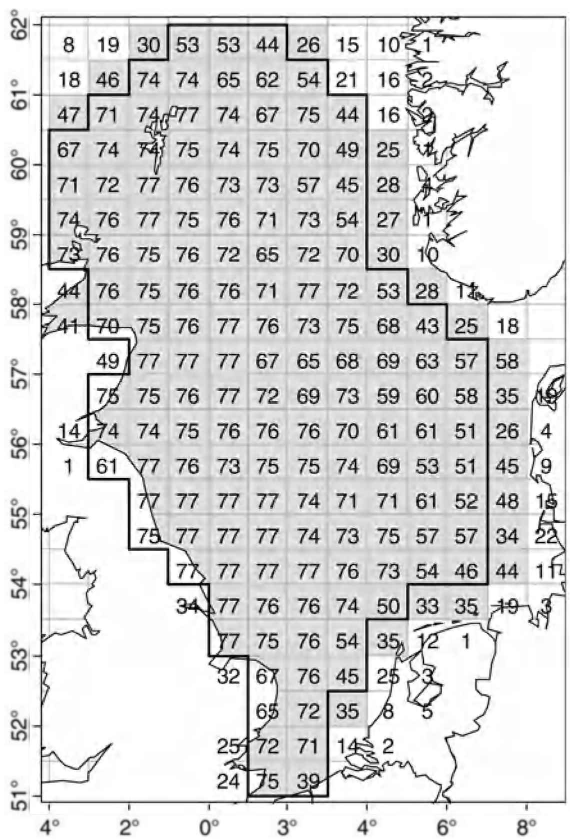

Figure 1. Map of the North Sea displaying, for each rectangle, the number of years in the 77-year time-series where British otter trawler cpue data were available (based on the rule that at least 10 h of fishing effort had occurred in the rectangle in the given year). The grey-shaded area encompasses those rectangles where we calculated cpue by year or decade for spatial distribution maps. The thick-lined polygon encompasses those rectangles included in analyses on centres of gravity of cpue distributions.

updated values provided online by the Climatic Research Unit, University of East Anglia, Norwich, UK (www.cru.uea.ac.uk/~timo/projpages/nao_update.htm; Figure 2a). The NAO is associated with speed and direction of westerly winds across the North Atlantic and is particularly important in winter when it exerts a strong influence on European weather patterns and on Atlantic water inflow into the North Sea; a positive NAO is generally linked with strong wind circulation and higher atmospheric and sea temperatures in western Europe (Hurrell, 1995; Jones *et al.*, 1997; Ottersen *et al.*, 2001). We also considered the Atlantic Multidecadal Oscillation (AMO), a climate mode that manifests itself as a 20–30-year cycle in de-trended sea surface temperature series for the North Atlantic. These data (back to 1871) were obtained from NOAA (Global Change Master Directory). A number of long-term coastal temperature time-series were examined from sites around the North Sea, including those from Marsdiep (Dutch coast; obtained from Mackenzie and Schiedek, 2007), Helgoland Roads (German coast; obtained from Wiltshire and Manly, 2004), and Dover (UK coast; obtained from www.cefas.co.uk/data.aspx). As a more generic indicator of sea temperature variations within the North Sea, the Hadley interpolated sea surface temperature (HadISST) time-series was used (Figure 2b). Annual mean of sea surface temperatures, interpolated to 1° latitude by 1° longitude, was used as described by Rayner *et al.* (2003), with updated values provided online by the UK Meteorological Office. For seabed temperature (SBT), no comprehensive time-series covering the entire span of this study was available, but for a shorter period (1980 on), winter SBT data were calculated as average SBT in 80 ICES rectangles sampled during the annual winter International Bottom Trawl Surveys (IBTS) of ICES (obtained from Dulvy *et al.*, 2008).

To describe the effects of fishing pressure, estimates of fishing mortality (F) on 4–8-year-old plaice for the years 1929–1937 and 1947–1992 were taken from Rijnsdorp and Millner's (1996) long-term study on North Sea plaice stock dynamics. Estimates of F for 4–8-year-old sole for the years 1957–1993 were taken

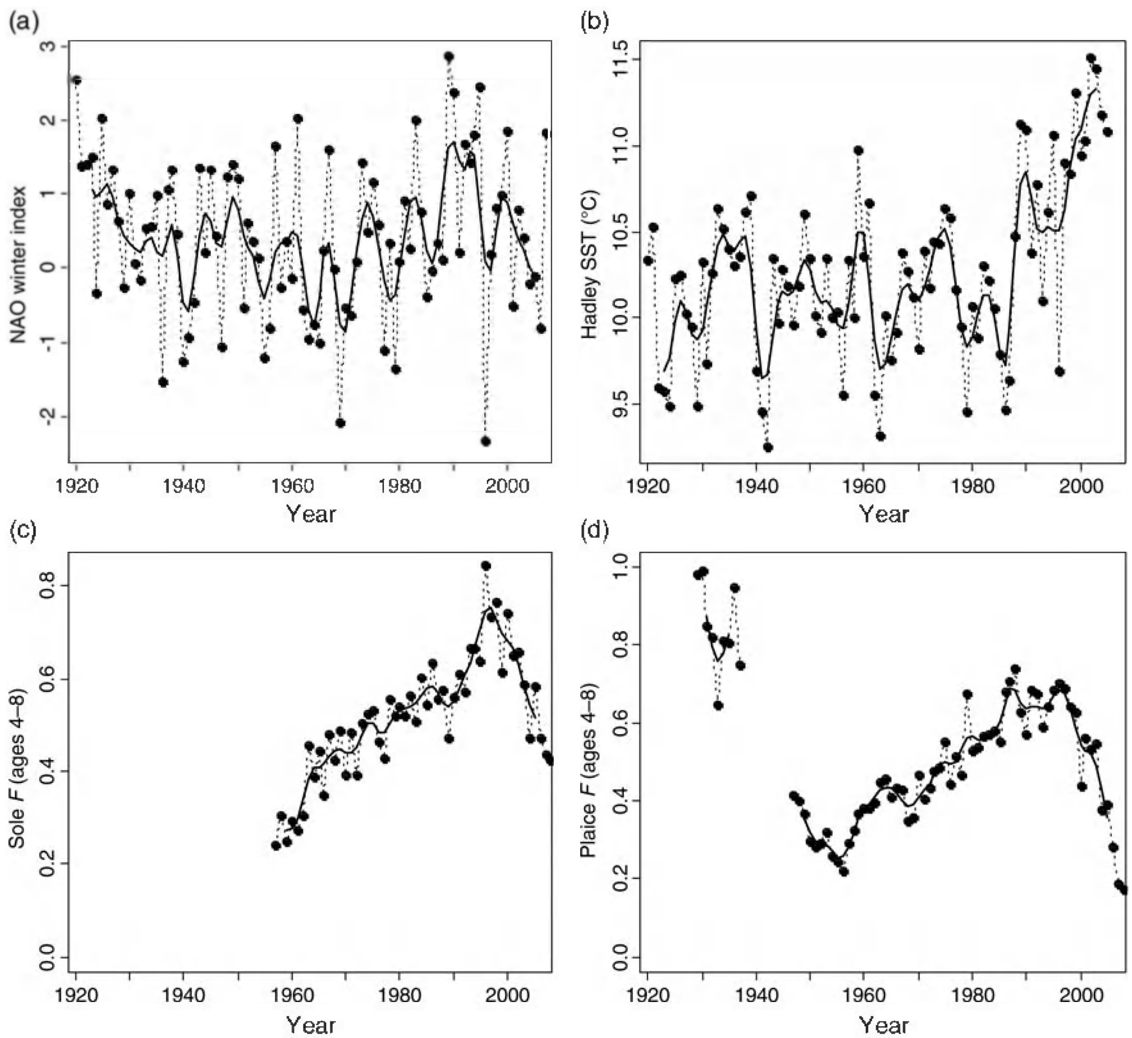

Figure 2. Time-series of environmental variables and fishing pressure examined here for possible relationships with North Sea sole and plaice distributions. (a) NAO winter index; (b) Hadley interpolated annual average sea surface temperature for the North Sea; (c) North Sea sole fishing mortality, averaged over ages 4–8 years (from Millner and Whiting, 1996); and (d) North Sea plaice fishing mortality, averaged over ages 4–8 years (from Rijnsdorp and Millner, 1996). Long-term variability is illustrated by heavy solid lines, representing values smoothed with a low-pass filter with five weights (1, 3, 4, 3, and 1) to remove fluctuations with periods <3 years (following Hurrell, 1995).

