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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

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Abstract

Patterns of mature cod and haddock abundance in the North Sea were estimated from International Council for the Exploration of the Seas (ICES) International Bottom Trawl Survey (IBTS) data acquired from 1980 to 1999 in the first quarter of each year. Relationships between abundances and environmental properties (water depth, bottom temperature and bottom salinity) were analysed through the use of generalised additive models (GAMs). Cod were tolerant of a wide range of environments found throughout the North Sea, but predominantly occurred in, either, shallower (depths less than 50 m), colder and less saline waters of the southern North Sea, or, deeper (depths greater than 100 m), warmer and more saline waters of the northern North Sea. In contrast, the bulk of the haddock population was confined to the northern North Sea. Greatest haddock abundances were found between 75 and 125 m, and abundances were positively related to temperature and salinity. While there was no decadal shift in haddock spatial distribution, the 1990s were associated with a displacement of cod towards deeper waters in the northern North Sea.

Keywords: Cod and haddock; Temperature; Salinity; Water column depth; Generalised additive modelling

1. Introduction

With recent decades bringing an increase in sea temperatures in the North Sea (Beaugrand, 2003), it has become increasingly important to understand the relationship between spatial distributions of stocks and the environment. Cod, for example, in the North Sea exist near to the southern temperature boundary of their habitat range (O'Brien et al., 2000), and thus it would be expected that significant increases in temperature would have an impact on this stock. In other cod populations, such as the northern cod stock off Newfoundland, shifts

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in spatial distribution have been observed which are thought to be related to environmental changes (Rose et al., 2000).

Currently, within the North Sea, populations of cod and haddock are spatially heterogeneous at a range of scales (Daan et al., 1990). Cod occur at selected locations throughout most of the North Sea continental shelf. Haddock occupy a less extensive area of the North Sea, mainly occurring in northern and central regions. The greatest abundances reported are to the east of Scotland, to the north of the Outer Hebrides, around the Orkneys, and to the west of the Norwegian Trench (Daan et al., 1990; Knijn et al., 1993).

Spatial distributions of cod and haddock are predominantly controlled by environmental properties such as temperature and salinity (Albert, 1994; O'Brien et al., 2000), although fishing and interaction with other fish species may modify these distributions. Cod occur in areas where water depths are less than 600 m, but are typically found where the depth is less than 200 m (Wheeler, 1969). They occur over a wide range of temperatures, from nearly freezing to approximately 20 °C, but have a preferred temperature range of 3–7 °C (Wise, 1961; Tremble and Sinclair, 1985; Brander, 1996) and have been seen to avoid temperatures less that 2 °C (D'Amours, 1993). They are tolerant of a wide range of salinities from near-freshwater to oceanic (approximately 35 ppt), with optimal salinities being between 30 and 35.5 ppt (Smith and Page, 1996). Haddock, by contrast, occur mainly in areas where the water depth is less than 300 m (Knijn et al., 1993), although they have been found at depths of up to 600 m (Albert, 1994). Smith et al. (1994) and Perry and Smith (1994) identified average temperatures and salinities at which haddock occurred on the eastern Scotian Shelf in March surveys as 5.0 °C and 32.9 ppt, respectively.

Statistical modelling is widely used to determine the relationships between fish abundance and causative factors (Rogers, 1992; Thompson and Hilden, 1987; Fromentin et al., 1998). However, two characteristics of fisheries data restrict the type of analysis possible. First, fisheries data typically have non-normal distributions and second, relationships between fisheries data and environmental properties are typically non-linear (Brander, 1994). Generalised linear models (GLMs) may be used to account for non-normality and non-linear relationships (McCullagh and Nelder, 1989). However, because these use parametric terms, they may be relatively inflexible if the relationships are complex. An alternative is to use generalised additive models (GAMs) (Hastie and Tibshirani, 1990). In a GAM, the response variable Y has a mean $\mu = E(Y|X_1, \ldots, X_P)$ which is linked to the predictors via:

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j(x_j) \quad (1)$$

where α is the intercept term, $g(\mu)$ the link function defining the relationship between the response and the additive predictor, and the f_js are arbitrary smooth functions. Use of GAMs within a fisheries context may be found in Swartzman et al. (1992), Daskalov (1999), Fox et al. (2000) and Maravelis et al. (2000).

