

Warm water occupancy by North Sea cod

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The North Sea has warmed in recent years and there is an ongoing debate into how this is affecting the distribution of fishes and other marine organisms. Of particular interest is the commercially important Atlantic cod (*Gadus morhua* L.), which has declined sharply in abundance in the North Sea over the past 20 years. Observations of the temperature experienced by 129 individual cod throughout the North Sea were made during a large-scale electronic tagging programme conducted between 1999 and 2005. We asked whether individual cod fully occupied the thermal habitat available to them. To this end, we compared the temperature experience of cod with independently measured contemporaneous sea-bottom temperature data. The majority of cod experienced a warmer fraction of the sea than was potentially available to them. By summer, most of the individuals in the south experienced temperatures considered superoptimal for growth. Cooler waters were within the reach of the cod and a small number of individuals migrated to areas that allowed them to experience lower temperatures, indicating that the cod had the capacity to find cooler water. Most did not, however, suggesting that the changing thermal regime of the North Sea is not yet causing adult cod to move to cooler waters.

Keywords: fishes; electronic tags; temperature; movement; distribution; population structure

1. INTRODUCTION

Climate change is predicted to have an increasing effect over the coming decades (Meehl *et al.* 2005). Forecasts of the effect of climate change on marine ecosystems vary (Hulme *et al.* 2002; ICES 2006), with predicted increases in average sea temperature much higher in some regions than others. The North Sea, being a relatively shallow shelf ecosystem within the northeast Atlantic, is perhaps particularly vulnerable to climate change. Since 1970, it has warmed by approximately 1.0°C (ICES 2006). Annual surface temperatures of the North Sea are forecast to warm by between 1 and 2.5°C during the next 50 years (Clark *et al.* 2003). Many ectothermic marine species, including crustaceans (Groeneveld & Branch 2002), cephalopods (Sims *et al.* 2001) and a number of commercially important fish species such as cod, plaice and mackerel (Metcalf *et al.* 2002) are highly mobile and undertake extensive migrations. In response to warming, the geographical ranges of cold-adapted marine species are predicted to become compressed or move towards the poles (Parmesan & Yohe 2003). As one of the most heavily fished seas in the world (Jennings *et al.* 1999; Kaiser *et al.* 2002), the consequences of changes in the distribution of commercial fish species in the North Sea will be significant (Beare *et al.* 2004).

The Atlantic cod (*Gadus morhua* L.) is distributed along the continental shelves of the North Atlantic between 40 and 80° of latitude. The North Sea cod stock has declined markedly in abundance in recent decades (Daan *et al.* 1994; Hislop 1996) and is precariously close to collapse (Cook *et al.* 1997; Christensen *et al.* 2003). Over-fishing has been blamed for the decline (Becker & Pauly 1996; Cook *et al.* 1997). However, the North Sea has also warmed

significantly in the past decades (O'Brien *et al.* 2000; Hulme *et al.* 2002; Hughes *et al.* 2003; ICES 2006) and this too has been implicated in the decline of the North Sea cod, be it on the basis of recruitment failure (O'Brien *et al.* 2000; Clark *et al.* 2003; Ottersen *et al.* 2006) or changes in the distribution of preferred habitat (Blanchard *et al.* 2005). Perry *et al.* (2005) reported a long-term northward shift of cod (and several other demersal fish species) in the North Sea that has coincided with its recent warming. Understanding the relative contribution of fishing pressure and climate change to the changes in stock distribution and abundance underpins effective fisheries management in the North Sea and elsewhere (Rose 2004; Horwood *et al.* 2006).

Throughout the geographical range of cod, the many stocks occupy mean annual seabed temperatures between 1 and 11°C, although the full thermal range extends from –1 to 19°C (Sundby 2000). Temperature influences vital processes such as growth rate (Pedersen & Jobling 1989; Brander 1995; Jobling 1988; Björnsson *et al.* 2001; Björnsson & Steinarsson 2002), metabolic rate (Claireaux *et al.* 2000; Lannig *et al.* 2004) and maturation (Yoneda & Wright 2005). Most fishes, being ectothermic, conform to their thermal environment and they must move if they are to maximize their exposure to suitable temperatures and optimize vital processes such as growth. Defining thermal optima is, however, complicated; laboratory studies suggest that the optimal temperature for cod growth decreases with size and age, with estimates varying from 17°C for newly hatched juveniles to 7°C for adults (Pedersen & Jobling 1989; Jobling 1988; Boutilier 1998; Björnsson *et al.* 2001; Björnsson & Steinarsson 2002). Furthermore, the specific effect of temperature will depend on a number of biotic factors that affect growth rate, such as food availability and haemoglobin genotype, both of which have been shown to underlie thermal

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Table 1. Summary statistics for number of tags deployed and DST temperature records successfully downloaded. (*T*, temperature (°C); s.d., standard deviation.)

region	release site	number of tags deployed	number of cod recaptured	number of tags with data returned	number of days at liberty	longest record (days)	min <i>T</i>	max <i>T</i>	mean <i>T</i>	s.d. <i>T</i>
southern North Sea	eastern channel	49	6	6	470	280	9.74	18.48	15.27	1.64
	Flamborough	54	16	10	650	308	5.49	9.17	7.41	0.69
	German Bight	100	8	6	1895	540	2.03	17.2	8.37	2.85
	southern Bight	209	65	64	5131	308	5.07	19.45	11.42	3.71
sub total		412	95	86	8146	540	2.03	19.45	10.61	3.79
northern North Sea	east Shetland	30	7	6	2280	909	6.86	14.36	9.52	1.91
	west Shetland	138	39	32	3674	337	6.27	13.29	9.08	1.84
	Moray Firth	94	5	3	233	131	6.85	9.61	7.79	0.85
	Viking Bank	7	3	2	278	152	5.64	8.51	7.63	1.86
sub total		269	54	43	6465	909	5.64	14.36	8.51	1.43
grand total		681	149	129	14 611					

preference in cod (Petersen & Steffensen 2003). Nevertheless, cod clearly has thermal distribution limits and, being a highly mobile species (Robichaud & Rose 2004), individuals would be expected to move either horizontally or vertically in order to remain at or close to a temperature optimal for growth.

