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Rindorf, Anna; Lewy, Peter

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Warm, windy winters drive cod north and homing of spawners keeps them there

Anna Rindorf and Peter Lewy

Danish Institute for Fisheries Research, Charlottenlund Castle, 2920 Charlottenlund, Denmark

*Corresponding author: Email: ar@dfu.min.dk, tel.: +4533963359, Fax: +45 33 96 33 33

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Summary

1. Climatic and anthropogenic effects often interact resulting in unexpected effects. For example, climate may lead to a change in the spatial distribution of a stock and thereby its vulnerability to exploitation. A stock which is currently under pressure from both environmental change and human exploitation is the North Sea cod stock. This stock has experienced a series of poor recruitments since the late 1990s and concomitant with the decrease in abundance, the distribution of cod has changed. Whilst it has been suggested that the change in distribution can be linked to increasing temperatures and fishing pressure, there is little actual evidence for this hypothesis.

2. Using winter and summer survey catches, we investigated whether a directional shift in the distribution of cod has taken place over the years 1983 to 2003. We then examined whether the change could be linked to climatic conditions, fishing mortality, stock size or limited directional movement of cod. Using the derived models, we investigated whether fishing has increased the sensitivity of the cod population to climate-induced distribution changes.

3. A series of winters characterised by high temperatures and southerly winds during the egg and larval phase of cod led to a northward shift in the distribution of juvenile North Sea cod the following year. A concomitant northern shift of mature fish around the time of spawning was linked directly to a tendency for northerly distributed juveniles to remain northerly throughout their life. This shift of the spawners further augmented that of the new recruits.

4. Although fishing mortality on a North Sea scale was not directly correlated to the displacement of any of the age groups, fishing has severely decreased the

number of fish in older age groups. This increases the sensitivity of the distribution of the cod stock to climatic changes.

5. *Synthesis and applications*. The centre of gravity of North Sea cod has moved north as a result of the effect of a series of warm, windy winters on the distribution of recently settled cod. The shift was followed by a northwards shift in the distribution of older age groups. Unless a series of cold and calm years combined with a reduced mortality in the southern areas allows a southern spawning population to rebuild, the cod stock is unlikely to return to its previous area of distribution. Protecting adult cod mainly in northern areas is furthermore unlikely to result in improved recruitment to the southern North Sea.

Keywords: climate change, fisheries management, North Sea cod, spatial distribution.

Introduction

Separating the impact of anthropogenic and environmental factors on declining species is a key topic in natural resource management. Unfortunately, this is often complicated as climate and human pressure interact to produce synergistic effects. In many cases, stocks are able to sustain the pressure from one factor but decline rapidly when the two are present together (O'Brien *et al*. 2000; MacKenzie & Köster 2004; Poloczanska *et al.* 2004, Hulme 2005). Often a decrease in stock size is accompanied by decrease in extent of the populated area (Myers & Stokes 1989; MacCall 1990; Swain & Kramer 1995). This concentrates remaining individuals in a small area and renders them more vulnerable to human impact (Jennings, Kaiser & Reynolds 2001). Alternatively, exploitation may alter the age distribution of the population and thereby

increase the vulnerability to a series of climatically-induced poor recruitment years (Jennings *et al.* 2001). Combined, exploitation and climate may lead to the disappearance of local aggregations. Thus long term effects of climate, distribution and exploitation depend on both the effect of climate on the distribution of the stock, the effect of exploitation on the susceptibility of the stock to local extinction and the rate of recolonisation following local extinction.

The Atlantic cod *Gadus morhua* L. has historically been a key species in several North Atlantic marine ecosystems but in recent years serious stock declines have placed it on the IUCN Red List of Threatened Species™. The North Sea population is currently at a historic low due to the combined effect of fishing and increased average temperatures during the egg and larval stage (O'Brien *et al*. 2000; ICES 2005). Historically, cod spawned throughout the North Sea (Daan 1978) but in recent years, surveys have found virtually no cod in south-eastern parts (ICES 2005), and the cause of this remains unclear. Fishing is an important source of mortality for North Sea cod and may have directly removed the southern individuals or may have acted indirectly through an increase of the sensitivity of the southern part of the stock to a series of poor recruitment years. Fishermen's organisations claim that cod have moved north in response to climatic changes (Anonymous 2004a). While this has also been suggested in the scientific literature (Pörtner *et al.* 2001, Perry *et al.* 2005), the nature of the mechanism remains unclear. If the distribution of adult cod has changed due to active movement, the stock should be able to return if environmental conditions improve. However, such movement would appear to be in contrast to the high degree of seasonal site fidelity generally found in cod (Bedford 1966; Daan 1978; Taggart 1997; Robichaud & Rose 2001). If the lack of cod in the south-eastern North Sea is instead

caused by decreased recruitment at south-eastern spawning sites, the prospects for the return of southern cod are less good. Areas where abundance has previously decreased due to fishing are only slowly colonized by cod from adjacent areas (Ruzzante *et al.* 2001). Even after a series of good recruitment years, south-eastern areas may therefore not be recolonized at the same rate as northern areas and stock recovery could take longer than currently assumed (ICES 2005).

Apart from active movements towards or away from specific temperatures (Clark & Green 1991; Swain & Kramer 1995), several factors influence the distribution of cod. Firstly, the distribution of late larvae reflects a combination of the distribution of spawning adults (Watson, Bye & Houghton 1977; Brander 1994; Ruzzante, Taggart & Cook 1996), and survival and drift of eggs and early larvae. Recruitment of cod in the North Sea is negatively correlated to sea surface temperature during the year of birth (Brander 2000; O'Brien *et al.* 2000), a fact which has been attributed to a negative correlation between temperature and food availability (Beaugrand *et al.* 2003). Drift of eggs and larvae depends on wind stress at the surface (Prandle 1984; Turrel 1992) and survival of early life stages are affected by both temperature (Iversen & Danielssen 1984) and wind (Sundby, Ellertsen & Fossum 1994; MacKenzie & Kiørboe 2000). Older fish may be affected by both bottom temperature and density dependent temperature selection (Swain & Kramer 1995). Fishing is an important source of mortality of older cod, and spatial differences in fishing effort may lead to distributional shifts (Appendix S1, see Supplementary material). Additionally, the distribution of a given age group is likely to reflect that of the cohort at previous times as tagging studies show marked seasonal site fidelity of individual cod (see above). In particular, spawning cod may exhibit homing to natal spawning sites (Ruzzante *et al.* 1996) and

the distribution of spawning cod reflects the distribution of the cohort as larvae or juveniles (Watson *et al.* 1977; Brander 1994; Ruzzante *et al.* 1996). A variety of factors may thus affect the distribution of cod, and the effect may differ between age groups.