In this paper, we estimated the spatial distribution of mature cod and haddock abundance in the North Sea in the first-quarter of each of the years from 1980 to 1999. We then examined relationships between these spatial distributions and environmental properties using GAMs. Spatial distributions were also derived for each species separately for the 1980s and 1990s and tested statically, following Syrjala (1996), to determine if there was any evidence of a change in spatial distribution. Syrjala's test is a randomization test based on the Cramer von Mises statistic extended to bivariate distributions. Previous studies have considered spatial distributions and environmental properties in the North Sea only over smaller areas or shorter time periods. This paper, therefore, takes a more synoptic approach.

2. Data

Data were collected in the North Sea between 50 and 62°N and between 5°W and 9°E (Fig. 1) from the International Council for the Exploration of the Seas (ICES) International Bottom Trawl Surveys (IBTS) between 1980 and 1999.

Two types of fisheries data were involved. Catch per unit effort (CPUE) data showed indices of abundances of cod and haddock at given lengths. Secondly, a sub-sample of these data had fish staged according to sex, maturity, age and length keys (SMALK). Data were geo-referenced to different resolutions: CPUE data were always geo-referenced to latitude and longitude, but SMALK data were geo-referenced to latitude and longitude, ICES statistical rectangle or roundfish

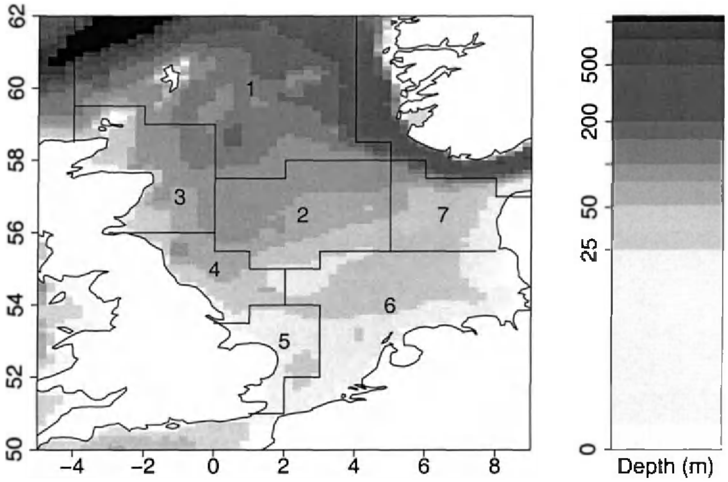

Fig. 1. The North Sea. Solid lines delineate roundfish areas (1–7); dashed lines delineate ICES statistical rectangles.

area depending upon which ships had acquired them. In addition to CPUE and SMALK data, age-specific estimates of the number of cod or haddock within the whole of the North Sea, created by virtual population analysis (VPA), were used. Data on bottom temperature and salinity in the first quarter of each year were obtained by ICES. Typically, these consisted of several measurements per ICES statistical rectangle, obtained concurrently with the fishing effort.

3. Methods

Spatial distributions of mature cod and haddock abundance were estimated by spatially resolving the VPA age-specific stock estimates to the resolution of the ICES statistical rectangle (1° longitude and 0.5° latitude) (Fig. 1). This is of a similar resolution to many previous studies which have used GAMs to analyse relationships between abundances of marine fish and environmental properties. For example, Swartzman et al. (1992) used a spatial resolution of approximately 0.6° longitude and 0.25° latitude, and Maravelis (1999) used a spatial resolution of 0.25°. The spatial distribution was estimated by using CPUE length data which were converted to numbers at age by using information from SMALK data on age at length. These were then used to spatially distribute the VPA estimates for age classes in the North Sea. SMALK data were then used to estimate the proportion of mature fish in each ICES statistical rectangle to give an estimate of absolute numbers of mature fish in each location (Fig. 2).