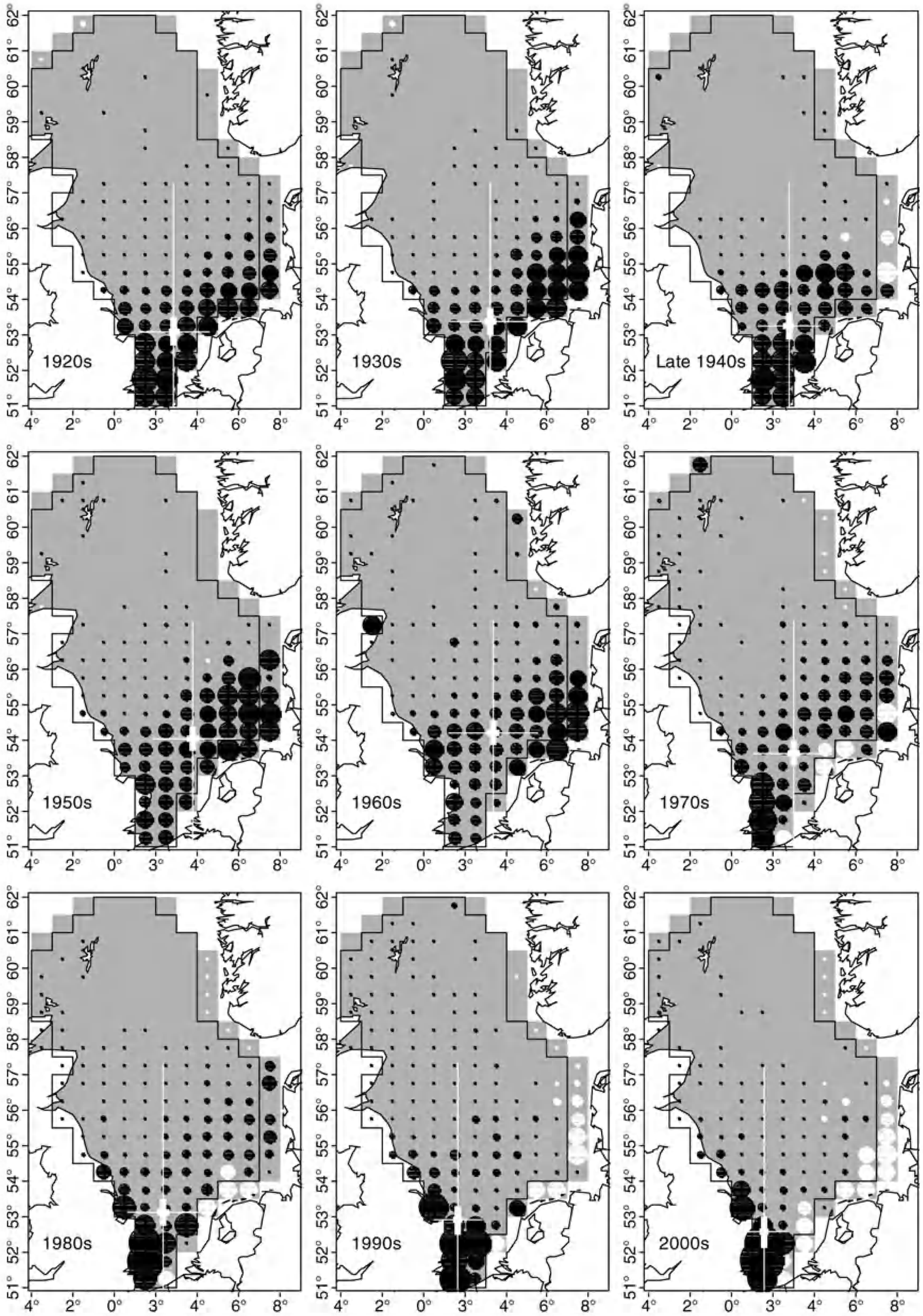

Figure 3. Long-term changes in relative sole cpue within the North Sea. For each decade, spatial distribution of sole cpue by British trawlers within the grey-shaded area is indicated by the area sizes of the black circles (proportional to cpue). In rectangles where no cpue data were available in a given decade (no effort), white circles represent the long-term average cpue. For each decade, the white cross indicates the centre of gravity of sole distribution, with its standard error (shorter, thick white lines) and standard deviation (longer, thin white lines) in the longitudinal and latitudinal directions.

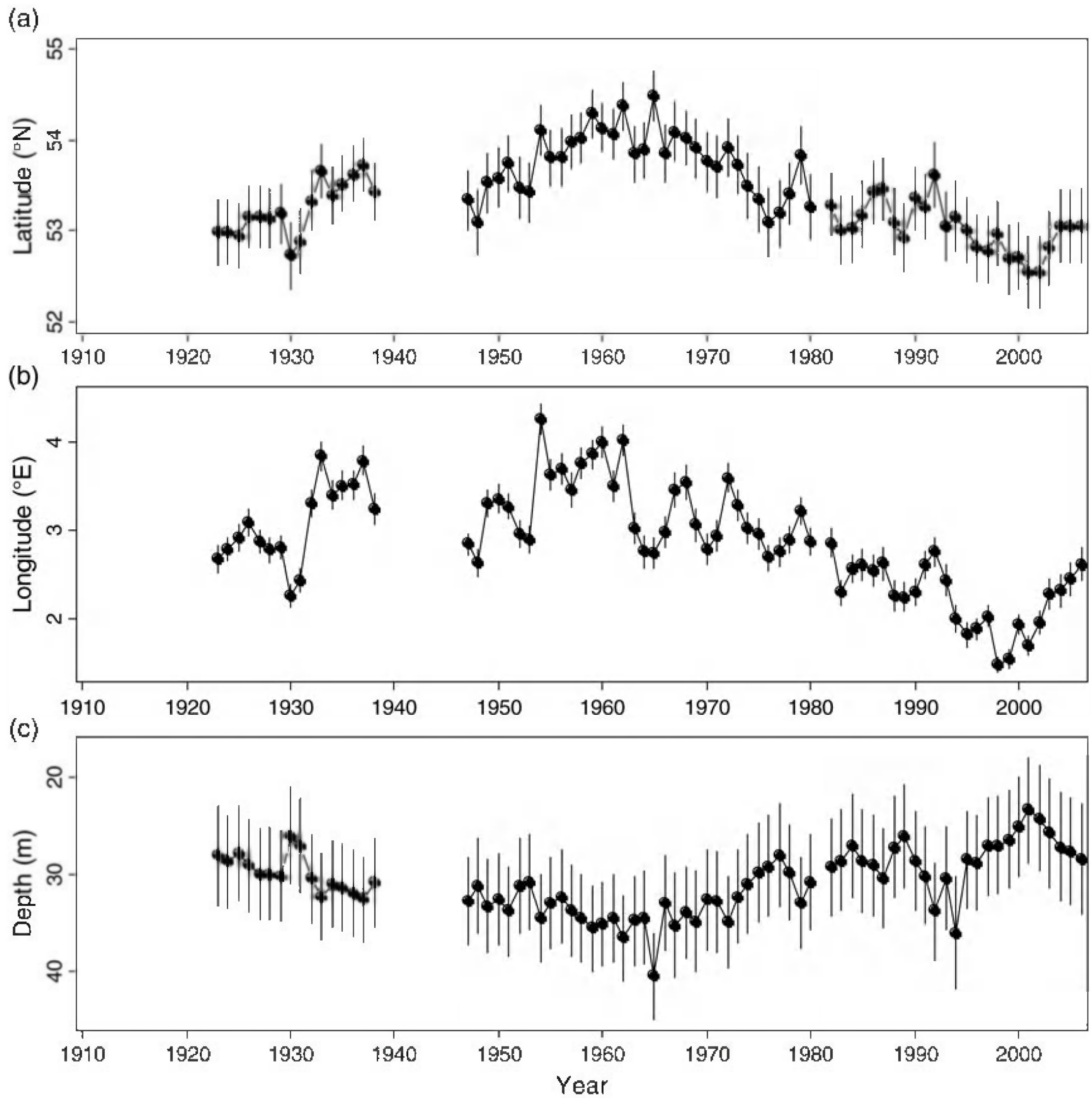

Figure 4. Long-term changes in (a) latitudinal and (b) longitudinal centre of gravity of North Sea sole distribution (calculated as the mean latitude and longitude weighted with sole cpue; bars indicate s.e. of weighted means); and (c) long-term changes in mean depth distribution of North Sea sole (with s.e.).

from Millner and Whiting (1996). Both F time-series were extended with recent data from ICES Working Group reports (ICES, 2009). These fishing mortality time-series are illustrated in Figure 2c and d.

We used correlations as a first approach to explore which environmental and/or fishing pressure variables might be associated with descriptors of sole and plaice distribution (latitudinal, longitudinal, and depth). Pearson's cross-moment correlations (r_p) were used, because none of the variables displayed distributions significantly different from normality (one-sample Kolmogorov–Smirnov tests, $p > 0.05$). There was, however, a moderate or weak autocorrelation between several time-series variables. To account for this, the test procedure for significance of correlations was adjusted following Pyper and Peterman [1998, Equation (1)], by reducing the "effective" degrees of freedom (and therefore p-values) according to the degree of autocorrelation (adjusted p-values are referred to here as p_{adj}).