Here we examine the winter and summer centre of gravity of the distribution of North Sea cod over the period from 1983 to 2003. We investigate whether distributional changes can be linked to climate, abundance, site fidelity or fishing mortality. The relationship between the centre of gravity and average temperature is examined to determine if changes in the centre were caused by active movement due to increased average temperatures. Furthermore, we relate the centre of gravity of juveniles to wind and temperature during the larval phase of the cohort and the centre of older fish to the location of the same cohort in previous years. To determine the direct effects of abundance and fishing, we further investigate the relationship between location of the centre and abundance of the cohort and the fishing mortality the cohort has sustained.

Methods

Study area

The study was confined to the North Sea area within 51ºN and 62ºN latitude and 4ºW and 9ºE longitude. Areas deeper than 200 m were not sampled by the surveys and were therefore excluded.

Estimation of centre of gravity and displacement

Our aim was to investigate the effect on distribution not only of current climatic conditions, but also of the climatic and distributional history of each cohort. In particular, we wished to investigate whether the distribution of juveniles could be linked

to particular conditions during and after spawning and whether the distribution of a cohort was retained in subsequent years. We estimated the distribution of cod in each age group from catch at age in the English and Scottish Groundfish surveys (August/September 1983 to 1990) and the International bottom trawl surveys (IBTS) coordinated by the International Council for the Exploration of the Sea (ICES)(February 1983 to 2003 and August/September 1991 to 2003, derived from the ICES International Bottom Trawl Survey Database). Although surveys were conducted before 1983, the coverage was poorer and methods less standardised, and the years before 1983 were therefore not used. The IBTS is conducted by several ships that each cover part of the North Sea. Demersal trawls are used to sample the abundance of cod and the total catch and length composition is recorded in each haul. Haul duration has varied from either 0.5 or 1 hour in the beginning of the period to 0.5 hour from the 1990s onwards and all catch rates are standardised to hourly values. Age length keys determined from otoliths are combined with the catch of each length group to provide the catch at age. The surveys conduct an average of two trawl hauls in each ICES statistical rectangle (1° longitude by 0.5^o latitude) and each haul is randomly allocated within trawlable areas. To avoid bias due to differences in survey coverage, only rectangles fished in at least 80% of the years were used. This resulted in 151 and 72 rectangles in winter and summer, respectively.

To examine the effect of homing of spawners, the age groups were divided into juveniles (1-year-olds), adults (2- and 3-year-olds) and potential spawners (4-year-olds and older)(Cook *et al.* 1999). As February marks the beginning of the spawning season for North Sea cod (Daan *et al.* 1990), only age 4+ cod caught in February are referred to as spawning fish and 4+-year-olds in summer are referred to as adults. We used an

alternative measure of the centre of gravity to describe the centre of the distribution of each age group (Appendix S2, see Supplementary material). The alternative measure of the centre of gravity of a given age, year and season was estimated as the average latitude and longitude weighted by the natural log of the average catch at age plus 1 in each statistical rectangle. This measure was used rather than the arithmetic centre of gravity as a simulation study indicated that the alternative estimate was homoscedastic whereas the arithmetic estimate was not (Appendix S2, see Supplementary material). Latitude and longitude of the centres of gravity of a given age, year and season were expressed in units of standard deviations from the mean of all years. When latitude and longitude of the centres were significantly correlated, principal component analysis of latitudes and longitudes of a given age and season was used to estimate the displacement of the centre, $L_{a,s,y}$, as the first principal component of standardised latitude and longitude. When no correlation was found, $L_{a,s,y}$ was estimated as the standardised latitude. In this way we obtained a single estimate of the directional displacement of each age in each year and season. This estimate of displacement has several advantages. First of all, it combines detailed information about distribution in a larger area in a single point which describes the location of an average cod. This facilitates the demonstration of yearly differences in distribution and the analyses of these. Secondly, the effects of the location of the cohort in previous years can be estimated by simply including the displacement of the centre of the cohort in former years in the model. Thirdly, some ships have changed trawl over the period, and this is likely to affect yearly average catch rates. However, if yearly differences in catchability are minor and ships sample widely within the North Sea, the change of trawl does not affect the centre.

Temperature and wind data

The effect of temperature on the distribution of cod is twofold: bottom temperature affects active movement of juveniles and adults and surface temperature affects survival of early life stages. Both bottom temperatures around the time of trawl sampling and surface temperature during the egg and larval phase were estimated from the North Sea temperature measurements in the ICES hydrographic database (www.ices.dk). Yearly average February bottom and surface temperatures (^{o}C), $T_{bottom,winter,y}$ and $T_{surface,winter,y}$, and August/September bottom temperatures, $T_{bottom,summer,y}$, were estimated as the average of temperatures averaged within ICES statistical rectangles. To avoid bias due to differences in the areas sampled, only rectangles sampled in at least 80% of the years in a given season were used. Data represent the temperature during the survey rather than the temperature history of the individual fish. However, monthly sea temperatures are highly positively autocorrelated (Cushing & Dickson 1976), and average bottom and surface temperatures were therefore assumed to reflect temperature over a period long enough for cod to have redistributed.