In the face of global warming, cod populations are predicted to retreat from warmer areas and expand into cooler areas on yearly (Blanchard *et al.* 2005) or decadal time-scales (Drinkwater 2005) within certain constraints to movements (Heessen & Daan 1994). Cod are known to be capable of moving distances in excess of the dimensions of the North Sea (approx. 1000 km; Robichaud & Rose 2004). In theory, therefore, individual cod could occupy almost any location within the North Sea. Cod in the North Sea are probably not as vagile as this, however, and conventional mark and recapture experiments (Robichaud & Rose 2004; Wright *et al.* 2006a; Righton *et al.* 2007) and genetic evidence (Hutchinson *et al.* 2001) suggest that populations from the northern North Sea (further than 57° N) do not intermix significantly with those from the southern North Sea (below than 56° N). Within these areas, however, we expect cod to maximize their exposure to the most suitable thermal habitat. Previous studies addressing thermal influences on fish distribution (Heessen & Daan 1994; Blanchard *et al.* 2005; Perry *et al.* 2005) have been derived from surveys that cut across large (thousands of kilometres) geographical areas and long (decadal) temporal scales. Such studies are insensitive to short-term, individual and regional variations in distribution. This can be a problem when addressing distribution patterns of spatially structured stocks such as cod (Hutchinson *et al.* 2001; Metcalfe 2006; Wright *et al.* 2006b) or species like cod that show high individual variability in migratory behaviour (Righton *et al.* 2001; Pálsson & Thorsteinsson 2003; Neat *et al.* 2006). Direct, individual-based evidence for thermal responses in fishes in the field is largely lacking and the consequences that individual behaviour could have for population-level range shifts have not been assessed.

The most direct means of evaluating whether or not cod actively moderate the range of temperatures they

encounter is by comparing the temperatures experienced by individual cod with the range of temperatures available to them in their habitat. To this end, we attached electronic data storage tags (DSTs) to several hundred individual cod in the North Sea to record the temperatures they experienced while at liberty (Metcalfe & Arnold 1997). We compared the temperature experience of individual cod released at a number of locations throughout the North Sea between 1999 and 2005 with contemporaneous, independently collated hydrographic data for the region. Our study aimed to assess the extent to which cod occupy the thermal habitat potentially available to them. We predicted that if cod select thermal habitat to maximize growth rates, they should avoid superoptimal temperatures by seeking cooler waters and that this should be evidenced by the DST records.

2. MATERIAL AND METHODS

(a) Data storage tags

Between 1999 and 2004, cod greater than 30 cm in length were captured in the North Sea from approximately 51° N in the south to 61° N in the north (table 1) and implanted with a DST. We used the 'LTD_1200' or 'LTD_1400' DST manufactured by Lotek Marine Technologies (Canada) or 'Centi' or 'Milli' DST manufactured by Star-Oddi Marine Device Manufacturing (Iceland). The DSTs recorded temperature to an accuracy of at least 0.1°C and a precision of at least 0.03°C. DSTs were programmed to record pressure and temperature every 10 or 20 min.

Since the southern and northern regions of the North Sea are physically and ecologically different and historical tagging experiments suggest a very limited mixing of cod between the two regions, we maintained this division in the design of our tagging experiment. Tagging was conducted during the autumn or spring and targeted locations were thought to contain discrete spawning groups based on past tagging studies and more recent genetic studies (table 1). Details of fish capture and tagging techniques can be found in Neat *et al.* (2006) and Righton *et al.* (2006). In brief, cod were captured by handline or with a modified trawl, anaesthetized and a DST implanted into the body cavity or attached externally

to the dorsal musculature, and released. The long-term (more than 1 year) effect of tags on growth has been found to be negligible (Righton *et al.* 2006). All work was carried out under UK Home Office regulations (Animals (Scientific Procedures) Act 1986).

(b) *Data sources and treatment*

Temperature records from returned DSTs were downloaded and summarized to give daily averages per individual. These data were then used to derive monthly median values for each of the release sites and for each region as a whole. For each region, the range and interquartile range (25–75%) were calculated. For comparison with seabed temperature data, we used data from cod released in the Southern Bight ($n=64$) and west of Shetland ($n=32$), because these were most representative of each area in terms of numbers of cod at liberty and coverage throughout the year.

Data from the International Council for the Exploration of the Sea (ICES) conductivity and temperature at depth (CTD) database were used to estimate seabed temperatures in each region during the years that the cod were at liberty. The two regions were bounded by 4° W to 4° E and 57° N to 61° N in the north (figure 1a) and by 1° W to 8° E and 51° N to 56° N in the south (figure 1b). These boundaries were selected to encompass suitable depth habitat for cod and typical cod home ranges inferred from conventional tagging studies (Robichaud & Rose 2004; Wright *et al.* 2006a; Righton *et al.* 2007). The data were filtered by a depth limit of 300 m to coincide with the greatest depth experienced by a tagged cod (298 m). For each region, the CTD data were inspected for trends across the period of study (1999 through 2002 in the south and 2002 through 2004 in the north) using multifactorial ANOVA (quarter, year and their interaction). While significant differences ($p < 0.01$) were detected between some quarters and years, there was no consistent trend in seabed temperature. The CTD data were thus pooled across years to achieve a better spatial coverage and split into quarters of the year. Temperature surfaces were created for each region and quarter of the year by interpolation with a long-range spherical (northern North Sea) or linear (southern North Sea) Kriging function. In the northern North Sea, a total of 1878 sample points between 2002 and 2005 gave good spatial (figure 1a) and temporal coverage for each quarter of the year with root mean square (RMS) less than 1°C in all the key areas. In the southern North Sea, despite 2256 sample points between 1999 and 2004, the CTD sampling stations in the waters between 50 and 53° N were widely spaced and relatively infrequently sampled (figure 1b), leading to high error estimates (RMS error > 1°C) in poorly sampled areas. To counter this, the southern North Sea region was gridded into cells of 10' north to south and 20' east to west and daily seabed temperature values for 1999, 2001 to 2003 (data for 2000 were not available) from a variant of the Princeton Ocean Model (Young 2002; Young *et al.* 2003) were used to populate those grid cells for which there were no CTD casts in a given quarter. Average temperature values were then calculated for each grid cell for each quarter. RMS was less than 1°C at any point in the resulting surfaces.

The area of seabed at each 0.5°C increment was calculated from the quarterly temperature surfaces, and a frequency distribution generated. Based on the proportion of the seabed within each 0.5°C temperature interval, the number of days equivalent to that for which DST data were available was calculated. Then for each region, the frequency distribution of seabed temperature days was compared with the frequency

distribution of DST temperature days. The Kolmogorov–Smirnov test for two samples was used to test for differences between the cumulative frequency distributions of seabed temperature and DST temperature.

3. RESULTS

(a) *DST recapture rates*

Out of 149 cod that were recaptured, 129 DSTs were returned and successfully downloaded (table 1). Forty-three of these tags were returned from the northern North Sea between 2002 and 2005 and yielded a total of 6465 days of temperature data. The longest record of temperature was 2.5 years (909 days) from a cod tagged east of Shetland. Eighty-six tags were returned from the southern North Sea from 1999 through 2004, and yielded 8146 days of temperature data. The longest record spanned 540 days from a cod tagged in the German Bight. During the 5 years of the study, data were available from at least six fishes at liberty in each region in each month of the year, peaking at 65 and 40 fishes in the southern North Sea and northern North Sea, respectively (figure 2a,b).

