TEMPERATURE DEPENDENT GROWTH AND DISTRIBUTION OF COD IN THE NORTH SEA

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1. SUMMARY

The temperature of the North Sea is a highly variable and is postulated to be a major determinant of growth rates in cod. Recent evidence also suggests that there are a number of cod populations within the North Sea. This report reviews recent evidence from laboratory studies of cod growth in relation to temperature and population source and the results of temperature experience and growth rates of wild cod captured and released with electronic data storage tags. The combined studies suggest that growth increases with temperature up to approximately 13 °C after which it plateaus and then declines. Cod originating from different areas appear to have different intrinsic growth rates. The report thus concludes that both temperature and region of origin are significant determinants of growth rate in cod.

2. INTRODUCTION

The North Sea is the most thermally variable marine ecosystem within which the Atlantic cod is found, ranging from 2 °C in some areas by the end of the winter to 19 °C by the end of the summer. Temperature influences vital processes in fishes such as growth rate (Pedersen and Jobling 1989; Bjornsson et al. 2001; Bjornsson & Steinarsson 2002), metabolic rate (Claireux et al. 2000; Lannig et al. 2004) and maturation (Yoneda & Wright 2005). Therefore we might expect large variance in growth rates of cod throughout the year and across the North Sea. 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 to (Pedersen & Jobling 1989; Bjornsson et al. 2001; Bjornsson & 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 preference in cod (Petersen & Steffensen 2003). There is a growing consensus that the North Sea cod stock is spatially structured (Hutchinson et al. 2001; Yoneda & Wright 2004; Wright et al. 2006). This would suggest that the constituent populations should experience different thermal environments. We might therefore expect these populations to show different thermal tolerances and growth responses. Until now, little information has been available to assess this potentially important issue.

Here we present and review recent evidence from laboratory and field studies of cod growth in relation to temperature and population source. First, a series of laboratory growth trials of cod from different regions is reported in which temperature was manipulated while controlling for factors such as food availability and density. Second, the results of a joint data storage tagging programme between FRS and CEFAS in which actual temperature experiences of cod throughout the North Sea were recorded. These data were analysed with respect to the thermal variability of the North Sea in order to assess the degree to which cod differentially occupy thermal habitat. Information on growth rates of these tagged individuals was investigated with respect to their known thermal experience.
3. LABORATORY GROWTH OF ADULT COD IN RELATION TO TEMPERATURE

Although cod tolerate temperatures as low as -1 °C and as high as 19 °C the range of temperatures that maximizes the scope for growth will be somewhere in between. The relationship between temperature and growth is predicted to be dome-shaped. Making specific predictions about growth requires an understanding of the precise shape of this relationship. For example, there may be a broad range of temperatures that facilitate good growth or there may be a very narrow range. In order to better understand this relationship, growth trials were undertaken on pre-spawning cod across the range of temperatures they would normally experience in Scottish waters.

Twenty cod from a cohort of cultured stock were used in the trial. Mean length of fish was 43 (± 4.2) cm at the start and 48 (± 4.8) cm by the end of the trial (n = 20). The temperature declined steadily by approximately 2 °C each fortnight from on average (± SD) 15.8 ± 0.3, 13.6 ± 0.4, 11.3 ± 0.5, 9.1 ± 0.4, 6.9 ± 0.5, 4.6 ± 0.3 °C. Fish were fed to excess so that food intake was not a constraint to growth. Photoperiod was set or 8 L:16 D according to late autumn/winter in high Scottish latitudes. At the end of each fortnightly treatment, the fish were weighed and measured and the daily specific growth rate (SGR) calculated as:

$$SGR = \frac{\ln(W_2) - \ln(W_1)}{D} \cdot 100$$

Where \(W_1\) and \(W_2\) are the weights at the beginning and end of the fortnight and \(D\) = number of days between weighing events (=14).