Relationships between standardised abundances of cod and haddock and environmental properties (water column depth, bottom temperature and bottom salinity) were estimated using GAMs. Abundances were standardised by division by their respective means to enable more effective comparison between GAMs. A Gaussian error model was assumed and the link function used was the identity function. GAMs were fitted between the standardized abundances and environmental properties using the lowess smoothing function with a span of 0.5 (Hastie and Tibshirani, 1990). This was done first with the entire data set, and then with the two decades separately.

Spatial distributions of abundance of cod and haddock were then compared between the two decades included in the data set. A randomization test was performed, Syrjala (1996), to determine if a statistically significant change in spatial distribution had occurred between the decades for each species.

4. Results

Greatest abundances of mature cod were found in two regions: in shallow coastal waters, predominantly in the southern North Sea (German Bight, Southern Bight) but also off the northeast coast of England; and secondly in deeper, more northerly waters along the

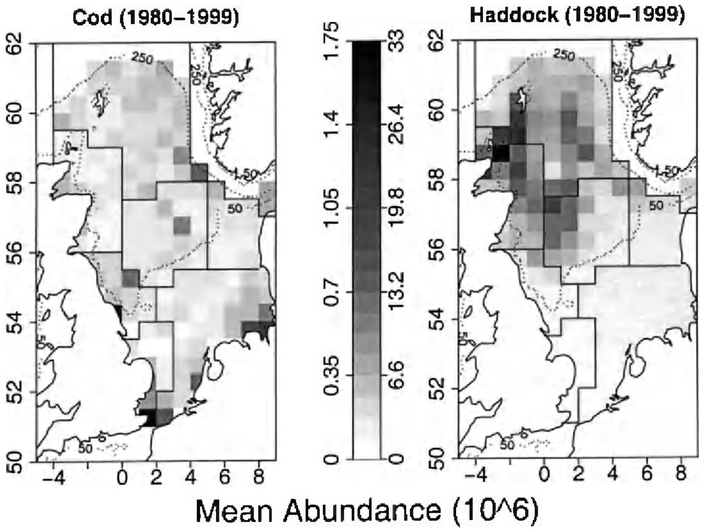

Fig. 2. Spatial distributions of mature cod and haddock abundance.

Norwegian Trench, particularly in the 1990s (Fig. 4). In contrast, the bulk of the mature haddock population was restricted to more northerly latitudes.

Greatest abundances of cod occurred where the water column depth was less than 50 m or greater than 150 m, whereas haddock favoured areas where the water column depth was between 75 and 125 m (Fig. 3). Cod were found over the entire temperature and salinity range of the North Sea. In contrast, abundances of haddock increased with increasing temperature and salinity (Fig. 3).

Of the three environmental properties considered, strongest GAM relationships existed between mature cod and mature haddock abundances and depth, although, in both cases, a high proportion of variation was not explained by the GAMs. Residual deviances as a proportion of null deviances were approximately 0.92 for cod and 0.59 for haddock: that is, the bulk of the variation in abundance, particularly for cod, was not explained through the use of a GAM (although P-values showed the models to be appropriate). Weaker GAM relationships existed between mature cod and haddock abundances and temperature and salinity. Residual deviances as a proportion of null deviances were approximately 0.97 for cod and 0.79 for haddock. Strongest fits occurred when fitting temperature and salinity additively with depth to cod and haddock abundance (Tables 1 and 2).

An inter-decadal temporal shift in spatial distribution existed for cod involving a displacement to the northern North Sea in the 1990s (Fig. 4). Using the test for change in spatial distributions in Syrjala (1996) this change was found to be statistically significant at the 5% level (P-value 0.02). An inter-decadal trend in relationships with environments existed for both mature cod and mature haddock (Fig. 5). The bulk of the cod

Table 1
Comparison of models for cod using anova

Response: resp. terms	Residual d.f.	Residual deviation	Test	d.f.	Deviance	F-values	P-value
1. D	2836.80	1482.88					
2. $D+T$	2832.42	1451.27	$+T$	4.39	31.61	14.23	<0.01
3. $D+T+S$	2827.47	1432.19	$+S$	4.94	19.08	7.63	<0.01

D: depth; T: temperature; and S: salinity.

