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Growth, temperature and density relationships of North Sea cod

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Abstract

This study presents an analysis of the relationship between ambient temperature, cod density, fishing mortality, prey fish biomass and growth of North Sea cod (*Gadus morhua*) as estimated from survey catches during the period from 1983 to 2006. Growth of young cod was positively related to temperature, but though temperature has increased, distribution of 1-year olds has changed concurrently, and no increase in length at age 1 has occurred. Growth from age 1 to 2 has decreased as ambient biomass of sandeel and density of cod has decreased whereas growth of cod older than 2 years decreased with increasing density of cod and increased with increasing biomass of demersal fish prey. Though growth of juveniles was strongly positively correlated to ambient temperature, no indication of direct temperature limitation of growth of older North Sea cod was found.

Key words: Growth, cod, prey abundance, temperature, North Sea

Introduction

The scope for somatic growth of fish is determined by temperature and food abundance (Brett 1979). This has led to the expectation that growth rate is likely to increase if a stock experiences increased temperatures (Brander 1995; Dutil et al. 1999) as food-unlimited growth is positively related to temperature below a certain level (Jobling 1988; Björnsson and Steinarsson 2002). In North Atlantic cod (*Gadus morhua*) stocks, the expectation of increased growth with increasing temperature is supported by a high correlation between average ambient temperature of the stock and size at age (Brander 1995; Campana et al. 1995). However, an analysis of the relationship between temperature and length at age in the North Atlantic does not reveal whether temperature acts directly on growth or indirectly through increasing food abundance. It remains an open question whether the relationship is retained locally and whether it affects growth up to a certain age only or is present throughout the lifetime of the fish. These aspects have important implications for management. Predictions of the effect of altered growth rates on exploitation rates have mostly focused on the beneficial effect of sustained growth increases on maximum sustainable yield (Steinarsson and Stefánsson 1996; Rätz and Lloret 2003). However, if increased growth is only exhibited by juveniles, the beneficial effect may be at least partly abated by the decreased efficiency of technical measures aimed at limiting catches of juveniles (Pinhorn and Halliday 2001). If increased growth of juveniles is furthermore followed by a decreased growth of old fish as seen in Northeast Arctic cod (Michalsen et al. 1998), the combined effect may be a decrease in the level of mortality the stock can sustain.

A stock which is currently facing the combined challenges of climatic changes, unsustainable exploitation and a decrease in the biomass of important fish prey is the North Sea cod stock. Over the past 20 years, recruitment has decreased severely, possibly due to a combination of a declining spawning stock biomass, increasing temperatures and changes in the zooplankton community

(O’Brien et al. 2000; Beaugrand et al. 2003). In addition to this, the stock has moved northwards within the North Sea (Hedger et al. 2004; Perry et al. 2005; Rindorf and Lewy 2006), a movement which seems to be caused by poorer recruitment in southern areas (Rindorf and Lewy 2006). The shift in distribution may have decreased average growth rate, as growth in northern areas is slower than in southern areas (Graham 1934; Daan 1974; Rijnsdorp et al. 1991). Furthermore, the distributional change may have limited the effect of the general increase in temperatures over this period (O’Brien et al. 2000), possibly abating any effect of temperature on growth, as there does not appear to be a clear correlation between average North Sea bottom temperature and weight of adult North Sea cod in the commercial catch (Clark et al. 2003). This suggests that the effect of temperature on growth has been limited thus far. Four of the most important fish prey of North Sea cod, namely Norway pout, sandeel, young whiting and young herring (Kikkert 1993), have decreased severely since the year 2000 (ICES 2005, 2006).

This study had three objectives: firstly, to investigate the changes in growth of North Sea cod over the past 20 years, secondly to determine if the observed changes were related to temperature and thirdly to determine whether growth was likely to be limited by prey fish biomass, cod density or fishing mortality. The shape of the relationship between growth and these variables depends on the life stage. Temperature thus affects growth of small cod differently from growth of large cod (Björnsson and Steinarsson 2002) and ontogenetic changes in diet composition (Kikkert 1993) leads to differences between life stages in the effect of the biomass of a specific prey. Therefore, the study was divided into three: an analysis of juvenile cod feeding mainly on invertebrates, an analysis of cod in the transition period between an invertebrate dominated diet and a piscivorous diet and an analysis of predominantly piscivorous cod.

Methods

Study area

The study area was confined to the area of the North Sea within 51°N and 62°N latitude and 4°W and 9°E longitude (Fig. 1). The areas northeast of 57.5°N and 8°E and areas deeper than 200 m were not sampled by the surveys and therefore excluded from the analyses.