The effect of temperature on growth rate was investigated using a linear mixed model. Mixed models extend standard linear models by allowing for random effects, here differences between fish, which are not of prime interest themselves, but must be accounted for when making inferences about the fixed effects of interest (temperature). Specific growth rate at 4.6°C was significantly lower than that at 6.9°C, but there was no consistent difference in the specific growth rates between 6.9°C and 13.6 °C, although growth declined significantly again at 15.8 °C (Figure 1). This suggests that there is a broad range of temperature in which cod attains good growth rates and it is only below 7 °C and above 14 °C that growth is significantly impaired.
Figure 1: Summary plot of mean daily specific growth rate (SGR) of cod for each fortnight at different temperatures. A line of best fit is shown for reference, but significance should not be placed on this due to the repeated measures nature of this experiment.
4. DIFFERENCES IN GROWTH OF JUVENILE COD FROM 2 SCOTTISH REGIONS

Controlled environment experiments were carried out to investigate thermal and population influences on growth in juvenile Atlantic cod *Gadus morhua* L. from two Scottish regions with a differing thermal regime. Juvenile 0-group cod were collected from the east and the west coast of Scotland. The two sample sites were St Andrews Bay (56° 21.6” N 2° 44.0” W) on the Scottish east coast and the Clyde Sea (55° 43.15” N, 4° 54.9” W) on the south west coast of Scotland. A series of growth trials were undertaken in order to test whether the populations differed from one another and how this varied with temperature. Details of the study can be found in Perutz *et al.* (submitted).

Linear mixed effects models were used to analyse the data. Cod from the Clyde Sea had a significantly higher growth rate than those from St Andrews Bay between 8 and 12°C. The growth rate of cod from both areas increased linearly and in parallel with temperature (Figure 2).

Figure 2: Specific growth rate of juvenile cod from the east coast (unfilled circles) and west coast of Scotland (filled circles) at different temperatures. Lines of best fit (solid = west coast, dashed = east coast) are shown for reference but significance should not be attached due to the repeated measures design of these experiments (data from Perutz *et al.* submitted).
These experiments suggest there are significant population differences in growth and that temperature had a significant but equal effect on both populations. Clyde Sea cod may have a higher genetic capacity for growth than St. Andrews Bay cod. The positive effect of temperature on growth rate is well documented (Brander, 1995; Purchase and Brown, 2001). The positive linear trend in growth rate with temperature, indicates that the range of temperatures (8-12 °C) at which the experiment was conducted was less than or at their optimal temperature for growth.

5. THERMAL EXPERIENCE OF WILD COD ACROSS THE NORTH SEA

A tag-recapture programme of cod was undertaken jointly by FRS and CEFAS between 1999 and 2005 using data storage tags (DSTs) that recorded the temperature and depth experience of free ranging cod. The project was funded in part by 2 EU contract projects; Codyssey and Metacod in addition to MF0756. Tagging was conducted during the autumn or spring and targeted locations thought to contain discrete spawning groups based on past tagging studies and more recent genetic studies. Details of techniques can be found in Neat et al. (2006), Righton et al. (2006) and Neat & Righton (2007). In order to compare the temperature experienced by the fish with that potentially available to the fish it was necessary to estimate seabed temperatures in each region. Data from the ICES CTD database was used to estimate sea bed temperatures in each region during the years that the cod were at liberty. The North Sea was split into two regions bounded by 4 °W to 4 °E and by 57 °N to 61 °N in the north (Figure 3a) and by 1 °W to 8 °E and by 51 °N to 56 °N in the south (Figure 3b). Temperature surfaces were created for each region and quarter of the year.

Figure 3: (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.
Figure 4: The left hand plot shows the proportion of the seabed at each 0.5 °C interval for the northern North Sea in the third quarter of the year between 2002-2004. Coloured bars indicate temperatures > 13 °C considered detrimental to cod growth. The right hand plot shows the same information for the southern North Sea for years 1999-2004.