Multiple linear regressions were then used as an approach to examine the relative importance of environmental and fishing pressure variables as determinants of sole and plaice distribution. As explanatory variables, these models included fishing pressure (sole F or plaice F), the NAO winter index, AMO, and Hadley SST (other sea temperature time-series were closely correlated with Hadley SST, and were not included to avoid the problem of multicollinearity). Initially, we started with a model with all considered explanatory variables, but no interactions. For example, for sole latitudinal distribution, the starting model was

$$\text{Sole latitude} \sim \text{Sole}\,F + \text{NAO} + \text{AMO} + \text{Hadley SST}. \quad (1)$$

However, only parameters that significantly contributed to the fit ($p < 0.05$) were retained in the model formulations. Finally, we checked whether any second-order interactions between climate and fishing pressure would significantly improve the fit ($p < 0.05$). For the final model, we give the standardized β coefficients,

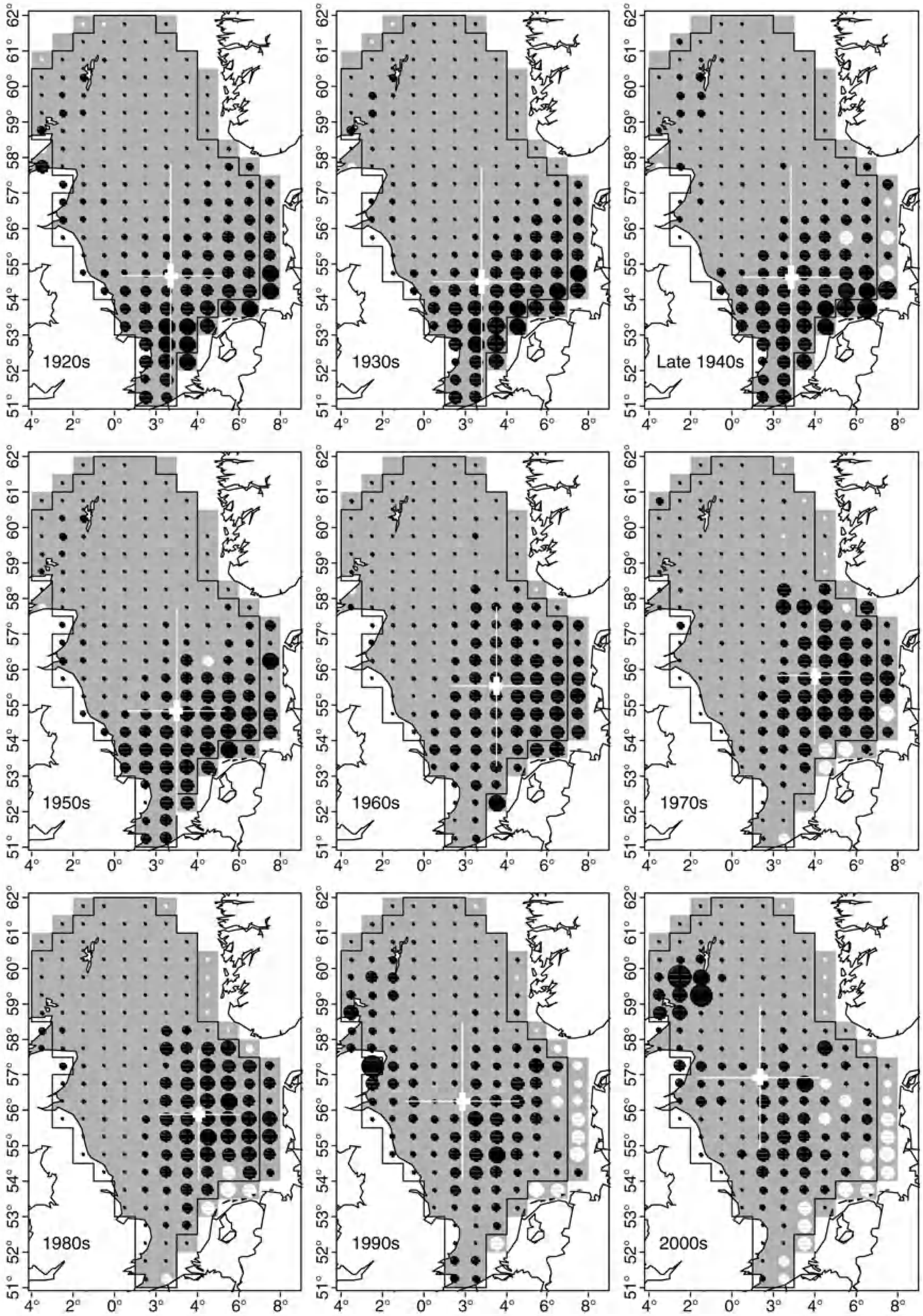

Figure 5. Long-term changes in relative plaice cpue within the North Sea. For each decade, spatial distribution of plaice cpue by British trawlers within the grey-shaded area is indicated by the area sizes of the black circles (proportional to cpue). In rectangles where no cpue data were available in a given decade (no effort), white circles represent the long-term average cpue. For each decade, the white cross indicates the centre of gravity of plaice distribution, with its standard error (shorter, thick white lines) and standard deviation (longer, thin white lines) in the longitudinal and latitudinal directions.

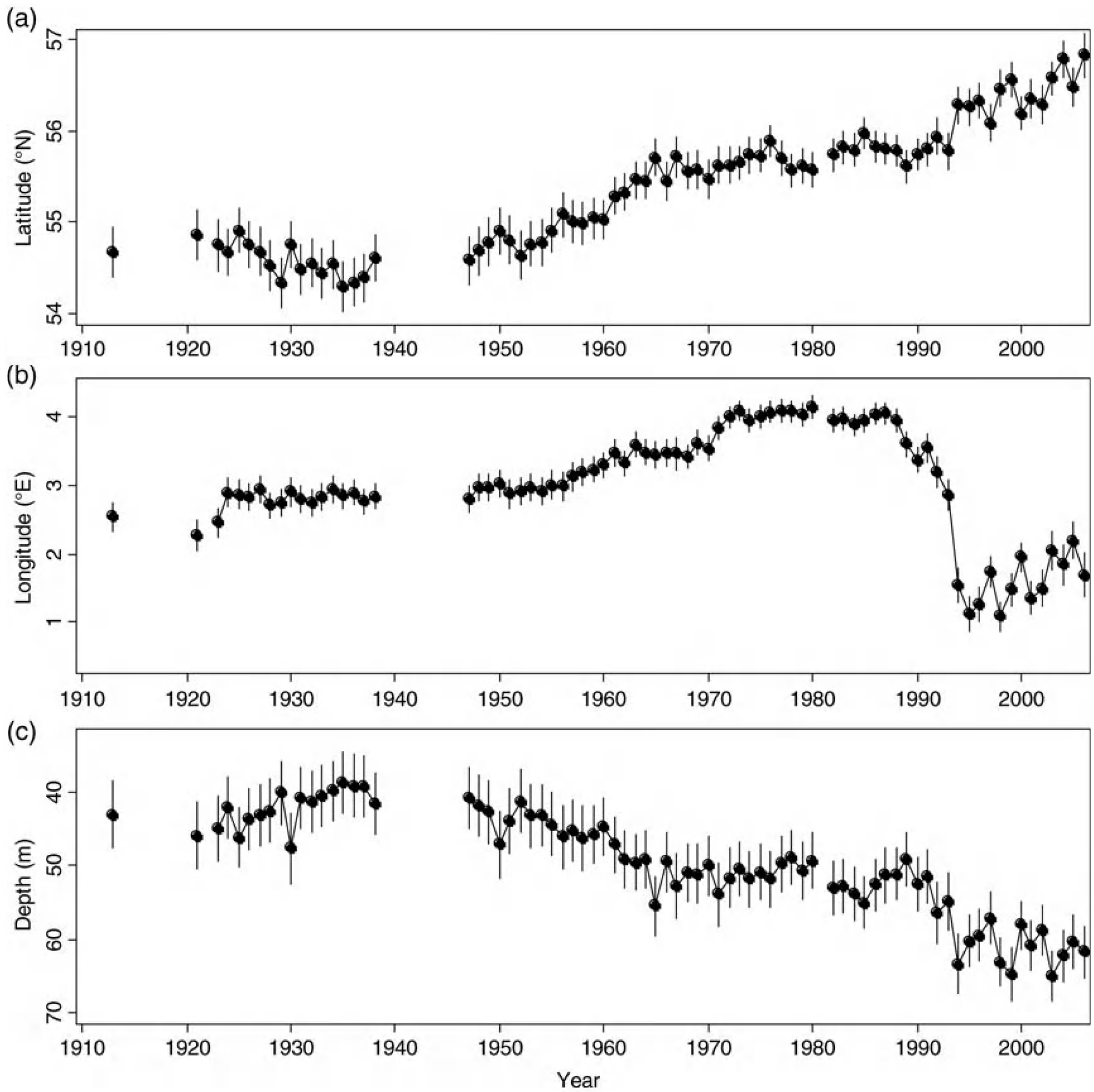

Figure 6. Long-term changes in (a) latitudinal and (b) longitudinal centre of gravity of North Sea plaice distribution (calculated as the mean latitude and longitude weighted with plaice cpue; bars indicate s.e. of weighted means); and (c) long-term changes in mean depth distribution of North Sea plaice (with s.e.).

obtained after standardization (subtracting the mean and dividing by the standard deviation) of the explanatory variables. The standardized β coefficients are indicative of the relative strength of the relationships between environment and fishing pressure with each fish distribution metric; it should be noted, however, that they cannot be directly interpreted as substantiating causative effects.