Survey data

Data on cod, clupeids and demersal fish prey were derived from catches in the English and Scottish Groundfish Surveys (August/September 1983 to 1990) and in the ICES International Bottom Trawl Survey (ICES International Bottom Trawl Survey Database, February 1983 to 2006 and August/September 1991 to 2005). The surveys use demersal trawls to sample the abundance of fish. Total catch and length composition of the majority of species is recorded in each haul. Haul duration generally varies between 0.5 and 1 hour, and all catch rates are standardised to hourly values. On average, two trawl hauls are conducted within each ICES statistical rectangle (0.5° latitude times 1° longitude, Fig. 1). The sampling intensity and spatial coverage of the 3rd quarter surveys increased in 1991, and areas just off the coasts on the eastern side of the North Sea were not covered in the 3rd quarter prior to this year. Additionally, the English Groundfish Survey used a Granton Trawl up to 1992. This trawl has been shown to have a low efficiency in catching small fish (Lewy et al. 2004).

Cod age-length keys were estimated using the method suggested by Rindorf and Lewy (Rindorf and Lewy 2001; Gerritsen et al. 2006). Age-length keys were estimated separately for each of 8 ICES roundfish sampling areas (ICES 1996, Fig. 1) where the number of fish aged was sufficient (Appendix). For the remaining areas, a common age-length key was estimated for combined two-roundfish areas (1 and 3, 2 and 4, 5 and 6 and 7 and 8). If this did not result in a sufficient number of observations, a common age-length key for the entire North Sea was used. Details of the estimation can be found in the Appendix. All fish ages were measured in years from February in the year of spawning and hence the age of a cod with one winter ring caught in September will be 1.5 years.

Length at age

The mean length at age a in a year y and season s, $\bar{l}_{a,y,s}$, was calculated by first estimating the average length of the age group within each statistical rectangle r, $\bar{l}_{a,y,s,r}$. $\bar{l}_{a,y,s}$ was then estimated as the average of $\bar{l}_{a,y,s,r}$ weighted by the average number of cod of age a caught per haul in rectangle r in year y and season s, $n_{a,y,s,r}$. In cases where $\sum_r n_{a,y,s,r} < 10$, no mean length at age was estimated.

Density and fishing mortality

To investigate density dependent growth, an index of the density of age-group a in a given year and season, $N_{a,y,s}$, was estimated by averaging the catch rate of age group a in each rectangle, $n_{a,y,s,r}$, over all rectangles. This survey based index was chosen rather than assessment based estimates as the latter provides an estimate of the number of fish once a year only and thus would not reflect changes from winter to summer.

Size selective fishing mortality affects length at age in some stocks (Hanson and Chouinard 1992; Riget and Engelstoft 1998; Sinclair et al. 2002*a*). To investigate whether increased fishing mortality is followed by a change in length at age, fishing mortality of age a in year y, $F_{a,y}$, was taken from the most recent stock assessment, including discard mortalities of cod (ICES 2006). This provided estimates for the period 1983 to 2005.

Estimation of amount of prey available

Three prey categories were considered: sandeel, clupeids and demersal fish. These prey types together constitute more than 40%, on average, of the stomach content of cod of age 2 and older (Fig. 2, Kikkert 1993). Though other prey types are also important to cod, no data were available to measure their abundance on the resolution of ICES statistical rectangles. A biomass index of clupeid and demersal prey fish was estimated from survey trawl catches. The fish biomass in the length range 5 to 15 cm caught per survey trawl hour was used. The lower length limit was used as the catchability of fish below this limit was considered highly variable. The upper limit corresponds roughly to the maximum prey size in medium to large sized cod (Kikkert 1993). As weight of the individual fish caught was not measured, biomass of clupeids and demersal fish within this size range was estimated from the length distribution by assuming that weight of a fish of length l was equal to $0.01l^3$. An index of the biomass of prey category j in rectangle r, quarter q and year y, $B_{j,y,q,r}$, was estimated as the average biomass caught per haul of this category. Flatfish were excluded as they are not a major prey of North Sea cod (with the possible exception of dab (*Limanda limanda*))(Kikkert 1993).