Table 2
Comparison of models for haddock using anova

Response: resp. terms	Residual d.f.	Residual deviance	Test	d.f.	Deviance	F-value	P-value
1. D	2836.80	2107.82					
2. $D+T$	2832.42	2048.25	$+T$	4.39	59.57	18.82	<0.01
3. $D+T+S$	2827.47	2039.97	$+S$	4.94	8.28	2.32	<0.05

D: depth; T: temperature; and S: salinity.

population was in shallow areas in the 1980s; but appears to have shifted to deeper areas in the 1990s in accordance with the spatial shift in distribution. Peak haddock abundance was found at approximately 6.5 °C in the 1980s; this had shifted to approximately 8 °C in the 1990s. In contrast to cod, the most favoured water depth for haddock did not change throughout the study period and there was no evidence of a spatial shift in distribution. The relationships with salinity appear unchanged for both species.

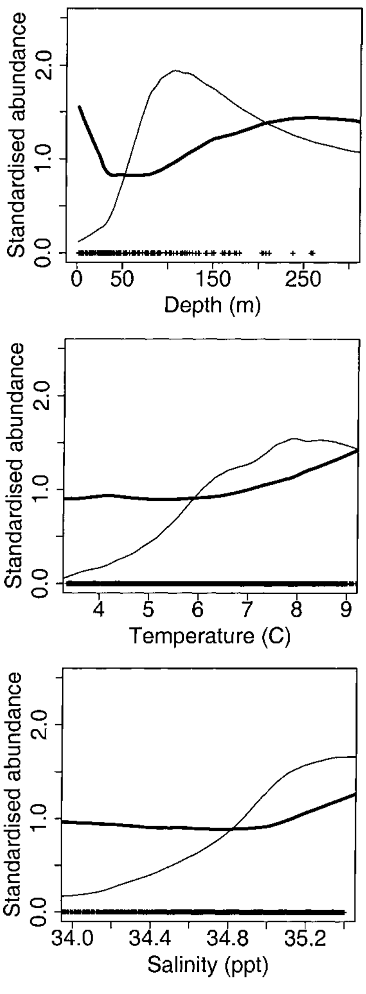

Fig. 3. GAM relationship between standardised cod abundance and haddock abundance and hydrographic properties (1980–1999). The thick line is for cod; the thin line is for haddock, data points are shown at the bottom of the graph.

5. Discussion

Although GAMS identified synoptic differences in spatial distributions, the strengths of the estimated relationships were weak. Partly, this was due to the nature of the sampling. With one or two hauls per ICES statistical rectangle acquired over a 3-month period, spatio-temporal variation in distributions of cod and haddock shoals at scales less than that of the statistical rectangle will have reduced the strength of relationships. Additionally, the limited range of the data used in this study, with all values lying within tolerance limits for cod, probably contributed towards the weakness of relationships. However, estimates of the spatial distributions of mature cod and haddock abundances were concordant with previous measurements (Daan et al., 1990; Knijn et al., 1993). Estimates of the spatial distributions of environmental properties were also concordant with previous estimates (ICES, 1962; Otto et al., 1990) and temporal variations followed similar patterns to those previously estimated (Becker and Pauly, 1966; Turrell et al., 1996). It was, therefore, reasonable to assume that the data used in this paper were representative enough for establishing relationships.