Results

Shifts in fish distributions

Over the past nine decades, both sole and plaice displayed long-term, multidecadal changes in spatial distribution. Magnitudes of each shift regarding "centres of gravity" of latitude and longitude were $\sim 1^\circ - 2^\circ$ for both species (corresponding to 142 km for plaice and 93 km for sole); those of depth distributions were $\sim$20 m for plaice, <10 m for sole. The direction and timing of shifts were, however, very different for the two species.

Sole distribution shifts

Sole have always been distributed in the shallow southern and southeastern North Sea, with only very small numbers in the northern North Sea, where they are absent from most rectangles.

Figure 3 shows the distribution of sole cpue over the North Sea by decade, from the 1920s to the 2000s. In the 1920s and 1930s, high sole cpue values were distributed evenly between the Southern Bight and German Bight, but the relative importance of the German Bight increased during the 1950s and 1960s. Since the 1970s, the importance of the German Bight has decreased, and from the 1980s on, sole cpue has been considerably higher in the Southern Bight, especially close to the Thames Estuary and southeastern England. Unfortunately, we lack British otter trawler cpue data for the southeasternmost part of the German Bight for much of the 1990–2000s.

North Sea sole have exhibited marked multidecadal fluctuations in their latitudinal centre of gravity (Figure 4a), which shifted from $\sim 53^\circ$N in the 1920s, northwards to $\sim 54^\circ$N in the

1960s, then southwards again to ~53°N in the 1990s (and to a southernmost latitude of 52.5°N in 2002). There have been less smooth and more irregular shifts in longitudinal centre of gravity (Figure 4b), notably a westward shift from ca. 1960 to 2000 (reflecting increased relative importance of the Thames Estuary region). There has been a more limited shift in depth distribution (Figure 4c), but this broadly parallels the latitudinal pattern.

Plaice distribution shifts

Plaice are generally more abundant in the southern and central parts of the North Sea than in the north. Their distribution differs from sole in being on average much more northern and encompassing most of the northern North Sea, where, although at lower cpue values, they are typically caught by otter trawlers in most rectangles, except for those that comprise the deepest waters in the northwest and the Norwegian Trench (Figure 5).

Plaice have over the past nine decades also exhibited major distribution shifts, but quite different from those observed for sole (Figure 5). During the 1920–1940s (and in 1913), the highest plaice cpue values were observed in the Southern Bight and the German Bight, in rectangles closest to the coast of southeastern England, the Netherlands and Germany, and with cpue values rapidly decreasing northwards and northwestwards. During the 1960–1980s, the east–central North Sea became far more important, including an offshore area stretching from the Dogger Bank north to the Great and Little Fisher Bank, but with relatively low cpue along most of the English and Scottish coasts. During the 1990–2000s, plaice cpue dropped markedly in the previously important east–central North Sea, especially in many rectangles close to Denmark and Germany, but remained high in the central North Sea. In the (late) 1990–2000s, there was a sudden, marked increase in relative plaice cpue off Scotland, Orkney, and Shetland.

From the start of our time-series in 1913 to World War II, the centre of gravity of North Sea plaice distribution remained constant regarding latitude, longitude, and depth. Since then, however, the centre of gravity has almost continuously shifted northwards by more than 2° latitude from the late 1940s to the 2000s (Figure 6a). Accordingly, plaice have moved offshore to greater depths by ~20 m since 1947 (Figure 6c), tracking the latitudinal shift and reflecting the north–south depth gradient in the North Sea. From the 1950s to the 1980s, there was an eastward longitudinal shift (Figure 6b) related to the temporary much greater importance of the east–central North Sea in this period. The centre of gravity "jumped" westwards by 3° longitude from 1988 to 1995 (and by >1° in 1993–1994 alone), the latter reflected an apparent population collapse in the east–central North Sea, but also the recently increased abundance off Scotland.

Correlations between environmental and fisheries variables

Before proceeding to examine correlations between climate variables and/or fishing pressure vs. sole and plaice distribution, it is necessary to determine whether such variables are themselves correlated. An analysis revealed that all sea surface and bottom temperature datasets (Hadley, Marsdiep, Helgoland, and Dover SST; IBTS winter SBT) were highly correlated (all $r_p > 0.75$, all $p_{adj} < 10^{-5}$, adjusted for autocorrelation). Similarly, the NAO winter index exhibited a strong positive correlation with Hadley SST ($r_p = 0.462$, $p_{adj} < 10^{-7}$), but by contrast, the AMO index was only weakly correlated with Hadley SST ($r_p = 0.227$, $p_{adj} = 0.04$), despite itself being derived from the combined Hadley SST and NOAA OI SST datasets.

Sole and plaice fishing mortality were strongly correlated with each other ($r_p = 0.678$, $p_{adj} < 0.0002$), but neither was significantly correlated with any of the climate variables (all $r_p < 0.24$, all $p_{adj} > 0.1$).

Because all sea surface temperature datasets were highly correlated, further analysis on relationships between climate and sole or plaice distributions was only carried out using the Hadley SST dataset (along with NAO and AMO), because this was judged to provide a representative index of regional hydroclimate.

Distribution shifts in relation to climate and fishing

All three measures of North Sea sole and plaice distribution—mean latitude, longitude, and depth—were strongly correlated with the Hadley annual index of sea surface temperature in the North Sea (Table 1). The direction of correlations was such that for sole, warmer temperatures were associated with more southern, western, and shallower distribution patterns (Figure 7, left panels). Conversely, for plaice, higher temperatures were associated with a more northwestern and a deeper distribution

Table 1. Correlations (r_p) between sole and plaice distribution in the North Sea (latitude, longitude, and depth) and variables related to climate and fishing pressure.

	Latitudinal shift		Longitudinal shift		Depth shift	
Variable	r_p	p_{adj}	r_p	p_{adj}	r_p	p_{adj}
Sole						
NAO winter index	**−0.246**	**0.035**	−0.174	0.138	−0.225	0.054
AMO index	−0.052	0.666	0.017	0.887	−0.107	0.374
Hadley SST	**−0.355**	**<0.005**	**−0.348**	**<0.005**	**−0.393**	**<0.005**
Sole *F* (ages 4–8)	**−0.781**	**<0.0001**	**−0.826**	**<0.0001**	**−0.631**	**<0.001**
Plaice						
NAO winter index	−0.015	0.900	−0.085	0.467	−0.022	0.850
AMO index	−0.085	0.478	**−0.530**	**<0.0002**	−0.054	0.652
Hadley SST	**0.431**	**<0.001**	**−0.443**	**<0.0005**	**0.455**	**<0.0005**
Plaice *F* (ages 4–8)	−0.098	0.449	−0.115	0.375	−0.046	0.718

There was weak or moderate autocorrelation within these variables. To account for this, the test procedure for significance of correlations was adjusted according to autocorrelation following Pyper and Peterman [1998; Equation (1)]. Correlations different from zero at adjusted $p < 0.005$ are shown emboldened.