(b) *Annual thermal variation in the two regions*

In the northern North Sea, temperatures were at their lowest around March and rose to a peak in September (figure 2a). This pattern varied across the region due to a number of thermally distinct areas; the areas to the northwest and northeast are heavily influenced by Atlantic inflow and were generally warmer, whereas the centrally located Fladden grounds were relatively colder, especially so in summer (figure 1a). In the southern North Sea, temperature dropped to a minimum in February before rising until September (figure 2b). From June onwards, the water column became stratified in the areas where water depth exceeded 50 m (generally north of 54° latitude; figure 1b). This resulted in the temperature range reaching a maximum, as deep areas remained cool and shallow areas warmed as high as 19°C (figures 1b and 2b).

(c) *Temperature experience of cod*

The annual range of temperatures was greater for cod in the southern North Sea than in northern North Sea (table 1). Overall, however, the majority of temperature experiences of cod in both of the regions closely followed the upper seasonal trend of sea bottom temperature (figure 2a,b). In the northern North Sea, experienced temperatures rarely exceeded 14°C and the cod released west of Shetland inhabited the warmest fraction of the area, particularly during the warmer months of the year (figure 2a). No cod from west Shetland moved to cooler waters and the variance between individuals was very low. In contrast, individuals released to the east of Shetland and on Viking Bank showed abrupt movements into cold fronts and prolonged occupancy of cooler areas (figure 3a). One cod (DST_66; figure 3a) was at liberty over 2 full years and experienced a very different thermal environment in each. In the first year, when the cod remained resident to its release site, it experienced the same seasonal rise and fall as its conspecifics. In the second year, the cod migrated and experienced much lower average temperatures with no obvious seasonal trend.

In the southern North Sea, all but two individuals released in the Southern Bight (figure 2b) migrated short

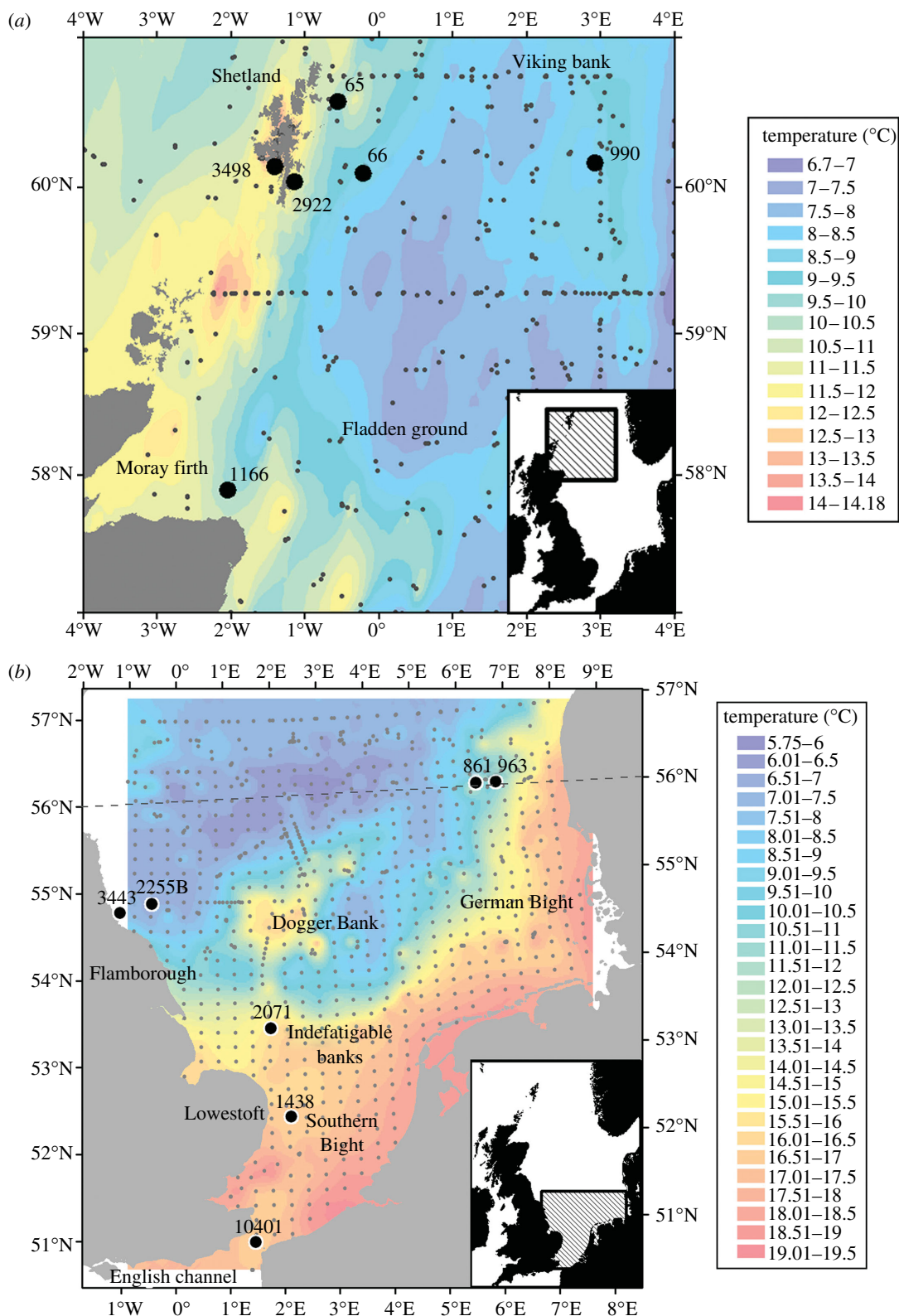


Figure 1. (a) Temperature surfaces for the seabed generated from CTD data for the northern North Sea in the third quarter of the year (July, August and September) averaged over 2002 to 2004. Black circles indicate recapture positions for cod profiled in figure 3a. Small grey circles show the location of CTD casts used to generate the temperature surface. Inset map shows the study area within the North Sea. (b) Equivalent plot for the southern North Sea for data averaged over 1999–2004. Black circles indicate summer location estimates for cod profiled in figure 3b. Small grey dots show the position of modelled data (regular grid) and CTD casts (outside the regular grid). Dashed grey line represents the northerly boundary of the region delimited as the southern North Sea.

distances and experienced temperatures well in excess of 14°C during late summer and autumn, with some experiencing temperatures up to 19°C (figure 3b). Individuals released in the English Channel also showed a similar

pattern (figure 3b), but individuals released in the German Bight experienced relatively low average temperatures in what appeared to be a more variable environment in the far north and east of the region (figure 3b). Although none of the