Wind affects drift and survival of eggs and larvae (Prandle 1984; Turrel 1992; Sundby *et al.* 1994; MacKenzie & Kiørboe 2000). Daily forecasts of directional average sea surface stress (N/m^{2}s) were obtained from the ECMWF data server (www.ecmwf.int). The data were used to estimate average sea surface stress over the months February to April in the directions west to east, W_{EW}, and south to north, W_{NS} covering the main spawning season of cod and hence the period in which pelagic eggs and early larvae are most abundant (Daan *et al.* 1990).

Abundance and fishing mortality

The number of cod of age a in year y, $N_{a,y}$, and the fishing mortality, $F_{a,y}$, endured by age a in year y was taken from the most recent stock assessment including discard mortalities (ICES 2005).

Models of displacement

The displacement of age group 1 in winter ($L_{1,winter,y}$) was analysed in a multiple regression model including the effects of displacement of potential spawners in the year of hatching ($L_{4+,winter,y-1}$), surface temperature in February in the year of hatching ($T_{surface,winter,y-1}$), bottom temperature during settling ($T_{bottom,summer,y-1}$), winter bottom temperature in the year of sampling ($T_{bottom,winter,y}$), average sea surface stress during the egg and larval stage ($W_{NS,y-1}$) and ($W_{EW,y-1}$), log abundance ($\ln N_{1,y}$), and the products $T_{bottom,winter,y} \ln N_{1,y}$, accounting for density dependent temperature selection, and $T_{surface,winter,y-1}W_{NS,y-1}$ and $T_{surface,winter,y-1}W_{EW,y-1}$, accounting for interactions between the effect of wind and temperature during the larval stage. The same effects were included in a multiple regression model of the displacement of 1-year-olds in summer except for the addition of the effect of the location of the cohort in the previous survey ($L_{1,winter,y}$) and the replacement of $T_{bottom,summer,y-1}$ with $T_{bottom,summer,y}$. Fish younger than 1 year are not landed by the fishery (ICES 2005), and fishing mortality was therefore not included.

The displacement of adult cod (age groups 2 to 3 in both seasons ($L_{2,s,y}$ and $L_{3,s,y}$) and age group 4+ in the summer ($L_{4+,summer,y}$)) was analysed in multiple

regression models including the effects of the displacement of the cohort 6 and 12

months earlier, log abundance ($\ln N_{a,y}$), the fishing mortality which the cohort had been

exposed to within the last year ($F_{a-1,y-1}$), bottom temperature at the time of the survey

($T_{bottom,winter,y}$ and $T_{bottom,summer,y}$ in winter and summer respectively), and the effect of

density dependent temperature selection as the product of bottom temperature and

$\ln N_{a,y}$.

The multiple regression model of potential spawners, $L_{4+,winter,y}$, analysed the same

effects as the model of adult fish, but as the group represents a plus group, the location

of potential spawners the previous year ($L_{4+,winter,y-1}$) was also included. To account for

homing to natal spawning sites, the location of 1-year-olds 3 years earlier ($L_{1,summer,y-3}$),

was included. Homing of cod older than 4 years was accounted for by the location of

spawning fish the previous year ($L_{4+,winter,y-1}$).

The residuals of the displacements were assumed to be normally distributed. All

statistical analyses were performed using SAS® version 8 for Windows®. Factors not

significant at the 5% level (*F*-statistic) were removed from the models. The non-

significant factors were tested one by one for effect on the reduced model to assure that

factors eliminated remained nonsignificant. Residuals were tested for trends and

autocorrelation (Pearson correlation coefficients) and for deviations from normality

(Shapiro-Wilks statistic).

Results

Displacement of the centre of gravity

Winter and summer centres of gravity shifted north as age increased from 1 to 4 years (Fig. 1) except for potential spawners which were further south than 3-year-olds in the same season. Latitude and longitude of the centre was significantly correlated for ages 1 and 2 in both seasons and ages 3 and 4+ in summer (correlations -0.62 to -0.85, $P<0.005$)(Fig. 1). The first principal component of latitude and longitude, $L_{a,s,y}$, explained more than 81% of the variation in latitude and longitude for these ages. The northwestwards shift over the period was significant for all ages and seasons except ages 2 and 3 in winter (correlations 0.33 and 0.41, $P=0.14$ and $P=0.07$, respectively)(Fig. 2).

Multiple regression models: juveniles

There was no effect of either bottom temperature or abundance on the displacement of juveniles. The reduced multiple regression model of the displacement of 1–year-olds in winter was:

$$\hat{L}_{1,winter,y} = 0.52^* L_{4+,winter,y-1} + 1.71^{***} T_{surface,winter,y-1} + 0.0079^* W_{NS,y-1}$$
$$- 0.0013^* T_{surface,winter,y-1} W_{NS,y-1} - 10.0^{**}$$

(r^2=0.61, * denotes significance levels of the parameters: *: 5%, **: 1%, ***0.1%). The displacement of 1-year-olds in the summer was highly correlated to the displacement of 1-year-olds in winter ($\hat{L}_{1,winter,y}$) with an additional effect of northwards sea surface stress in the year of spawning ($W_{NS,y-1}$):

$$\hat{L}_{1,summer,y} = 0.77^{***} L_{1,winter,y} + 0.0013^{***} W_{NS,y-1} - 0.82^{**}$$

(r^2=0.70). Hence, 1-year-olds were located northwest of the average if northwards surface stress ($W_{NS,y-1}$) or temperature ($T_{surface,winter,y-1}$) was high during the egg and

larval stage, and spawners were located north of the average. Only northwards surface stress affected displacement whereas eastwards stress had no detectable effect. Wind effect dominates the displacement completely in years with a high northwards surface stress, eliminating the effect of temperature (Fig. 3). In years with low northwards sea surface stress, temperature has a pronounced effect on displacement, leading to a south-eastern location of the centre in cold years and a northwestern location in warm years. Since 1993, only three years were predicted to have produced juveniles southeast of the average if the spawners had not moved (Fig. 3). In contrast to this, seven years in the period 1983 to 1992 should have produced southeastern centres. The changes in wind and temperature alone would have been sufficient to move the centre of 1-year-olds northwestwards over the period even if the spawners had not moved (Fig. 4a). However, the sustained displacement since 1990 was caused by the displacement of spawners rather than a direct effect of climate (Fig. 4a).