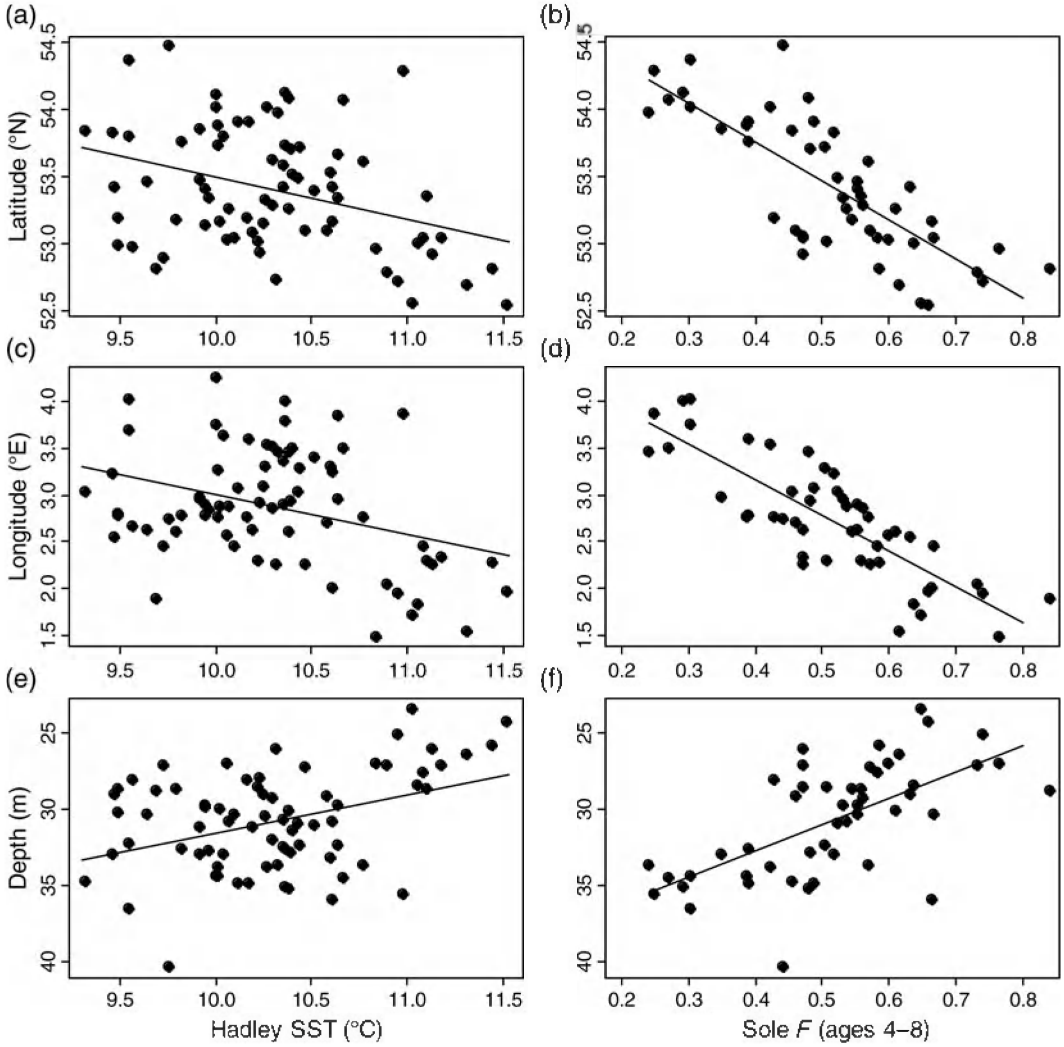

Figure 7. Relationships of Hadley SST (left) and sole fishing pressure (right) with metrics of North Sea sole distribution: (a and b) latitudinal centre of gravity; (c and d) longitudinal centre of gravity; and (e and f) mean depth distribution. Regression lines indicate significant relationships.

pattern (Figure 8, left panels). Each of the correlations with Hadley SST was significant beyond the $p_{adj} < 0.005$ level.

The NAO winter index was significantly correlated only with the latitudinal distribution of sole and not very strongly ($p_{adj} = 0.035$); the correlation with the depth distribution of sole approached significance ($p_{adj} = 0.054$), such that a more negative phase of the NAO would be associated with more southern and perhaps deeper distribution of sole (Table 1). The NAO winter index was not correlated with sole longitudinal distribution and with none of the measures of plaice distribution. However, plaice longitudinal distribution was strongly correlated with the AMO index ($p_{adj} < 0.0002$), such that a more positive phase of AMO was associated with a more western distribution of this species.

Fishing mortality on sole (averaged over ages 4–8 years) was correlated highly significantly with the latitudinal, longitudinal, as well as depth distribution (Table 2 and Figure 7, right panels). Higher fishing mortality on sole was associated with an on average more southern, western, and shallower distribution of the species. In contrast, fishing mortality on North Sea plaice (Figure 7, right panels) was not correlated significantly with either the latitudinal, longitudinal, or depth distribution of the species.

Multiple regression analyses were conducted to explore the relative strength of relationships of climate and fishing pressure variables with distributional responses of sole and plaice (Table 2). Regression models confirmed that Hadley SST was a highly significant predictor of the latitudinal, longitudinal, and depth responses of both fish species (all $p < 0.0005$); also that fishing mortality was a significant predictor for sole ($p < 10^{-5}$), but not plaice distribution. The NAO winter index, however, was rejected as a predictor for sole or plaice distribution ($p > 0.05$) by any regression model that also included Hadley SST, the latter displaying far greater explanatory power. In contrast, the AMO was retained as a significant predictor of plaice longitudinal distribution ($p < 10^{-5}$), also with the inclusion of Hadley SST (a high AMO being associated with a westward displacement). The AMO was also a significant predictor of plaice latitudinal and depth distribution, but only in models that included Hadley SST as covariate.

There was no evidence that interactions between climate and fishing mortality provided additional explanatory power. For

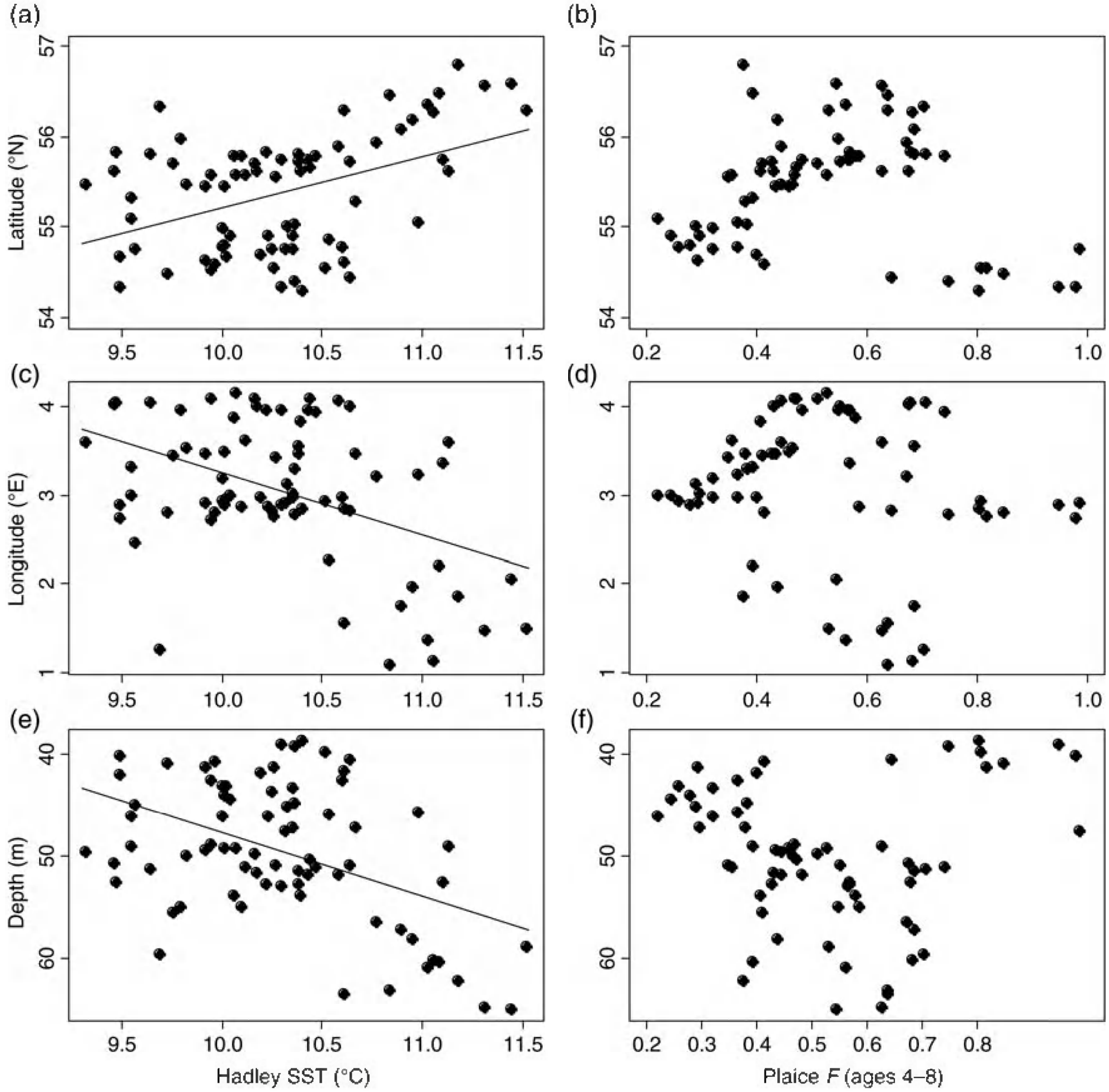

Figure 8. Relationships of Hadley SST (left) and plaice fishing pressure (right) with metrics of North Sea plaice distribution: (a and b) latitudinal centre of gravity; (c and d) longitudinal centre of gravity; and (e and f) mean depth distribution. Regression lines are included only where correlations are significant ($p < 0.05$, adjusted for autocorrelation).

sole, the interaction Hadley SST × sole F did not explain latitudinal, longitudinal, or depth responses significantly (all $p > 0.2$). For plaice, the interactions Hadley SST × plaice F (all $p > 0.6$) and AMO × plaice F (all $p > 0.4$) did not explain any of the responses in distribution metrics.