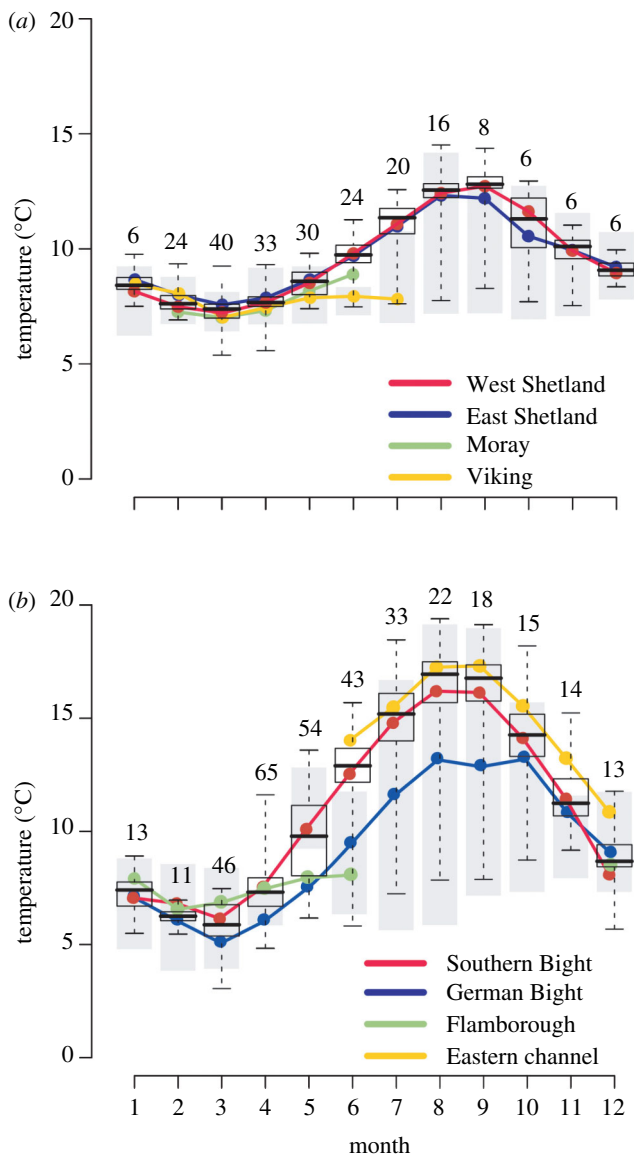


Figure 2. (a) Sea bottom temperatures and the monthly thermal experience of cod in the northern North Sea. The limits of the boxes show 25 (upper) and 75% (lower) quartile temperature ranges, while the black line shows the median temperature. Error bars/whiskers show the full range of the temperature experience. Numbers above the error bars indicate the number of cod at liberty during each month. Average monthly temperature experiences of cod from each release site are shown by colours. The range of CTD data in each month is represented by filled grey bars. (b) Same plot for the southern North Sea.

tagged cod released off Flamborough survived through to the end of the summer, they appeared to occupy lower than average temperatures (figure 3b). The lowest temperatures were experienced by the two individuals that were tagged off Lowestoft, but moved north into deeper water (more than 50 m) and by individuals tagged in the German Bight (figure 3b).

(d) Comparison of hydrographic data with DST data

In both regions of the North Sea, cooler water was available for the cod to move into during all quarters of the year except the first, when temperatures were low and relatively uniform (figure 4). In the northern region during the third and fourth quarters of the year, a large fraction of

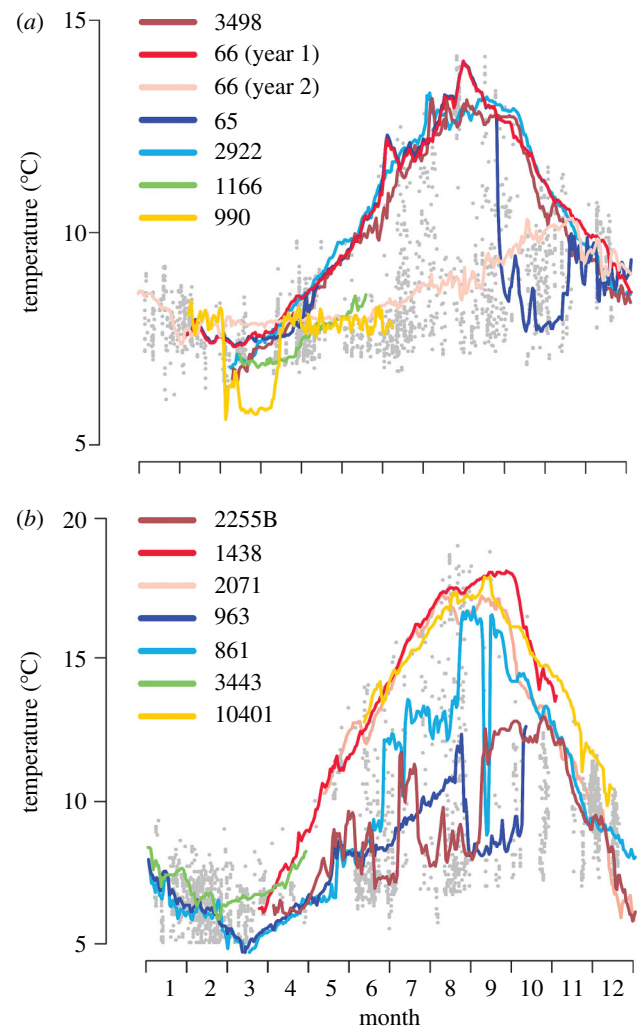


Figure 3. (a) Individual cases of DST records illustrating variation in the mean daily thermal experience of cod in the northern North Sea. The legend refers to the tag ID number: 3498 (west Shetland), 66, 65 and 2922 (east Shetland), 1166 (Moray Firth) 990 (Viking bank). (b) DST records from the southern North Sea. Tag ID numbers: 2255B, 1438, 2071 (Southern Bight), 963, 861 (German Bight), 3443 (Flamborough), 10401 (Eastern Channel). CTD data (daily resolution) are represented by filled grey dots.

the area, particularly around the Fladden ground (figure 1a), was cooler than the conditions that the majority of cod experienced. Cod released to the west of Shetland tended to be in the warmest fraction of water (figure 4), although this only approached statistical significance in the third quarter (table 2). In the southern North Sea, cooler areas were found in deep water north of 54° latitude (figure 1b). Most individuals, however, occupied the warm shallow waters in the south, and during the third and fourth quarters, they experienced significantly warmer temperatures than they would have done had they simply occupied a representative proportion of the thermal habitat available (figure 4, table 2).