Multiple regression models: adults

Neither bottom temperature, abundance nor fishing mortality affected the displacement of adults. However, all age groups except the 3-year-olds in winter were significantly correlated to the displacement of the cohort at previous sampling times ($\hat{L}_{a-1,summer,y-1}$, $\hat{L}_{a,winter,y}$ or $\hat{L}_{a-1,winter,y-1}$). The reduced models took the form

$$\hat{L}_{2,winter,y} = 0.40^* L_{1,summer,y-1} + 0.07$$

$$\hat{L}_{2,summer,y} = 0.42^* L_{1,summer,y-1} + 0.47^* L_{2,winter,y} + 0.05$$

$$\hat{L}_{3,summer,y} = 0.54^{**} L_{2,summer,y-1} + 0.08$$

$$\hat{L}_{4+,summer,y} = 0.55^* L_{4+,winter,y} + 0.02$$

No intercepts were significant, indicating that a cohort placed in the average location tended to remain at the average location at older ages. Although the models were all significant, the r^2s were rather low (0.19 to 0.42).

Multiple regression models: potential spawners

Bottom temperature, abundance and fishing mortality had no affect on the displacement of potential spawners. The analysis of the displacement of the 4+ group in winter revealed significant effects not only of the displacement of 3-year-olds last year ($L_{3,winter,y-1}$) but also of the displacement of 1-year-olds 3 years earlier ($L_{1,summer,y-3}$):

$$\hat{L}_{4+,winter,y} = 0.55^{**} L_{3,winter,y-1} + 0.33^* L_{1,summer,y-3} + 0.12$$

(r^2=0.61).

The potential spawners thus tended to be located south of the average if the 3-year-olds were southeast of the average the previous year. However, in addition to this effect, a southwards displacement of the cohort as juveniles resulted in a southwards displacement of the spawners. Hence cod did not simply remain at the locations where they were present the year before but exhibited a response which could be interpreted as a homing of adults to areas where they were themselves spawned. The shift in the location of the spawners was mainly caused by this homing effect as the model predicts that the centre of the spawning cod would not have changed directionally in the absence of a shift in the location of the recruits (Fig. 4b).

The residuals were not significantly autocorrelated, did not exhibit trends and did not deviate significantly from a normal distribution in any of the models ($P > 0.05$ in all cases).

Time series analyses

As the displacement of juveniles is linked to that of spawners the previous year and the displacement of spawners is linked to that of juveniles three years earlier, the displacement of spawners becomes an autoregressive model with an external input in the form of temperature and wind forcing. Autoregressive processes may be stationary (the system returns to an equilibrium value after a perturbation) or non-stationary (a perturbation remains in the system and the system moves away from the start location). The parameters in the autoregressive model are the factors which determine whether the system is stationary. We wanted to investigate whether the model of the displacement of spawners and recruits was stationary within the space defined by the confidence limits of the parameter estimates and whether the properties depended on the age distribution of the stock.

The multiple regression models demonstrated that the displacements of 1-year-olds in summer could be predicted as:

$$\hat{L}_{1,summer,y} = 0.77\,\hat{L}_{1,winter,y} + 0.0013W_{NS,y-1} - 0.82 = 0.77\big(0.52L_{4+,winter,y-1}$$
$$+ 1.71T_{surface,winter,y-1} + 0.0079W_{NS,y-1} - 0.0013T_{surface,winter,y-1}W_{NS,y-1} - 10.0\big) + 0.0013W_{NS,y-1}$$
$$- 0.82$$

The parameters for the displacement of ages 4 and older were set to the upper 85% quartile to obtain an example where a broad age distribution results in stationarity but a narrow age distribution did not. The resulting model was

$$\hat{L}_{4,winter,y} = 0.76\hat{L}_{3,winter,y-1} + 0.49\hat{L}_{1,summer,y-3} + 0.11$$

To use the above model to predict $\hat{L}_{4,winter,y}$, a prediction of $\hat{L}_{3,winter,y-1}$ (the location of 3-year-olds in the previous year) is needed. One option is to simply assume no shift in the location of 3-year-olds, i.e. $\hat{L}_{3,winter,y-1} = 0$. However, correlation analyses showed that $\hat{L}_{3,winter,y-1}$ was significantly correlated to $L_{4+,winter,y-1}$ (correlation=0.63, P =0.0028). Hence assuming that the location of 3-year-olds did not shift though that of 4+ year-olds did, seemed unreasonable. Instead we assumed that the location of 3-year-olds in a given year followed that of 4+year-olds in the same year. This reduces the prediction of the location of 4+-year-olds to

$$\hat{L}_{4,winter,y} = 0.76\hat{L}_{4+,winter,y-1} + 0.49\hat{L}_{1,summer,y-3} + 0.11$$

To demonstrate the presence or absence of stationarity under changing climatic conditions, we estimated the displacement of 1-year-olds in summer, $\hat{L}_{1,summer,y}$, under alternating 5-year periods of warm ($T_{surface,winter}$=6.5ºC, W_{NS}=1100) and cold ($T_{surface,winter}$=5ºC, W_{NS}=300) weather and a variable displacement of spawners, $\hat{L}_{4,winter,y}$. The displacement of the spawners was estimated as the weighted average $\hat{L}_{a,winter,y}$ of ages 4 to 7. $\hat{L}_{a,winter,y}$ was estimated as

$$\hat{L}_{a,winter,y} = 0.76L_{a-1,winter,y-1} + 0.11, 4<a\leq7.$$ This corresponds to the relationship between the displacement of 3- and 4+-year-olds ($L_{3,winter,y-1}$ and $L_{4+,winter,y}$) detected in the regression analysis. The average displacement was weighted by the proportion a-year olds in the spawning biomass of age 4+ cod in 1963 and 2003 (from ICES 2005) to

provide an example of a population with a wide and narrow age distribution of spawners, respectively.