A comparison of the standardized β coefficients in final models (Table 2) lent support to the notion that between fishing mortality and Hadley SST, the former was the stronger predictor of sole latitudinal, longitudinal, and depth distribution responses, although both variables were highly significant predictors. For plaice, where the effect of fishing mortality on distribution was insignificant, the Hadley SST and AMO contributed approximately equally to the distribution responses.

Discussion

Over the past nine decades, both sole and plaice exhibited long-term, multidecadal changes in spatial distribution within the North Sea. Magnitudes of each shift regarding "centres of gravity" of latitude and longitude were ~1°–2° for both species; those of depth distributions were ~20 m for plaice, <10 m for sole. The direction and timing of shifts were, however, very different in the two species: since the 1950s mainly northeastwards and to deeper waters in North Sea plaice, but mainly southwestwards and to shallower waters in North Sea sole (by 142 and 93 km, respectively). Both species displayed correlations with the Hadley SST, but in opposite directions; for sole, but not plaice, a close correlation with fishing mortality was also observed.

Unlike in recent studies based on IBTS (Perry *et al.*, 2005; Dulvy *et al.*, 2008), we used data derived from commercial catch records, so it is necessary to consider whether or not these provide a representative and non-biased picture of fish distribution in the past or simply a reflection of favoured fishing localities. Improvements in fishing power of UK otter trawlers have clearly happened (Engelhard, 2008), but this problem was

Table 2. Regression models on distribution responses of North Sea sole and plaice (latitudinal, longitudinal, and depth) to variables related to climate and fishing pressure.

Response variable	Predictor	$\beta_{standardized}$	s.e.	t	p-value
Sole latitudinal shift	Hadley SST	−0.161	0.036	−4.426	0.00006
	Sole F (ages 4–8)	−0.350	0.039	−9.045	<0.00001
Sole longitudinal shift	Hadley SST	−0.148	0.045	−3.330	0.002
	Sole F (ages 4–8)	−0.473	0.047	−9.974	<0.00001
Sole depth shift	Hadley SST	−1.348	0.353	−3.821	0.0004
	Sole F (ages 4–8)	−1.993	0.376	−5.303	<0.00001
Plaice latitudinal shift	AMO index	−0.209	0.074	−2.828	0.006
	Hadley SST	0.322	0.071	4.529	0.00003
Plaice longitudinal shift	AMO index	−0.423	0.082	−5.181	<0.00001
	Hadley SST	−0.298	0.079	−3.786	0.0003
Plaice depth shift	AMO index	−1.778	0.788	−2.256	0.028
	Hadley SST	3.502	0.759	4.614	0.00002

Final models are presented following a backward selection procedure, from a full model that included the NAO winter index, AMO, Hadley SST, and fishing mortality as main effects. Only the terms that significantly explained the distribution metric ($p < 0.05$) were retained. None of the interactions between environmental variables and fishing pressure was significant ($p > 0.05$). Standardized β coefficients are displayed here, obtained after standardization of the explanatory variables and indicative of the relative strength of these in explaining the response variable.

overcome, because no attempt was made to estimate the absolute biomass in any particular area. Instead, relative spatial distributions of cpue were used. Spatial distributions of cpue could be influenced by the level of targeting of a species by the fleet (Gillis *et al.*, 2008; Quirijns *et al.*, 2008). However, although North Sea plaice and particularly sole are targeted extensively by beam trawlers, they are merely important bycatch species for the UK otter trawl fleet used here to provide cpue indices; this fleet primarily catches roundfish (e.g. cod and haddock) in a mixed fishery (Bannister, 2004).

Further evidence of representativeness of our cpue maps for "true" sole and plaice abundance distributions is provided by great similarity with spatial distributions based on IBTS available for recent decades (Perry *et al.*, 2005; Dulvy *et al.*, 2008). This being said, the patterns in recent decades may be affected by the competition between otter trawlers and beam trawlers (Rijnsdorp *et al.*, 2008), because an analysis of the Dutch demersal fleet since the 1950s has revealed that the otter trawl fleet has been outcompeted and largely displaced to deeper waters by the highly efficient beam trawl fleet that operates in this region. Although this would be expected to affect the total effort expended by the otter trawl fleet in an area, we would not generally anticipate an impact on catch rates (i.e. cpue). However, commercial fishers may interact on local grounds and "interference competition" between vessels has been observed. In such cases, this is known to affect the relationship between cpue and fish stock biomass (Gillis and Peterman, 1998; Poos and Rijnsdorp, 2007).

It has also been important to establish that climate variables and fishing pressure are not significantly correlated, i.e. that the two factors are not confounded, because this has been one of the major concerns voiced about earlier studies (Perry *et al.*, 2005; Dulvy *et al.*, 2008). It was not surprising that the various North Sea temperature time-series were highly correlated, because this was also observed by Mackenzie and Schiedek (2007). However, it is important and useful to note that in the long term, there were no significant correlations between fishing mortality (in either species) and any climate variable. This offers the hope that a longer-term analysis of fish distributions could start to pin down the primary influences that are confounded in the shorter term and also the possibility of any effects of the interaction between climate and fishing pressure on distribution responses. Although no support for an interactive effect was found in this study, the importance of not only examining climate and fishing effects separately, but also their potential interaction, has been emphasized recently (Perry *et al.*, 2010). Although clear relationships were found between SST and flatfish distributions, the effects of SBT could not be fully explored, because of the lack of data for most of the earlier decades; where time-series overlapped, SST and SBT were closely correlated. Note that although sole and plaice are benthic as adults/late juveniles, their eggs and early juveniles are found in the pelagic zone, close to the sea surface. It is currently unclear whether the dominant climate-related impact on fish distribution patterns happens through processes that occur during the early life-history stages (as suggested by Rindorf and Lewy, 2006), or through temperature tolerances/preferences during the adult phase, and consequently whether SST or SBT is the most appropriate environmental variable to consider.

Plaice seem to have responded largely to climate changes with a shift to the north, the west, and to deeper waters, fully in line with expectations assuming a north–south SST gradient in the northern hemisphere (Perry *et al.*, 2005; Dulvy *et al.*, 2008; Rijnsdorp *et al.*, 2009). The lack of a relationship with fishing mortality suggests that climate is the dominating driver on plaice distribution, and not fishing. In the North Sea, juvenile plaice are typically concentrated in shallow inshore waters and move gradually offshore as they become larger. Surveys in the Wadden Sea have demonstrated that 1-group plaice are now almost absent from the area where they were once very abundant. The "plaice box" (an area of the Dutch and German coast closed to most plaice fishing under the EU Common Fisheries Policy since 1989: Pastoors *et al.*, 2000) is now considered much less effective as a management measure than 10 or 15 years ago, and this has been attributed to the distribution shift resulting from long-term climate change (van Keeken *et al.*, 2007). Marine protected area boundaries, such as those associated with the "plaice box", may have to be "adaptive" in future and move with the fish they are trying to protect. It is interesting to note that the apparent bimodal distribution pattern of plaice distribution in recent years (1990s and 2000s in Figure 5), such that high cpue values were recorded in the central North Sea, but also off northeast Scotland. This sudden occurrence of large numbers of plaice off

Scotland could result from an invasion from the west (this might be an explanation for the sudden "jump" in longitude; Figure 6), as well as a gradual shift in the centre of gravity from the southeast. ICES stock assessments and fishery-independent surveys provide little evidence of a shift in plaice populations from the west to the east side of Scotland, because plaice populations have only ever been relatively small off the Scottish Highlands and islands.

From our analyses, sole seem to have responded to climate change and fishing, and the relationship with fishing seems particularly strong. This is in line with extensive targeting of this highly priced species by the large North Sea beam trawl fleet, often in preference to plaice (Pilling *et al.*, 2008). Contrary to simple expectations regarding the manifestation of climate change, sole have exhibited a southwestward shift to shallower waters with warming, in line with Perry *et al.* (2005). In the North Sea, the north tends to be colder than the south in summer, but the south tends to be colder than the north in winter. Some southern North Sea species, such as sole, have been previously excluded from large areas of shallow inshore habitat along the continental coast in winter, because these waters cool down to well below 3°C, a critical temperature below which sole suffer impaired physiological function and increased mortality (Woodhead, 1964a, b). Consequently, in the past, sole tended to overwinter in deeper waters before returning to the shallows in spring, to avoid the lethally cold winter temperatures (Henderson and Seaby, 2005). However, there is evidence that sole have started spawning in coastal waters earlier, because of the rapidly warming seas in winter since the 1980s (Teal *et al.*, 2008). During severe winter conditions, such as those experienced in the 1960s and in 1996, sole were excluded from the shallows to the extent that mass mortality events were reported (Woodhead, 1964a; Horwood and Millner, 1998). A similar mass mortality event for sole was reported in early 1929 (Lumby and Atkinson, 1929), notably on the Terschelling ground off the Dutch coast. This coincided with seawater temperatures that were 5°C colder than were considered "normal" for that time of year. Better accessibility to shallow, inshore waters in winter might also explain why several other small, warm-tolerant southern species have recently displayed southward, "shallowing" distribution shifts (Dulvy *et al.*, 2008). This is equally a manifestation of changing climate conditions in the North Sea as the more widely known (and reported) "northward" shift of marine organisms in recent years.