Figures 3 (b) and 4 demonstrate that by the third quarter of the year a large portion of the southern North Sea was warmer than 13 °C suggesting it may be detrimental to growth of cod. By contrast in the northern North Sea only a tiny fraction of the sea area was warmer than 13 °C. In order to see if the cod tagged with DSTs were avoiding warm temperatures at any time of the year a comparison was made between the temperature experienced by the cod and the range of temperature potentially available to them based on the previous analysis. Temperature records from returned DSTs were summarised 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 inter-quartile range were calculated. For comparison with sea-bed 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 (Figure 5).
The temperature experience of the majority of cod followed the upper range of temperatures and the cod thus experienced a warmer fraction of the sea than was 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. 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.
6. **GROWTH OF WILD ADULT COD IN THE NORTH SEA IN RELATION TO TEMPERATURE**

Information on the temperature experience of cod provided by DSTs can be used to directly assess the influence of temperature on growth. For this study only fish that had been at liberty for > 90 days were used because often there is weight loss over the weeks following capture and tagging, especially if done at or before spawning. An analysis was undertaken on 22 cod tagged in the northern North Sea and 30 from the southern North Sea. The overall average annual increase in length was 9.9 cm in the northern North Sea and 11.9 cm in the southern North Sea. A simple measure of temperature experience is the overall average temperature that the fish experienced during its time at liberty. In the northern North Sea there is a positive relationship with temperature as cod rarely experience super-optimal temperatures (Figure 6). However, in the southern North Sea the relationship appears to be parabolic with growth rates declining when temperatures exceed 13 °C. This is broadly in agreement with the laboratory experiments.

![Graph](image)

**Figure 6**: Specific growth rate of DST tagged fish in relation to the average temperature they experienced. Upper panel depicts cod tagged in the northern North Sea (>57 °N). Lower panel cod tagged in the southern North Sea (< 56 °N).
7. DISCUSSION AND CONCLUSIONS

The growth rate of cod growth is strongly influenced by temperature. A dome shaped relationship between growth rate and temperature was evident from both laboratory and field studies. It should be noted, however, that much individual variability lies around this relationship and that at least in the wild many other factors such as food availability will strongly influence growth. Such a pattern is broadly in agreement with previous laboratory studies (Purchase & Brown 2000; Bjornsson et al. 2002) and field observations (Brander 1995). It suggests that while cod may tolerate temperatures as low as 2 and as high as 19 °C in the North Sea, the range of temperatures that allow for high growth rates lies between 7 and 13 °C.

There is much variation in temperature across the North Sea. At the extremes, a cod from Lowestoft experienced 14 °C of annual temperature variation whereas an individual released east of Shetland experienced less than a 3 °C change over the year. The range of sea-bottom temperatures in the North Sea means that cod will be subjected to temperatures below and above the range that allows for high growth. This may be particularly important in the third quarter of the year when much of the southern North Sea is above 13 °C and therefore potentially detrimental to growth. Given that temperatures greater than 13 °C appear to be detrimental to growth, at least in adult cod, it might be expected that the cod would seek cooler waters either by moving to deeper water or by moving to more northerly latitudes. The data from electronic tags allowed testing of this hypothesis (Neat & Righton 2007). Although areas of the North Sea below 13 °C were available throughout the year and some of the tagged cod did move significant distances, most did not show any sign of moving away from temperatures in excess of 13 °C. It is not clear why the cod expose themselves to temperatures that result in poor growth rates, but there may be costs to migration. 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. The DST data show that fish 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 in the North Sea and suggests that simple search strategies to find suitable temperatures would not necessarily succeed. In spite of exposure to temperatures that appear to be detrimental to short-term growth for significant periods of time, the annual growth rate of southern North Sea cod is still significantly higher than their northern counterparts. Thus they must have very high growth rates in spring and early summer that compensates for the low growth incurred during the high late summer period.

In agreement with a growing consensus that the North Sea cod stock is spatially structured (Hutchinson 2001; Yoneda & Wright 2004; Wright et al. 2006) these new data suggests the cod populations within the North Sea experience quite different thermal environments. We might expect these populations to show different thermal tolerances and growth responses. This appears to be the case in populations of cod from the east and west coasts of Scotland. The laboratory growth trials suggested that juvenile cod from the west coast consistently grew at a faster rate than cod from the east coast. Differences in growth rates between northern North Sea cod and southern North Sea cod have also recently been demonstrated in laboratory trials (Perutz, Neat & Wright, unpublished data) which is in accordance with field observations.
8. REFERENCES