As temperature and wind only affects displacement during the early life stages, the effect of climate on the displacement of spawners exhibits a temporal lag (Fig. 5). Furthermore, as the spawning stock consists of several age groups, the displacement of adult fish changes smoothly even when climatic factors show abrupt year-to-year changes. This smoothing renders the spawning stock partially resilient to climatic conditions in individual years. The homing of adults to natal spawning displacements introduces a delayed augmentation of prolonged climatic displacement.

The stationarity of the time series models depends on the parameter estimates, and cases where both wide and narrow age distribution provided stationarity or lack of stationarity can be found within the confidence limits of the estimated parameters. However, a range of parameter combinations resulted in stationarity with a wide age distribution of spawners, whereas a narrow age distribution of spawners resulted in a continued displacement of the centre (Fig. 5).

Discussion

Temperature and wind affected displacement of early life stages but had no effect on displacement of the centre of distribution of adult fish. There was thus no evidence to suggest that the adult cod population moved to avoid high temperatures. However, there was ample evidence that cohorts tended to retain a northerly distribution throughout their lives, in particular when becoming mature. The lack of temperature effect on older stages introduces a temporal lag in the relationship between climate and the displacement of spawners. Because of this lag, a series of warm, windy years followed by a series of cold calm years will not immediately result in a shift of the

centre of the spawners. The resilience of the location of the spawners depends both on the parameters in the models and on the age structure of the spawners. A spawning stock consisting of few age groups is susceptible to a lasting change in displacement over a greater range of parameter combinations than a spawning stock biomass consisting of several age groups. This renders the spatial distribution of a stock consisting of several age groups more likely to be stable.

The effect of surface stress on displacement of juveniles agreed with a simple effect of northwards surface stress on the drift of eggs and larvae, resulting in a more northerly distribution in years with a high stress. When the northwards wind stress was low, the early life stages presumably drifted less from where they were spawned (Prandle 1984; Turrel 1992) and the displacement of the centre was highly dependent on temperature. Years with high temperatures are characterized by a lower availability of larval food (Beaugrand *et al.* 2003), and may result in a disproportionately large decrease in the survival of cod larvae in the southeastern North Sea. There was no effect of eastwards surface stress, indicating that the effect was not due to turbulence induced mortality (MacKenzie & Kiørboe 2000). Had this been the case, the effect of eastwards surface stress should have exceeded that of northwards surface stress, as westerly stress were generally greater than southerly stress during the egg and early larval stages (Fig. 2f).

The lack of effect of ambient temperature after the first year of life is supported by the low correlation between local temperature and abundance of cod seen in other cod stocks (Perry & Smith 1994; Swain 1999; Begg & Marteinsdottir 2002). However, the low r^2 of the models of adults indicate that other factors than distributional history affects displacement. Obvious candidates are food abundance and mortality, in

particular fishing mortality. Though we did not detect an effect of fishing mortality on a North Sea wide scale, there may be local effects which are not detected in this type of analysis. If fishing mortality was highest in the southern part of the area, this could have moved the centre north (Appendix S1). Unfortunately, it is impossible to investigate this aspect further due to a lack of spatially disaggregated data on fishing effort. The 2- and 3-year–old cohorts consist of varying proportions of mature fish (Cook *et al.* 1999) and if the mature and immature fish move differently, the yearly differences in the proportion of mature fish will add to the variance in the displacement. This could be investigated by estimating the centre of both mature and immature 3-year-olds but such analyses were considered beyond the scope of the present study.

Homing to natal spawning sites has been demonstrated for Canadian cod (Taggart 1997; Robichaud & Rose 2001), but genetic analyses have not rendered conclusive evidence of separate spawning populations in the central North Sea (Hutchinson, Carvalho & Rogers 2001). However, a lack of genetic differentiation does not imply that cod do not exhibit homing, but merely that the homing response is not 100% accurate. Spawning in the North Sea has historically taken place at a number of more or less closely connected sites (Daan 1978) and as the geographical distance between neighbouring sites is small, minor inaccuracies in the homing response of the fish may lead to substantial genetic mixing.

Site fidelity has profound implications for management of the cod stock. Even though the stock is not necessarily divided into distinct substocks, it is not a unit stock which redistributes and spawns throughout the North Sea. Protecting cod mainly in the northern part of their range as has been suggested (Anonymous 2004b) may aggravate the northwards displacement. If cod disappear entirely from parts of the North Sea due

to the combined effects of fishing and global warming (King 2005), a potential stock recovery following more favourable environmental conditions and substantially reduced fishing pressure may not repopulate these areas. Rather, the return of cod must be through immigration which is a slow process (Ruzzante *et al.* 2001). Fishing is likely to have increased the sensitivity of the cod stock to climate-induced distributional changes by reducing the number of older cod in the population. The probability that a displacement of the recruits would initiate a lasting displacement of the adults has increased over the years as the average age of spawners has decreased: cod of age 5 years and older constituted 57% of the spawning biomass in the years 1963 to 1972 but only 33% from 1994 to 2003 (ICES 2005). A wider age distribution of spawners would increase the probability that spawning and hence recruitment would take place throughout the North Sea even after a period of warm, windy years.

Acknowledgements

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Appendix S1

The effect of non-uniformly distributed fishing mortalities.