There are many examples in the literature where fish distribution and/or abundance has been related to the NAO (Ottersen *et al.*, 2001; Attrill and Power, 2002; Henderson, 2007). Here, a correlation of the NAO with sole latitudinal (and perhaps depth) distribution was found, but no significant relationships in a regression model that also included the Hadley SST. It is perhaps not surprising that stronger correlations were identified with sea temperatures within the North Sea, because temperature is the physical variable experienced directly by the fish and known to affect their growth and behaviour. The NAO would have a much more indirect influence (see also Engelhard and Heino, 2006). In addition, this study provided evidence indicating the importance of the AMO, an index that is becoming increasingly popular in studies of fish and climate in the North Atlantic (Nye *et al.*, 2009). The AMO was significantly related to plaice (but not sole) distribution, especially if the effect of sea temperature was accounted for in regression models; this suggested that apart from immediate temperature effects, long-term fluctuations in thermohaline circulation and hence shifts in temperature regime affected plaice distribution (Nye *et al.*, 2009). Elsewhere in the North Sea, Attrill and Power (2002) demonstrated that patterns in the NAO coincided with variation in the structure of the fish assemblage, explaining 54% of variation, and that the growth of many juvenile fish, including sole, were also influenced by the NAO. A study of the changing fish community in the Bristol Channel (Henderson, 2007) identified two periods of discrete change in the fish community over the past 25 years. The first change happened in the late 1980s and involved an abrupt shift in the relative abundance of the "permanent" members of the community, coinciding with observed changes in the plankton of the northeast, and was correlated with the winter NAO. A second discrete change, affecting the total species assemblage, happened in the early 1990s. This was marked by a sudden alteration in the set of "occasionally occurring" species. This change was correlated with average seawater temperature (and possibly the AMO) rather than NAO.

Apart from climate and fishing, other factors may also have had an important influence on plaice and sole distributions throughout the twentieth century. These may have included habitat modification, changes in prey resources and/or overall system productivity, and changes in precipitation and run-off patterns. Perhaps fish populations have been affected by successive loss of important southern plaice (and sole) nursery grounds. The Dutch and Belgian coasts were previously very good nursery grounds for plaice (Wimpenny, 1953), but several anthropogenic changes have strongly altered this. In particular, the closure of the Zuiderzee in the early 1930s and the closure of estuaries of the Rhine, Meuse, and Scheldt in the 1960s and 1970s (Heip, 1989) will have likely reduced the recruitment from these nursery grounds and hence may have affected the abundance and distribution of older age groups in the North Sea (Rijnsdorp *et al.*, 1992; Rochette *et al.*, 2010).

In the coastal waters of the western Mediterranean and the Bay of Biscay, which are affected by the run-off of the Rhone and the Loire, respectively, sole recruitment and growth has been positively affected by the river run-off subsidising the benthic foodweb with addition of nutrients and terrestrial organic matter (Salen-Picard *et al.*, 2002; Le Pape *et al.*, 2003). Plaice expansion northwards in the North Sea during the 1950–1980s might have happened because of nutrient enrichment and eutrophication of the coastal zone, because the plaice growth rate is known to correlate strongly with various eutrophication parameters (e.g. phosphorus inputs), and there is evidence of increased benthic productivity in large areas of the North Sea during this period. Sole and plaice in the German Bight have been particularly heavily influenced by river run-off and nutrient inputs that increased in the 1960s and 1970s, but which have subsequently declined (Colijn *et al.*, 2002; Philippart *et al.*, 2007).

The decrease in relative abundance in the German Bight in recent decades may be due to the increase in small-bodied, small-mouthed flatfish, such as solenette *Buglossidium luteum* and scaldfish *Arnoglossus laterna*, which may compete with plaice and sole in this region (Jennings *et al.*, 2008; van Hal *et al.*, 2010), in conjunction with changes in the productivity of the benthic ecosystem. An analysis of plaice and sole diets in 1996 compared with the beginning of the twentieth century has revealed that polychaetes have increased and bivalves decreased (Rijnsdorp and Vingerhoed, 2001). These results might reflect a change in system productivity, but equally they are consistent with the hypothesis that beam trawling has improved the feeding conditions for the two flatfish species, by enhancing the abundance of small opportunistic benthic species, such as polychaetes, in the heavily trawled areas. However, the changes in diet may also be related to eutrophication and pollution. A recent comparison of plaice diet in the central North Sea (JKP, unpublished data) during the early 1900s (1902–1909), 1950s (1950–1959), and early twenty-first century (2004–2009) has revealed similar changes in diet, with a switch away from bivalves such as *Spisula* and *Ensis* towards polychaetes, crabs, and sandeels. This suggests that it is not eutrophication or pollution that has affected diets (and therefore growth and possibly distribution) in the central North sea, and that the cause is more likely to be increased trawling pressure, allied with long-term climate change.

Conclusions

The analyses carried out here support hypothesis 1 that long-term shifts at least in plaice distribution are better explained by climate variables than by fishing pressure. However, the situation for sole is more complicated; sole have responded to climate change and fishing, and their temperature response is opposite to that of plaice.

The results also provide support for hypothesis 2, about the usefulness of long time-series for disentangling climate and fishing effects. In the short term, climate and fishing variables are confounded, but over a longer period, these factors are clearly separable, and we have been able to attribute the shift in plaice distribution to climate rather than to fishing (although other factors may have played an important role).

We have also confirmed hypothesis 3, by demonstrating that data from commercial fisheries can yield useful insight into the long-term implications of climate change, especially when the data are "normalized" and not used to provide absolute biomass or abundance estimates. Commercial catch data have the benefit of being collected over far greater temporal and spatial scales than fishery-independent survey data. They are usually collected systematically and consistently over long periods, and the data tend to be less noisy than survey data because of the much greater sampling effort. However, proper acknowledgement of potential biases (e.g. misreporting, interaction between fishing fleets, technological improvements, etc.) is a prerequisite in such analyses.

Acknowledgements

GHE, JKP, and ADR were supported through the EU FP6 project RECLAIM; GHE, JKP, and LTK were also supported through the UK's Department for Food, Environment and Rural Affairs (contracts MF1201, MA010, and MF1108), and LTK was also supported by the EU UNCOVER project (contract 022717). JKP thanks the conveners of the International Symposium on Climate Change Effects on Fish and Fisheries for inviting him to present this material and CLISAP (an excellence cluster at the University of Hamburg) in supporting his attendance at the symposium. William Cheung, Nick Dulvy, Christopher Lynam, David Maxwell, and one anonymous referee gave valuable feedback and advice on the statistical analysis.

References

Attrill, M. J., and Power, M. 2002. Climatic influence on a marine fish assemblage. Nature, 417: 275–278.

Bannister, R. C. A. 2004. The rise and fall of cod in the North Sea. *In* Management of Shared Fish Stocks, pp. 316–338. Ed. by A. I. L. Payne, C. M. O'Brien, and S. I. Rogers. Blackwell Publishing, Oxford, UK.

Beare, D. J., Burns, F., Greig, A., Jones, E. G., Peach, K., Kienzle, M., McKenzie, E., *et al.* 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Marine Ecology Progress Series, 284: 269–278.

Bevington, P. R. 1969. Data Reduction and Error Analysis for the Physical Sciences, 2nd edn. McGraw-Hill, New York.

Colijn, F., Hesse, K. J., Ladwig, N., and Tillmann, U. 2002. Effects of the large-scale uncontrolled fertilisation process along the continental coastal North Sea. Hydrobiologia, 484: 133–148.

Coutant, C. C. 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada, 34: 739–745.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology, 45: 1029–1039.

Engelhard, G. H. 2005. Catalogue of Defra historical catch and effort charts: six decades of detailed spatial statistics for British fisheries. Science Series Technical Report, 128. Cefas, Lowestoft. 42 pp.

Engelhard, G. H. 2008. One hundred and twenty years of change in fishing power of English North Sea trawlers. *In* Advances in Fisheries Science: 50 Years on from Beverton and Holt, pp. 1–25. Ed. by A. Payne, J. Cotter, and T. Potter. Blackwell Publishing, Oxford, UK.