4. DISCUSSION

The North Sea has warmed in recent decades and there is evidence to suggest that the geographical distributions of several fish species, including cod, have shifted north towards cooler waters (Beare *et al.* 2004; Perry *et al.* 2005; Rindorf & Lewy 2006). Not all evidence is consistent with

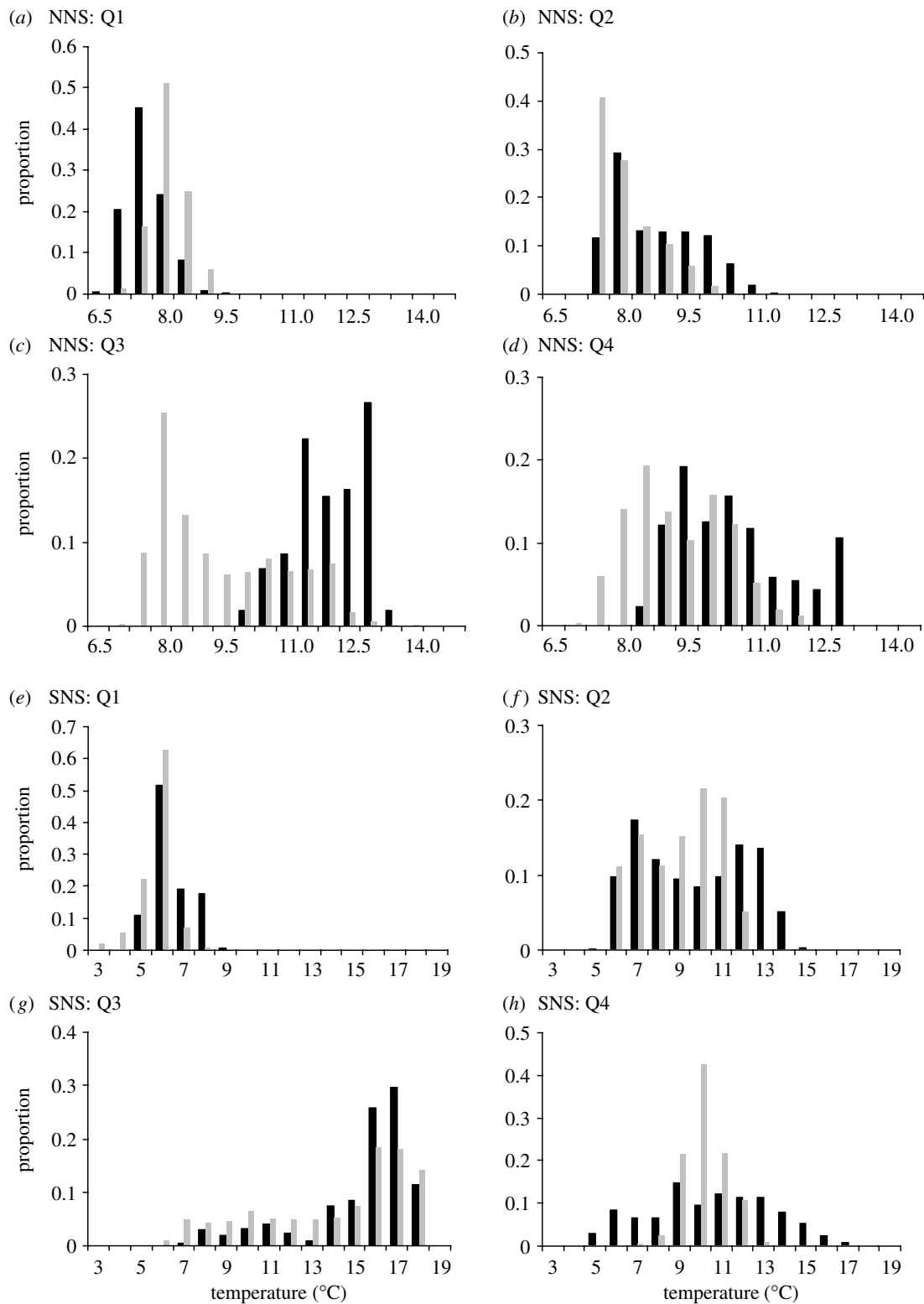


Figure 4. Frequency histograms representing proportion of DST data (black bars) and sea bottom data (grey bars) at 0.5°C intervals for each quarter (Q) of the year; (a)–(d) northern North Sea; (e)–(h) southern North Sea.

Table 2. Results of Kolmogorov–Smirnov tests (KS) on equivalent frequency distributions for the seabed temperatures and DST records for each quarter of the year (Q) for cod from the Southern Bight and west Shetland.

region	Q1	Q2	Q3	Q4
northern North Sea	KS = 0.28, $p=0.96$	KS = 0.33, $p=0.73$	KS = 0.46, $p=0.07$	KS = 0.18, $p=0.99$
southern North Sea	KS = 0.31, $p=0.58$	KS = 0.33, $p=0.19$	KS = 0.48, $p=0.003$	KS = 0.56, $p<0.001$

this scenario, however; Heessen & Daan (1994) observed that cod aged 3 and 4 years (equivalent to those in our study) tended to be found in higher numbers in the warmer fraction of the North Sea. The present study suggests that while cod were capable of finding cooler waters, the majority occupied the upper fraction of thermal habitat available. Although this does not contradict Perry *et al.*'s (2005) conclusion, we should consider why, if rising temperatures have pushed cod north, we did not observe any response to temperature at the individual level. Perry *et al.*'s (2005) and Rindorf & Lewy's (2006) data were drawn from across the entire North Sea. This can be a concern because there is mounting evidence that the North Sea cod stock shows a high level of population structure (Hutchinson *et al.* 2001; Metcalfe 2006; Wright *et al.* 2006b). What may seem like a distribution shift may, in fact, represent changes in the abundance and distribution of local populations as a consequence of the effects of population dynamics, fishing pressure and variation in migration (Hedger *et al.* 2004). The present study, however, being reliant on regionally explicit, individual-based data collected throughout the year, better captures the thermal habitat associated with the spatial dynamics of cod. If adult movement drives distribution shifts, then our data suggest that a shift has been unlikely and that the observation of Perry *et al.* (2005) is more likely to be explained by local depletion of cod in the south. If, on the other hand, cod has indeed shifted northward, our data suggest that the mechanism by which it has occurred is via recruitment or settlement rather than adult movement.