Changes in overall fishing mortality in an area affects the distribution of fish if fishing mortality is spatially heterogeneous. Assume that an area is divided into two areas, N and S. Fish in area N are subject to the fishing mortality of F_N and the number of fish in area N at the beginning of year t is $N_{N,t}$. Similarly, in area S fish are subject to the fishing mortality F_S and the number of fish at the beginning of year is $N_{S,t}$. In the absence of migration and recruitment, the number of fish present in the two areas after 1 year is

$$N_{N,t+1} = N_{N,t}e^{-F_N-M}$$
$$N_{S,t+1} = N_{S,t}e^{-F_S-M}$$

where M is natural mortality ($M = M_N = M_S$). The proportion of fish located in area N in the beginning of year t is

$$\frac{N_{N,t}}{N_{N,t} + N_{S,t}} \qquad\qquad \text{eqn A1}$$

After 1 year, the proportion located in area N is

$$\frac{N_{N,t+1}}{N_{N,t+1} + N_{S,t+1}} = \frac{N_{N,t}}{N_{N,t} + N_{S,t}e^{F_N-F_S}} \qquad\qquad \text{eqn A2}$$

As A2≠A1 unless $F_S=F_N$, unequal fishing mortalities change the distribution of the stock. If fishing mortalities in both areas are increased by a factor a, the proportion of fish in area N after 1 year becomes

$$\frac{N_{N,t+1}}{N_{N,t+1} + N_{S,t+1}} = \frac{N_{N,t}}{N_{N,t} + N_{S,t}e^{a(F_N-F_S)}} \qquad\qquad \text{eqn A3}$$

As A3$\neq$A4 unless $F_S=F_N$, changing fishing mortality in both areas by the same factor

leads to a change in distribution from that obtained at F_S and F_N.

Appendix S2

Statistical properties of measures of the centre of gravity

To use the centre of gravity in analyses such as ordinary multiple regression models, the variance of the yearly estimates must be homogeneous. We conducted a simulation experiment to compare ability to fulfil this assumption of the traditional measure of the centre of gravity with that of an alternative measure.

The estimation of the variances of the two measures was based on simulations of a series of trawl samples taken along a transect line. The distribution of cod along this line was assumed to be bimodal and shifts in the centre of gravity were caused by variation in the relative importance of the two modes. This spatial distribution was obtained by letting the density of fish, *f*, at any given point *x*, be described by the sum of two normal distributions:

$$f_w(x) = N_w \bullet \left(w\varphi(x \mid \mu_1, \sigma_1) + (1-w)\varphi(x \mid \mu_2, \sigma_2) \right) \quad 0 \leq w \leq 1 \qquad \text{eqn A5}$$

where

$$\varphi(x \mid \mu_m, \sigma_m) = \frac{1}{\sigma_m 2\sqrt{\pi}} e^{-\frac{1}{2}\left(\frac{x-\mu_m}{\sigma_m}\right)^2}$$

and μ_m and σ_m are the mean location and standard deviation of aggregation *m*, *w* describes the relative importance of mode 1 of the distribution and

$$N_w = \frac{N_0}{\sum_x w\varphi(x \mid \mu_1, \sigma_1) + (1-w)\varphi(x \mid \mu_2, \sigma_2)}$$

where N_0 is the total number of fish present at all locations x. N_w ensures that the total number of fish along the transect remains constant for all values of *w*.

We now turn to the simulation of trawl samples along the transect. Several authors have found that a delta-distribution (Atchinson & Brown 1957) adequately describes the error structure of trawl catches (Pennington 1983; Stefánsson 1996). The delta-distribution is a combination of two distributions: a binomial distribution describes the probability p of obtaining a non-zero catch and a log-normal or gamma distribution describes the distribution of the number of fish caught in non-zero catches. In the lognormal case, the delta distribution $D(p, \gamma, \tau)$ is defined as:

$$P(C < 0) = 0$$
$$P(C = 0) = 1 - p$$
$$P(C \leq c) = pLN(c|\gamma, \tau) \quad , c > 0$$

where C is the catch in numbers and $LN(c|\gamma, \tau)$ is the distribution function of a log-normal distribution with mean γ and standard deviation τ.

The expected catch at a given location x, $E(C_w(x))$, is proportional to $f_w(x)$ if catchability, q, is constant (Hilborn and Walters 1992):

$$E(C_w(x)) = qf_w(x) = qN_0 \frac{w\varphi(x \mid \mu_1, \sigma_1) + (1-w)\varphi(x \mid \mu_2, \sigma_2)}{\sum_x w\varphi(x \mid \mu_1, \sigma_1) + (1-w)\varphi(x \mid \mu_2, \sigma_2)} \qquad \text{eqn A6}$$

Note that q enters equation only as the product qN_0.

Preliminary investigations of the survey catches indicated a positive correlation between the average proportion of trawl hauls taken in a given year and season which contained a particular age group and the average of non-zero catches of this age group. Hence p and $E(C \mid C > 0)$ are not independent. The relationship between the two was adequately described by

$$p = 1 - (1 + E(C \mid C > 0))^{-\lambda} \qquad \text{eqn A7}$$

where λ is a positive constant (r^2=0.61, no trends in the residuals). λ was estimated to be 0.81, and as this value was close to 1, λ was set to 1. This reduces (A7) to

$$p = \frac{E(C \mid C > 0)}{1 + E(C \mid C > 0)}$$

As the expected catch at a given location x is

$$E(C_w(x)) = p_w(x)E(C_w(x) \mid C_w(x) > 0) \qquad \text{eqn A8}$$

$p_w(x)$ can also be expressed as

$$p_w(x) = \frac{E(C_w(x))}{E(C_w(x) \mid C_w(x) > 0)}$$

Inserting $E(C_w(x)) = qf_w(x)$ (from (A6)) and rearranging, we get

$$p_w(x) = \frac{1}{2}\left(\sqrt{(qf_w(x))^2 + 4qf_w(x)} - qf_w(x) \right) \qquad \text{eqn A9}$$

as $p_w(x)>0$.

To ensure that (A6) and (A8) are fulfilled, the parameter $\gamma_w(x)$ must be

$$\gamma_w(x) = \ln(qf_w(x)) - \ln(p_w(x)) - \frac{\tau^2}{2} \qquad \text{eqn A10}$$

Hence, if τ^2 and q are constant and known, $\gamma_w(x)$ and $p_w(x)$ can be estimated directly from $f_w(x)$.