Engelhard, G. H., and Heino, M. 2006. Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. Oecologia, 149: 593–603.

Gillis, D. M., and Peterman, R. M. 1998. Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. Canadian Journal of Fisheries and Aquatic Sciences, 55: 37–46.

Gillis, D. M., Rijnsdorp, A. D., and Poos, J. J. 2008. Behavioral inferences from the statistical distribution of commercial catch: patterns of targeting in the landings of the Dutch beam trawler fleet. Canadian Journal of Fisheries and Aquatic Sciences, 65: 27–37.

Greenstreet, S. P. R., Spence, F. B., Shanks, A. M., and McMillan, J. A. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. II. Trends in fishing effort in the North Sea by UK registered vessels landing in Scotland. Fisheries Research, 40: 107–124.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Bridson, J. 2004. Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using generalised additive models. Fisheries Research, 70: 17–25.

Heino, M., Engelhard, G. H., and Godø, O. R. 2003. Variations in the distribution of blue whiting in the Barents Sea: climatic influences or year class effects ? ICES Document CM 2003/Q: 03. 11 pp.

Heip, C. 1989. The ecology of the estuaries of Rhine, Meuse and Scheldt in the Netherlands. Scientia Marina, 53: 457–463.

Henderson, P. A. 2007. Discrete and continuous change in the fish community of the Bristol Channel in response to climate change. Journal of the Marine Biological Association of the United Kingdom, 87: 589–598.

Henderson, P. A., and Seaby, R. M. 2005. The role of climate in determining the temporal variation in abundance and growth of sole *Solea solea* in the Bristol Channel. Journal of the Marine Biological Association of the United Kingdom, 85: 197–204.

Hiddink, J. G., and ter Hofstede, R. 2008. Climate induced increases in species richness of marine fishes. Global Change Biology, 14: 453–460.

Horwood, J. W., and Millner, R. S. 1998. Cold induced abnormal catches of sole. Journal of the Marine Biological Association of the United Kingdom, 78: 345–347.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science, 269: 676–679.

ICES. 2009. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak—Combined Spring and Autumn (WGNSSK). ICES Document CM 2009/ ACOM: 10. 1028 pp.

Jennings, S., Alvsvåg, J., Cotter, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., *et al.* 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. Fisheries Research, 40: 125–134.

Jennings, S., van Hal, R., Hiddink, J. G., and Maxwell, T. A. D. 2008. Fishing effects on energy use by North Sea fishes. Journal of Sea Research, 60: 74–88.

Jones, P. D., Jonsson, T., and Wheeler, D. 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and South-West Iceland. International Journal of Climatology, 17: 1433–1450.

Le Pape, O., Chauvet, F., Désaunay, Y., and Guérault, D. 2003. Relationship between interannual variations of the river plume and the extent of nursery grounds for the common sole (*Solea solea*, L.) in Vilaine Bay. Effects on recruitment variability. Journal of Sea Research, 50: 177–185.

Lumby, J. R., and Atkinson, G. T. 1929. On the unusual mortality amongst fish during March and April 1929, in the North Sea. Journal du Conseil Permanent International pour l'Exploration de la Mer, 4: 309–332.

MacKenzie, B. R., and Schiedek, D. 2007. Long-term sea surface temperature baselines-time series, spatial covariation and implications for biological processes. Journal of Marine Systems, 68: 405–420.

Millner, R. S., and Whiting, C. L. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine Science, 53: 1185–1195.

Nye, J. A., Link, J. S., Hare, J. A., and Overholtz, W. J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series, 393: 111–129.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. Ch. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128: 1–14.

Pastoors, M. A., Rijnsdorp, A. D., and van Beek, F. A. 2000. Effects of a partially closed area in the North Sea ("plaice box") on stock development of plaice. ICES Journal of Marine Science, 57: 1014–1022.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Perry, R. I., Curry, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. Journal of Marine Systems, 79: 427–435.

Philippart, C. J. M., Beukema, J. J., Cadee, G. C., Dekker, R., Goedhart, P. W., van Iperen, J. M., Leopold, M. F., *et al.* 2007. Impacts of nutrient reduction on coastal communities. Ecosystems, 10: 95–118.

Pilling, G. M., Kell, L. T., Hutton, T., Bromley, P. J., Tidd, A. N., and Bolle, L. J. 2008. Can economic and biological management objectives be achieved by the use of MSY-based reference points? A North Sea plaice (*Pleuronectes platessa*) and sole (*Solea solea*) case study. ICES Journal of Marine Science, 65: 1069–1080.

Pinnegar, J. K., Engelhard, G. H., and Daskalov, G. M. 2010. Changes in the distribution of fish. *In* Resolving Climatic Impacts on Fish Stocks, pp. 94–110. Ed. by A. D. Rijnsdorp, M. A. Peck, G. H. Engelhard, C. Möllmann, and J. K. Pinnegar. ICES Cooperative Research Report, 301.

Poos, J. J., and Rijnsdorp, A. D. 2007. An "experiment" on effort allocation of fishing vessels: the role of interference competition and area specialization. Canadian Journal of Fisheries and Aquatic Sciences, 64: 304–313.

Pyper, B. J., and Peterman, R. M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Canadian Journal of Fisheries and Aquatic Sciences, 55: 2127–2140.

Quirijns, F. J., Poos, J. J., and Rijnsdorp, A. D. 2008. Standardizing commercial CPUE data in monitoring stock dynamics: accounting for targeting behaviour in mixed fisheries. Fisheries Research, 89: 1–8.

Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., Kent, E. C., *et al.* 2003. Global analysis of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research, 108: ACL2.1–ACL22.9.

Rijnsdorp, A. D. 2010. Sole. *In* Resolving Climatic Impacts on Fish Stocks, pp. 193–198. Ed. by A. D. Rijnsdorp, M. A. Peck, G. H. Engelhard, C. Möllmann, and J. K. Pinnegar. ICES Cooperative Research Report, 301.

Rijnsdorp, A. D., and Millner, R. S. 1996. Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. ICES Journal of Marine Science, 53: 1170–1184.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66: 1570–1583.

Rijnsdorp, A. D., Poos, J. J., Quirijns, F. J., HilleRisLambers, R., de Wilde, J. W., and den Heijer, W. M. 2008. The arms race between fishers. Journal of Sea Research, 60: 126–138.

Rijnsdorp, A. D., van Beek, F. A., Flatman, S., Miller, J. M., Riley, J. D., Giret, M., and de Clerk, R. 1992. Recruitment of sole, *Solea solea* (L.), in the Northeast Atlantic. Netherlands Journal of Sea Research, 29: 173–192.

Rijnsdorp, A. D., and Vingerhoed, B. 2001. Feeding of plaice *Pleuronectes platessa* L., and sole *Solea solea* (L.) in relation to the effects of bottom trawling. Journal of Sea Research, 45: 219–229.

Rindorf, A., and Lewy, P. 2006. Warm, windy winters drive cod north and homing of spawners keeps them there. Journal of Applied Ecology, 43: 445–453.

Robinson, R. 2000. Steam power and distant-water trawling. *In* England's Sea Fisheries: the Commercial Sea Fisheries of England and Wales since 1300, pp. 206–216. Ed. by D. J. Starkey, C. Reid, and N. Ashcroft. Chatham Publishing, London.

Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. 2010. Effect of nursery habitat degradation on flatfish population: application to *Solea solea* in the eastern Channel (western Europe). Journal of Sea Research, 64: 34–44.

Salen-Picard, C., Darnaude, A. M., Arlhac, D., and Harmelin-Vivien, M. L. 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. Oecologia, 133: 380–388.

Teal, L. R., de Leeuw, J. J., van der Veer, H. W., and Rijnsdorp, A. D. 2008. Effects of climate change on growth of 0-group sole and plaice. Marine Ecology Progress Series, 358: 219–230.

van Hal, R., Smits, K., and Rijnsdorp, A. D. 2010. How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. Journal of Sea Research, 64: 76–84.

van Keeken, O. A., van Hoppe, M., Grift, R. E., and Rijnsdorp, A. D. 2007. Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. Journal of Sea Research, 57: 187–197.

Wiltshire, K. H., and Manly, B. F. J. 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. Helgoland Marine Research, 58: 269–273.

Wimpenny, R. S. 1953. The Plaice (being the Buckland Lectures for 1949). Edward Arnold & Co., London. 145 pp.

Woodhead, P. J. M. 1964a. The death of North Sea fish during the winter of 1962/63 particularly with reference to the sole, *Solea vulgaris*. Helgoländer Wissenschaftliche Meeresuntersuchungen, 10: 283–300.

Woodhead, P. J. M. 1964b. Changes in the behaviour of sole, *Solea vulgaris*, during cold winters and the relation between the winter catch and sea temperature. Helgoländer Wissenschaftliche Meeresuntersuchungen, 10: 328–342.