The northern and southern regions of the North Sea are hydrographically distinct. The northern region is strongly influenced by the Atlantic inflow (Turrell *et al.* 1992, 1996) and being deeper, has a lower and more stable thermal regime. Thermally distinct areas establish in the summer when the cooler water becomes isolated beneath a thermally stratified water column. In the south, where water depths rarely exceed 50 m, a high degree of mixing and a strong influence of continental air temperature lead to a highly variable thermal environment. The thermal variability across the two regions is clearly reflected in the DST records. At the extremes, a cod released in the Southern Bight experienced 14°C of annual temperature variation, whereas an individual released east of Shetland experienced less than a 3°C change over the year. In the shorter term, the greatest thermal variation (a 7°C decrease in temperature over 3 days, followed by a return to the previous temperature over 2 days) was experienced by cod in the German Bight during summer, where they occupied water at the interface of the stratified and mixed regions of the southern/central North Sea. Across the entire North Sea, however, it is the cod in the south that should be the most likely to exhibit behavioural thermoregulation and move north or into cool deep waters.

A key assumption in our argument is that the cod had the capacity to occupy any location within the delimited areas. In a week or two after release, the temperatures experienced will be locally biased to conditions within the vicinity of the release site. However, cod, like other large demersal fish species, e.g. plaice (Hunter *et al.* 2004) and sea bass (Pawson *et al.* 1987), is a highly mobile species capable of long migrations between feeding and spawning grounds (Robichaud & Rose 2004). Historical records of the tagged adult cod in the North Sea suggest average

movement rates of 0.5 km per day and up to 11 km per day in the northern North Sea (Wright *et al.* 2006a), and movements rates of more than 1.5 km per day and up to 30 km per day in the southern North Sea (with a maximum distance between release and recapture of more than 650 km; Righton *et al.* 2007). In either region, cod needed to move only in the region of 50–200 km to find cooler water. Therefore, given the number of cod at liberty (129) and the number of days of observation in this study (nearly 15 000), we would expect that if the cod had cause to move to cooler water they had sufficient opportunity to do so. They did not, and so occupied the upper range of temperatures that were potentially available to them. This result is perhaps not surprising for cod from the northern North Sea where summer temperatures were rarely above 13°C, but many cod in the southern North Sea experienced periods of up to four months in temperatures (above 15°C) considered detrimental for adult growth (Jobling 1988). While a small number of individuals did move in such a way that caused them to experience a significantly lower range of temperatures, this really only serves to reinforce our assumption that the cooler waters were available for occupancy.

Our sampling of North Sea cod was inevitably biased by higher returns in some areas than in others for a variety of reasons including number of tags released and differences in fishing effort across the North Sea. As a consequence, the temperature experienced by the cod may have been biased by the propensity of the particular spawning group to migrate (Robichaud & Rose 2004). Cod in the southern North Sea show a range of migratory behaviours; off Flamborough, the German Bight and the Eastern Channel, they are largely resident, whereas Southern Bight cod can be highly migratory (Hutchinson *et al.* 2001; Robichaud & Rose 2004). Similarly, in the north, cod on the west of Shetland appear to be strongly site-attached throughout the year (Neat *et al.* 2006), whereas those on the east side are a mixture of residents and migrants (Wright *et al.* 2006b). However, this variability was equally represented in our study, and since cod tagged in the Southern Bight were especially well represented and they were the group predicted to migrate to avoid warm temperatures, this should not be a serious concern.

This lack of observed thermal response can be interpreted in a number of ways. First, that temperature is not the primary driver for cod habitat choice. Other biotic factors, such as prey availability, density-dependent effects (Swain 1999; Swain *et al.* 2003; Blanchard *et al.* 2005) and demographic change (Ottersen *et al.* 2006) may have important consequences for cod distribution and behaviour (Righton *et al.* 2001). Since the abundance of cod in the North Sea has remained below biologically safe limits since 1999, it is possible that reduced competition for habitat and food resources reduces movement rates and thereby influences habitat choice. Blanchard *et al.* (2005), however, suggest that cod are more likely to occupy the most suitable habitat when abundance is low. Addressing this issue seriously, however, would require reconstruction of the long-term feeding patterns of the individual fishes, which is not yet possible (Righton *et al.* 2001). Second, the costs of searching for and finding a narrow range of optimal temperatures in a highly variable environment like the North Sea may outweigh the benefits of finding them. Our knowledge of how fishes detect

thermal gradients, or gradients in other aspects of their environment, is limited (Brown 2003; Sims *et al.* 2006). Our data show that fishes at different times of the year and in different areas of the North Sea can experience sometimes very similar and sometimes very different thermal conditions. This illustrates the temporal and spatial complexity of the thermal habitat and suggests that simple search strategies to find suitable temperatures would not necessarily succeed. Third, thermal tolerance and optima may have been inadequately described by laboratory experiments; natural or regional variance in thermal tolerance of cod may permit residence in apparently unsuitable areas. Studies of haemoglobin genotypes have shown that the Hb1-1 genotype is associated with warm water preference in juvenile cod (Petersen & Steffensen 2003) and the Hb1-1 allele is found at its highest frequency in cod from warmer areas, particularly the southern North Sea (Sick 1965; Husebø *et al.* 2004). Unfortunately, we were not able to determine Hb genotype of the tagged cod due to the difficulties of undertaking the analysis at sea and our concern that blood sampling may have compromised the survival of tagged fishes. Growth of cod of all Hb genotypes appears to be optimized at 14°C (Jordan *et al.* 2006). However, recent evidence suggests that the ability of cod to extract oxygen from seawater is maximized at around 12°C, regardless of Hb genotype (Colosimo *et al.* 2003). Combined, these studies suggest that cod in water significantly warmer than 14°C should benefit by moving to cooler water.

The North Sea is predicted to gradually warm for the next 50 years (Clark *et al.* 2003). If this will further exacerbate the decline of North Sea cod, this study concurs with conclusions of Heessen & Daan (1994), O'Brien *et al.* (2000), Beaugrande *et al.* (2003) and Ottersen *et al.* (2006) by suggesting that the mechanism by which it occurs must be at the level of recruitment or early settlement rather than adult behaviour. Our finding is also consistent with fishing mortality on cod in southern areas having been higher and as a consequence caused the distribution to contract in the south. There is a growing consensus that the North Sea cod stock is spatially structured (Hutchinson *et al.* 2001; Yoneda & Wright 2004; Wright *et al.* 2006a) and this study suggests that the cod populations it supports experience quite different thermal environments. We might therefore expect these populations to show different thermal tolerances and growth responses. Our data provide the first direct measurements of the temperature experienced by cod in the North Sea and as such provide an assessment of the occupancy of thermal habitat that accounts for spatial structuring and individual variation. They do not suggest any consistent pattern with respect to thermally selective behaviour or movement; therefore, they do not support the idea that adult cod are being forced north by rising sea temperatures.