The centre of gravity was estimated by parametric bootstrap (Davison & Hinkley 1997). It was assumed that two trawl hauls were taken at each site x and the number of fish caught in haul i, $c_{w,i}$, was simulated from the delta distribution with parameters $\gamma_w(x)$ and $p_w(x)$ given by (A9) and (A10). The observed standard deviation, $\hat{\tau}$, of the trawl catches throughout the North Sea was around 1 for all ages. However, as this estimate includes spatial variation in density, we used $\tau = 0.5$ for the simulation.

Further, we assumed $q=1$. The density of fish at each site, $f_w(x)$, was calculated by (A5). The number of sites was set to 23, located at 0.5 intervals from $x=51$ to $x=62$. The parameters of f_w were $(\mu_1, \sigma_1) = (52,1.5)$, $(\mu_2, \sigma_2) = (60,2)$ and $N_0=100$. These values of x were chosen to represent observed cod catches. A directional shift in the location of the centre was achieved by calculating $f_w(x)$ for nine equally spaced values of w in the interval 0.1 to 0.9. Increasing w increases the latitude of the centre of the distribution (Fig. S1).

The arithmetic centre of gravity was estimated as

$$\hat{G}_{arithmetic,w} = \frac{\sum_x \bar{c}_w(x) * x}{\sum_x \bar{c}_w(x)}$$

where $\bar{c}_w(x) = \frac{1}{2}\left(c_{w,1}(x) + c_{w,2}(x)\right)$. An alternative measure of the centre of gravity was estimated as

$$\hat{G}_{\ln,w} = \frac{\sum_x \overline{\ln(c_w(x)+1)} * x}{\sum_x \overline{\ln(c_w(x)+1)}}$$

where $\overline{\ln(c_w(x)+1)} = \frac{1}{2}\left(\ln\left(c_{1,w}(x)+1\right) + \ln\left(c_{2,w}(x)+1\right)\right)$.

100000 replications were carried out and the empirical mean and variance of the two measures were calculated for each value of w. The displacement was larger for the arithmetic than for the alternative measure, but the two were highly correlated (correlation=0.996)(Fig. S2a). The variance of the arithmetic measure varies between 0.063 and 0.197 while that of the alternative measure varies between 0.066 and 0.083 (Fig. S2b). The variance of the alternative measure was fairly constant and generally less than that of the arithmetic estimate. We concluded that the assumption of

homoscedasticity of the alternative measure can be considered reasonable. This is not the case for the arithmetic measure.

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Figure legends

Fig. 1. Location of the centre of gravity of cod in winter (a) and summer (b) in the years 1983 to 2003. Cod age 1 (●), 2 (▲), 3 (▲) and 4+ (●).

Fig. 2. Displacement from the average of ages 1 to 4+ (a to d), winter surface and summer bottom temperature (e) and average sea surface stress$*10^{-3}$ (f) in February to April. a to e: Solid line: winter. Hatched line: summer. f: Westerly (hatched) and northerly (solid) wind stress.

Fig. 3. Displacement of the centre of 1-year olds in summer as a function of northwards surface stress and winter temperature. Displacement was predicted by assuming that spawners remained at their average displacement. Green shades indicate centres of 1-year olds northwest of the average, yellow to red centres southeast of the average. Degree of shading indicates distance from the average. Symbols indicate observed northwards surface stress and temperature in the years 1982 to 1992 (●) and 1993 to 2002 (○).

Fig. 4. Displacement from the average of age 1 in summer (a) and of age 4+ in winter (b). Observed displacement (solid black line) and model predicted displacements (hatched line) of 1-year olds in the summer and 4+-year olds in winter. Grey lines depict the displacement if spawners (a) or 1-year olds (b) remained at the centre observed in 1983.

Fig. 5. Effect of having a broad age distribution of spawners on the resilience of the displacement of recruits (broken lines) and spawners (solid lines) over a period of 50 years. Displacement is driven by alternating 5 year periods of warm and cold weather. The displacement of spawners for a wide (black) and narrow (grey) age distribution.

Fig. S1. Density of fish, $f(x)$, at site x along the transect for three different values of the relative importance of mode 1 of the distribution, w. $w=0.1$ (hatched), $w=0.55$ (solid black) and $w=0.9$ (grey).