Spatial distributions of mature cod differed greatly from those of mature haddock because of their different relationships with environmental properties. Cod were found throughout the North Sea in either shallower coastal waters or deeper and more oceanic waters. It is possible that separate stocks exist—tagging data by Daan (1978) suggest that North Sea cod may

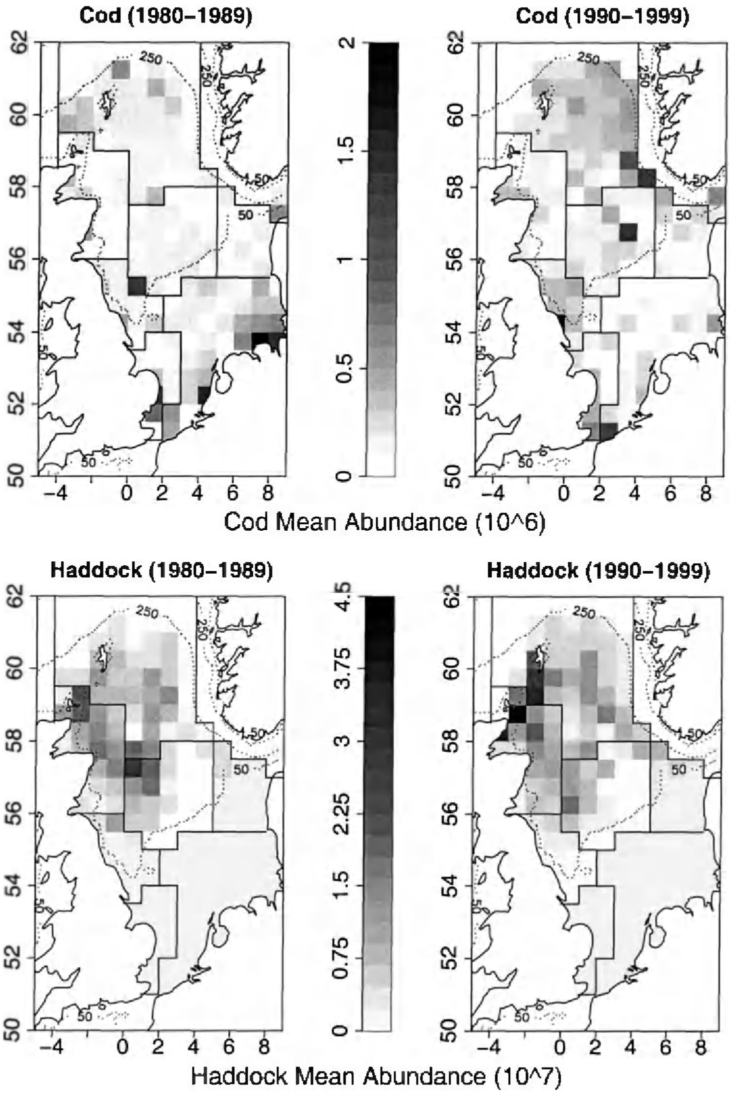

Fig. 4. Temporal trends in spatial distributions of mature cod and haddock abundance: 1980–1989 and 1990–1999.

exist as southern, central and northern stocks—and that these stocks differed as to their optimal environments. As mentioned in the results section, there was evidence of a shift in spatial distribution for cod, resulting in a change in the relationship to depth between the 1980s and 1990s (Fig. 5). This shift may have been caused by the warming of the North Sea (Beaugrand, 2003) as the relationship to temperature has changed little between decades (Fig. 5), and so it would be expected if cod in the North Sea are truly at the southern temperature boundary of their habitat range (O'Brien et al., 2000). There are other instances where a shift in cod distribution is thought to have been at least partially caused by an environmental change, for example Rose et al. (2000) consider a shift in the distribution of Newfoundland cod stocks.