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REFERENCES

- Beare, D., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E. & Reid, D. 2004 An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biol.* **10**, 1209–1213. (doi:10.1111/j.1529-8817.2003.00790.x)
- Becker, G. A. & Pauly, M. 1996 Sea surface temperature changes in the North Sea and their consequences. *ICES J. Mar. Sci.* **53**, 887–898. (doi:10.1006/jmsc.1996.0111)
- Beaugrande, G., Brander, K. M., Lindley, J. A., Souissi, S. & Reid, P. C. 2003 Plankton effect on cod recruitment in the North Sea. *Nature* **426**, 661–664. (doi:10.1038/nature02164)
- Bjornsson, B., Steinarsson, A. & Oddgeirsson, M. 2001 Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). *ICES J. Mar. Sci.* **58**, 29–38. (doi:10.1006/jmsc.2000.0986)
- Björnsson, B. & Steinarsson, A. 2002 The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **59**, 494–502. (doi:10.1139/f02-028)
- Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D. & O'Brien, C. M. 2005 Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. *Can. J. Fish. Aquat. Sci.* **62**, 2001–2009. (doi:10.1139/f05-109)
- Boutilier, R. G. 1998 Physiological ecology in cold ocean fisheries: a case study in Atlantic cod. In *Cold ocean physiology* (eds H. O. Pörtner & R. C. Playle), pp. 463–469. Cambridge, UK: Cambridge University Press.
- Brown, B. R. 2003 Sensing temperature without ion channels. *Nature* **421**, 495. (doi:10.1038/421495a)
- Brander, K. M. 1995 The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES J. Mar. Sci.* **52**, 1–10. (doi:10.1016/1054-3139(95)80010-7)
- Christensen, V., Guénette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D. & Pauly, D. 2003 Hundred year decline of North Atlantic predatory fishes. *Fish Fish.* **4**, 1–24.
- Claireaux, G., Webber, D. M., Lagardère, J.-P. & Kerr, S. R. 2000 Influence of water temperature and oxygenation on the aerobic metabolic scope of Atlantic cod (*Gadus morhua*). *J. Sea Res.* **44**, 257–265. (doi:10.1016/S1385-1101(00)00053-8)
- Clark, R. A., Fox, C. J., Viner, D. & Livermore, M. 2003 North sea cod and climate change—modelling the effects of temperature on population dynamics. *Global Change Biol.* **9**, 1669–1680. (doi:10.1046/j.1365-2486.2003.00685.x)
- Colosimo, A., Giuliani, A., Maranghi, F., Brix, O., Thorkildsen, S., Fischer, T., Knust, R. & Poertner, H. O. 2003 Physiological and genetical adaptation to temperature in fish populations. *Cont. Shelf Res.* **23**, 1919–1928. (doi:10.1016/j.csr.2003.06.012)
- Cook, R. M., Sinclair, A. & Stefánsson, G. 1997 Potential collapse of North Sea cod stocks. *Nature* **385**, 521–522. (doi:10.1038/385521a0)
- Daan, N., Heesen, H. J. L. & Pope, J. 1994 Changes in the North Sea cod stock during the twentieth century. *ICES Mar. Sci. Symp.* **198**, 229–243.
- Drinkwater, K. 2005 The response of Atlantic cod to future climate change. *ICES J. Mar. Sci.* **62**, 1327–1337. (doi:10.1016/j.icesjms.2005.05.015)
- Groeneveld, J. C. & Branch, C. M. 2002 Long distance migration of South African deep water rock lobster *Palinurus gilchristi*. *Mar. Ecol. Prog. Ser.* **232**, 225–238.