Fig. S2. Average centre of gravity (a) and variance of the centre of gravity (b). Arithmetic measure (solid) and modified measure (hatched).
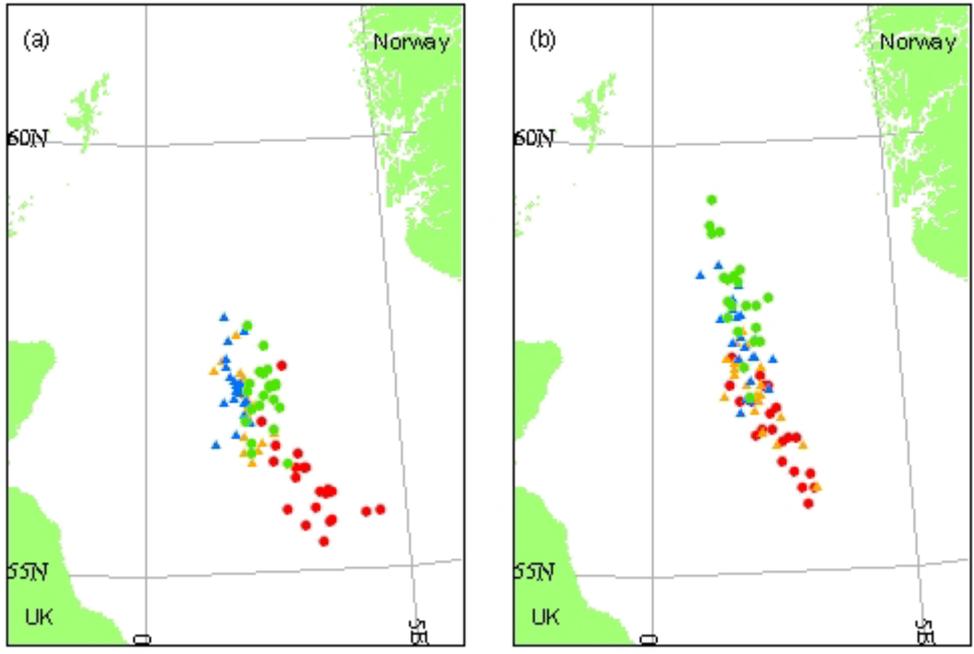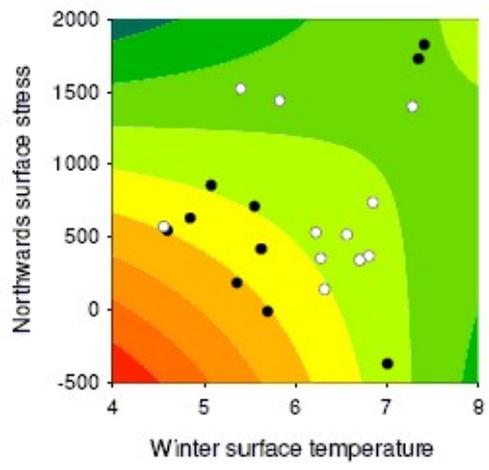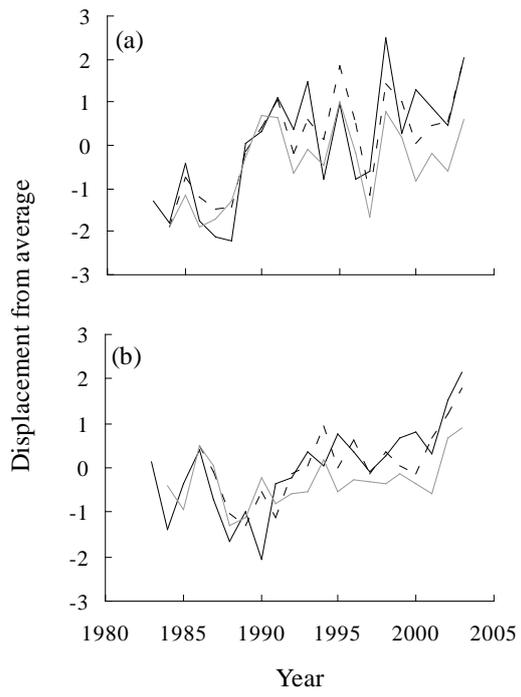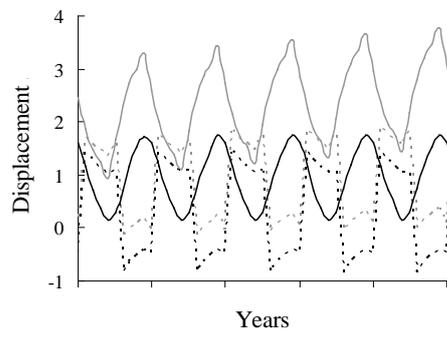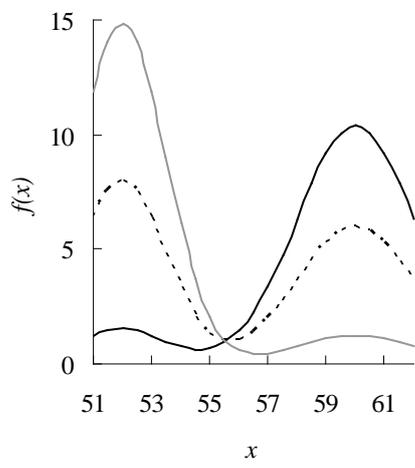
Fig. 1

Fig. 2
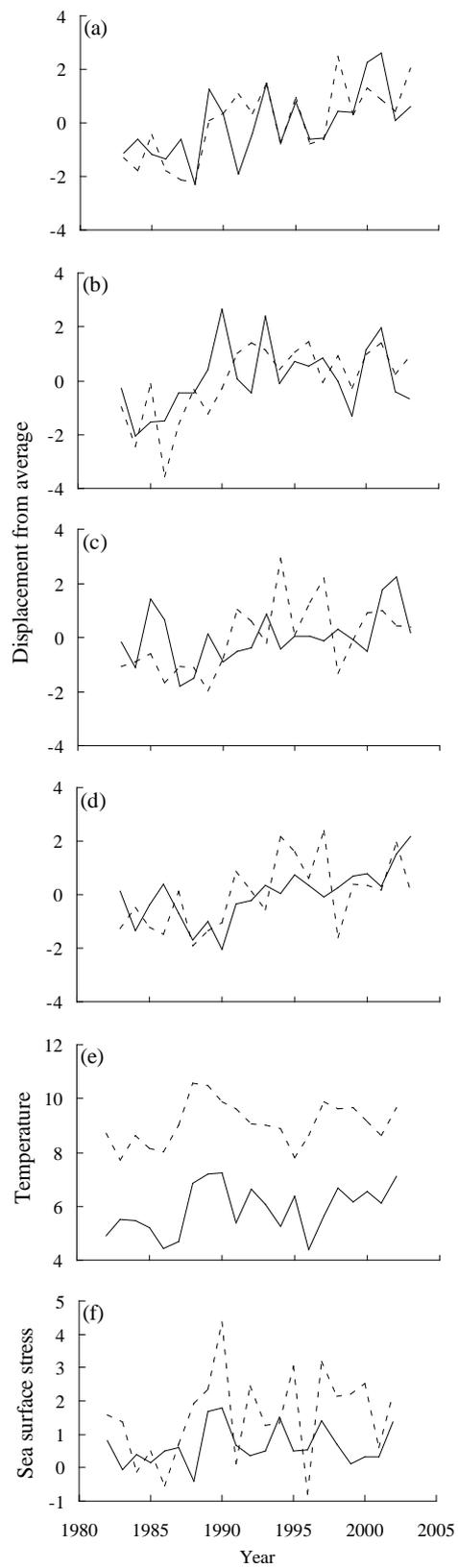
Fig. 3

Fig. 4

Fig. 5

Fig. S1

Fig. S2