In contrast, there appears to be only one haddock stock, with the bulk of the population occurring within an envelope of environmental characteristics: depths between 75 and 125 m, bottom temperatures greater

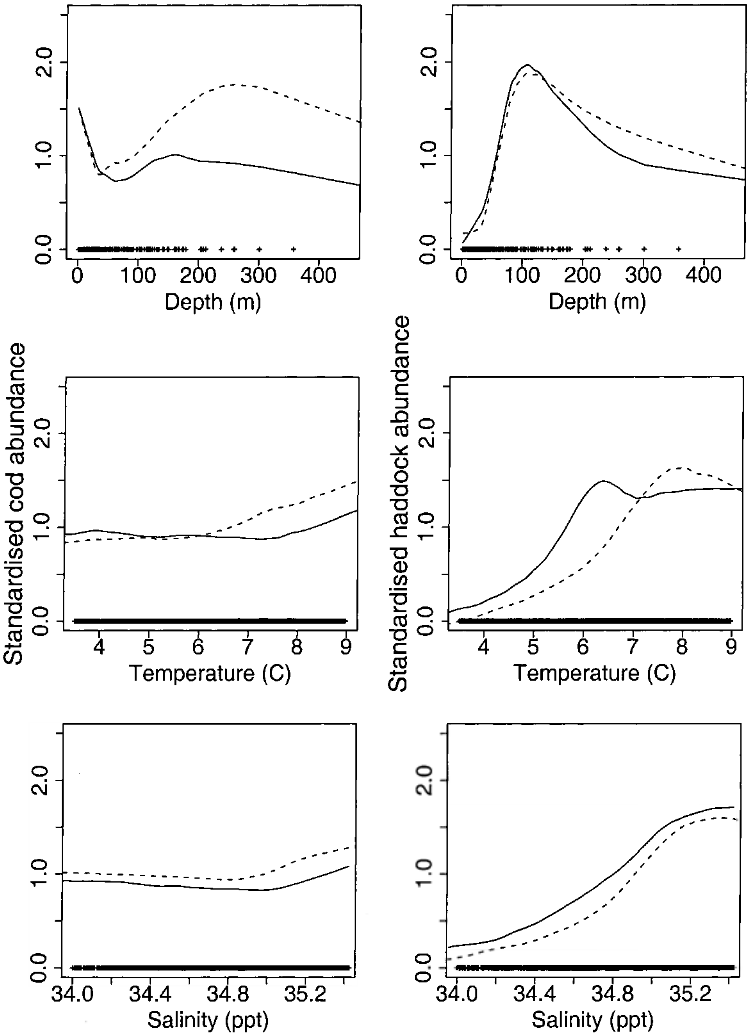

Fig. 5. Temporal trends in GAM relationships between standardised cod and haddock abundance and hydrographic properties: water column depth, bottom temperature and bottom salinity. The solid line is for years 1980–1989; the dashed line is for years 1990–1999 while data points are shown at the bottom of the graph.

than 6 °C, and salinities greater than 34.5 ppt. Depth played an important role in determining spatial distributions of mature haddock. Throughout the 1980s and 1990s, there was a trend of increasing bottom temperatures (the mean first quarter bottom temperature of the 1980s was 5.99 °C, that of the 1990s was 6.55 °C). Haddock favoured the same region (waters of depths between 75 and 125 m) regardless of temperature change. This may be seen in Fig. 5 where the peak haddock abundance is found at greater temperatures in the 1990s than in the 1980s, because haddock have remained in a constant position in the now warmer seas.

6. Conclusions

Cod were tolerant of a wider range of conditions, being found across the range of depth, temperature and salinity in the North Sea. As a result, they were found in two regions: first, in shallow coastal areas, predominantly in the southern North Sea; and second, in deeper more oceanic areas along the Norwegian Trench. This supports the hypothesis that separate cod stocks exist in the North Sea, with different stocks favouring different optimal environments. The shift in distribution between decades suggests that the southern North Sea may be becoming too warm to support a large resident cod population. It is unclear, however, whether cod in this region are migrating north or dying out.

In contrast, haddock were restricted to the northern North Sea. They showed stronger relationships with the environment, favouring deeper, warmer and more saline areas. Of these, it may be inferred that depth was the most important determinant of spatial distributions of haddock: an increase in temperature from the 1980s to the 1990s did not result in a marked change in spatial distributions, with haddock still exhibiting the same relationship with depth.

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