- Hedger, R. E., McKenzie, E., Heath, M., Wright, P. J., Scott, B., Gallego, A. & Andrews, J. 2004 Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using general additive modelling. *Fish Res.* **70**, 17–25. (doi:10.1016/j.fishres.2004.07.002)
- Heessen, H. & Daan, N. 1994 Cod distribution and temperature in the North Sea. *ICES Mar. Sci. Symp.* **198**, 244–253.
- Hislop, J. R. G. 1996 Changes in the North Sea gadoid stocks. *ICES J. Mar. Sci.* **53**, 1146–1156. (doi:10.1006/jmsc.1996.0140)
- Horwood, J., O'Brien, O. & Darby, C. 2006 North Sea cod recovery? *ICES J. Mar. Sci.* **63**, 961–968. (doi:10.1016/j.icesjms.2006.05.001)
- Hughes, S. L., Turrell, W. R. & Newton, A. 2003 Hydrobiological variability on the northwest European continental shelf during the 1990s and its relation to changes in fish stocks. *ICES Mar. Sci. Symp.* **219**, 421–425.
- Hulme, M. *et al.* 2002. Climate change scenarios for the United Kingdom: the UKCIP02 scientific report. Tyndall Centre for Climate Change Research, Norwich.
- Hunter, E., Metcalfe, J. D., Holford, B. H. & Arnold, G. P. 2004 Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables II. Reconstruction of plaice ground tracks. *Mar. Biol.* **144**, 787–798. (doi:10.1007/s00227-003-1242-1)
- Husebø, Å., Imsland, A. K. & Nævdal, G. 2004 Haemoglobin variation in cod: a description of new variants and their geographical distribution. *Sarsia* **89**, 369–378. (doi:10.1080/00364820410002631)
- Hutchinson, W. F., Carvalho, G. R. & Rogers, S. I. 2001 Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters as revealed by microsatellites. *Mar. Ecol. Prog. Ser.* **223**, 251–260.
- ICES 2006 ICES report on ocean climate 2005. *ICES Cooperative Res. Report* **280**, 1–47.
- Jennings, S., Alvsvåg, J., Cottera, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., Rijnsdorp, A. D. & Smedstad, O. 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. *Fish. Res.* **40**, 125–134. (doi:10.1016/S0165-7836(98)00208-2)
- Jobling, M. 1988 A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. *Aquaculture* **70**, 1–19.
- Jordan, A. D., Lampe, J. F., Grisdale-Helland, B., Helland, S. J., Shearer, K. D. & Steffansen, J. F. 2006 Growth of Atlantic cod (*Gadus morhua* L.) with different haemoglobin subtypes when kept near their temperature preference. *Aquaculture* **257**, 44–52. (doi:10.1016/j.aquaculture.2006.03.015)
- Kaiser, M. J., Collie, J. S., Hall, S. J., Jennings, S. & Poiner, I. R. 2002 Modification of marine habitats by trawling activities: prognosis and solutions. *Fish Fish.* **3**, 114–136.
- Lannig, G., Bock, C., Sartorius, F. J. & Portner, H. O. 2004 Oxygen limitation of thermal tolerance in cod, *Gadus morhua* L., studied by magnetic resonance imaging and on-line venous oxygen monitoring. *Am. J. Physiol.* **287**, R902–R910.
- Meehl, G. A., Washington, W. M., Collins, W. D., Arblaster, J. M., Hu, A., Buja, L. E., Strand, W. G. & Teng, H. 2005 How much more global warming and sea level rise? *Science* **307**, 1769–1772. (doi:10.1126/science.1106663)
- Metcalfe, J. D. 2006 Fish population structuring in the North Sea: evidence, processes and mechanisms. *J. Fish. Biol. Suppl. C*, 48–65.
- Metcalfe, J. D. & Arnold, G. P. 1997 Tracking fish with electronic tags. *Nature* **387**, 665–666. (doi:10.1038/42622)
- Metcalfe, J. D., Arnold, G. & McDowall, R. 2002 Migration. In *Handbook of fish biology & fisheries*, vol. 1 (eds P. J. B. Hart & J. D. Reynolds), pp. 175–199. Oxford, UK: Blackwell Scientific.
- Neat, F. C., Wright, P. J., Zuur, A. F., Gibb, I. M., Gibb, F. M., Tulett, D., Righton, D. A. & Turner, R. J. 2006 Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). *Mar. Biol.* **148**, 643–654. (doi:10.1007/s00227-005-0110-6)
- O'Brien, C. M. C., Fox, J., Planque, B. & Casey, J. 2000 Climate variability and North Sea cod. *Nature* **404**, 142. (doi:10.1038/35004654)
- Ottersen, G., Hjermann, D. O. & Stenseth, N. Chr. 2006 Changes in the spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fish. Oceanogr.* **15**, 230–243. (doi:10.1111/j.1365-2419.2006.00404.x)
- Pálsson, O. K. & Thorsteinsson, V. 2003 Migration patterns, ambient temperature and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. *Can. J. Fish. Aquat. Sci.* **60**, 1409–1423. (doi:10.1139/f03-117)
- Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- Pawson, M. G., Kelley, D. F. & Pickett, G. D. 1987 The distribution and migrations of bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by tagging. *J. Mar. Biol. Assoc. UK* **67**, 183–217.
- Pedersen, T. & Jobling, M. 1989 Growth rates of large, sexually mature cod *Gadus morhua*, in relation to condition and temperature during an annual cycle. *Aquaculture* **81**, 161–168. (doi:10.1016/0044-8486(89)90242-1)
- Perry, A. L., Lowe, P. J., Ellis, J. R. & Reynolds, J. D. 2005 Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915. (doi:10.1126/science.1111322)
- Petersen, M. F. & Steffensen, J. F. 2003 Preferred temperature of juvenile Atlantic cod *Gadus morhua* with different haemoglobin genotypes under normoxia and moderate hypoxia. *J. Exp. Biol.* **206**, 359–364. (doi:10.1242/jeb.00111)
- Righton, D., Metcalfe, J. & Connolly, P. 2001 Different behaviour of cod in the North and Irish Seas. *Nature* **411**, 156. (doi:10.1038/35075667)
- Righton, D., Kjesbu, O. S. & Metcalfe, J. 2006 A field and experimental evaluation of the effects of data storage tags on the growth of cod. *J. Fish Biol.* **68**, 385–400. (doi:10.1111/j.0022-1112.2006.00899.x)
- Righton, D., Quayle, V., Hetherington, S. & Burt, G. 2007 Movements and distribution of cod in the southern North sea and English Channel: results from conventional and electronic tagging experiments. *J. Mar. Biol. Assoc.*
- Rindorf, A. & Lewy, P. 2006 Warm, windy winters drive cod North and homing of spawners keeps them there. *J. Appl. Ecol.* **43**, 445–453.
- Robichaud, D. & Rose, G. A. 2004 Migratory behaviour and range in the Atlantic cod: inference from a century of tagging. *Fish Fish.* **5**, 185–214.
- Rose, G. A. 2004 Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Can. J. Fish. Aquat. Sci.* **61**, 1553–1557. (doi:10.1139/f04-173)
- Sick, K. 1965 Haemoglobin polymorphism of cod in the North Sea and North Atlantic Ocean. *Hereditas* **54**, 49–69.

- Sims, D. W., Genner, M. J., Southward, A. J. & Hawkins, S. J. 2001 Timing of squid migration reflects North Atlantic climate variability. *Proc. R. Soc. B* **268**, 2607–2611. (doi:10.1098/rspb.2001.1847)
- Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J. & Metcalfe, J. D. 2006 Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proc. R. Soc. B* **273**, 1195–1201. (doi:10.1098/rspb.2005.3444)
- Sundby, S. 2000 Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* **85**, 277–298.
- Swain, D. P. 1999 Changes in the distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence—effects of environmental change or change in environmental preferences? *Fish. Oceanogr.* **8**, 1–17. (doi:10.1046/j.1365-2419.1999.00090.x)
- Swain, D. P., Sinclair, A. F., Castonguay, M., Chouinard, G. A., Drinkwater, K. F., Fanning, L. P. & Clark, D. S. 2003 Density versus temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence and on the Scotian Shelf. *Fish. Res.* **59**, 327–341. (doi:10.1016/S0165-7836(02)00027-9)
- Turrell, W. R., Henderson, E. W., Slessor, G., Payne, R. & Adams, R. D. 1992 Seasonal changes in the circulation of the northern North Sea. *Cont. Shelf Res.* **12**, 257–286. (doi:10.1016/0278-4343(92)90032-F)
- Turrell, W. R., Slessor, G., Payne, R., Adams, R. D. & Gillibrand, P. A. 1996 Hydrography of the East Shetland Basin in relation to decadal North Sea variability. *ICES J. Mar. Sci.* **53**, 899–916. (doi:10.1006/jmsc.1996.0112)
- Wright, P. J., Galley, E., Gibb, I. M. & Neat, F. C. 2006a Fidelity of adult cod to spawning grounds in Scottish waters. *Fish. Res.* **77**, 148–158. (doi:10.1016/j.fishres.2005.10.008)
- Wright, P. J., Neat F. C., Gibb F. M., Gibb, I. M. & Thordarson, H. 2006b Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J. Fish Biol. Suppl. C*, 181–199.
- Yoneda, M. & Wright, P. J. 2004 Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. *Mar. Ecol. Prog. Ser.* **276**, 237–248.
- Yoneda, M. & Wright, P. J. 2005 Effects of varying temperature and food availability on growth and reproduction in first-time spawning female Atlantic cod. *J. Fish Biol.* **67**, 1225–1241. (doi:10.1111/j.1095-8649.2005.00819.x)
- Young E. F. 2002 Tidal validation of a three-dimensional primitive equation model for the North Sea region. CEFAS internal report, Pakefield Rd, Lowestoft, UK.
- Young, E. F., Brown, J., Aldridge, J. N., Horsburgh, K. J. & Fernand, L. 2003 Development and application of a three-dimensional baroclinic model to the study of the seasonal circulation in the Celtic Sea. *Cont. Shelf Res.* **24**, 13–36. (doi:10.1016/j.csr.2003.09.003)