Two indices of average prey fish biomass were calculated: one was a North Sea average and the other was an estimate of the ambient prey biomass of each age group. The latter estimate accounts for differences in the spatial overlap between prey and predator whereas the former does not. The North Sea average biomass index in year y and season s, $B_{j,NS,y,s}$, of clupeids ($j=clupeid$) and demersal fish ($j=demersal$) was estimated as the average of the biomass index in the given year and season and the biomass index estimated 6 months earlier, where the biomass index of a given year and season was estimated as the average of all rectangles sampled. Ambient or cod-weighted biomass is an index of the ambient biomass of prey to an average cod of a given age. It is obtained by weighting the indices of prey biomass within a rectangle by the proportion of cod of a given age which are present in the rectangle. This produces an index of the current ambient prey biomass. However, to compare prey biomass indices with growth within the last 6 months, an estimate which refers to the 6 months prior to the survey is required. This necessitates an assumption on the spatial distribution of predators and prey in the time between the surveys. As an approximation, it was decided to assume that the distribution of fish changed instantaneously on the 1st of June and the 1st of December (midway between the surveys). Average ambient biomass indices, $B_{j,a,y,s}$, of clupeids and demersal fish were estimated as the average of the current ambient prey biomass and that experienced by the cohort 6 months earlier. The biomass indices of both clupeids and demersal fish are likely to be biased by the change in spatial coverage and survey gear around 1991.

Sandeels are poorly represented in survey trawls, and the biomass index of sandeel in the water column was therefore estimated from commercial catches per day in the Danish sandeel fishery from 1983 to 2005 (Appendix). The total biomass of sandeel caught per day was used directly as an estimate of available prey. No correction for the size distribution was necessary as sandeels are generally smaller than 15 cm in the North Sea. Unfortunately, not all areas are fished in every year and to achieve full spatial coverage of the estimates throughout the period, it was necessary to assume that the spatial distribution of sandeel remained constant over the years. Further, the sandeel biomass available in squares which were fished by less than 5 boats over the entire period was assumed to be zero (or at least negligible compared to that in other squares) as was the sandeel biomass available from September to March, the period when sandeel are buried in the sediment most of the time (Winslade 1974). 2nd and 3rd quarter estimates were produced. The 2nd quarter biomass index consists mainly of sandeels 1-year old and older whereas the 3rd quarter index may include young of the year. To use this information, indices of sandeel biomass available in the 2nd and 3rd quarter ($B_{s2,NS,y,summer}$ and $B_{s3,NS,y,summer}$, respectively) was estimated separately by averaging the biomass indices in the North Sea over statistical rectangles. Following the estimation of the ambient biomass index of clupeids and demersal fish prey, the ambient or cod-weighted biomass index of sandeel in the second and third quarter ($B_{s2,a,y,summer}$ and $B_{s3,a,y,summer}$, respectively) was obtained by weighting the indices of sandeel biomass within a rectangle by the proportion of cod of a given age which are present in the rectangle in the September survey. As sandeel were assumed to be unavailable in winter, ambient and North Sea average sandeel biomass of cod in February was zero. Note that if survey changes in 1991 bias all cod catches by a common factor, the index of ambient sandeel biomass is unaffected by changes in gear (Appendix).

Estimation of average temperature

Bottom temperature data are not available on a monthly basis from all ICES statistical rectangles in the North Sea. To achieve this kind of resolution, it is necessary to use predictions from a hydrodynamic model. We used output from the ECOSMO model (Schrum et al. 2006) which provides estimates of temperature with a horizontal resolution of 10 km, a vertical grid spacing of 5 m at depths less than 40 m and a larger grid spacing below this level. The hydrodynamic part of the model is based upon the non-linear primitive equation model HAMSOM (HAMburg Shelf Ocean Model, Schrum and Backhaus 1999). Several studies have demonstrated the ability of model to provide realistic simulations of North Sea hydrodynamics (Schrum et al. 2000; Janssen et al. 2001; Janssen 2002). Though the model does not capture all weekly variations (deviations of up to 2°C occur in a few cases), yearly average temperatures are accurately reproduced as is the temporal development over the study period (Janssen et al. 2001). Average temperature, T, in each year and rectangle was extracted for the months March to May, June to August, September to November and December to February. The groups were selected to provide 3 month intervals prior to and after the surveys. Temperature estimates were not available for the area north of 60°N or for the year 2005.

Two temperature estimates were calculated in each year and season: a North Sea average and an estimate of average ambient temperature of a given age (Heesen and Daan 1994). The latter estimate accounts for the spatial distribution of the age group whereas the former does not. Two temporal scales were considered: for the comparison with average length of fish younger than 2 years, an accumulated average temperature over their entire life time was estimated starting from the time of settling and for the comparison with growth rates of cod older than 1.5 years, estimates of average North Sea temperature within the last 6 months were estimated.

The accumulated average temperature over the entire life time of juvenile cod was estimated starting from the time of settling. Cod are at least partly demersal from June onwards in their first year (Bromley and Kell 1995) and hence the average demersal lifetime temperature of 0.5-year olds is the average temperature from the 1st of June to the 1st of September whereas that of 1-year olds is the average from the 1st of June to the 1st of March and that of 1.5-year olds is the average from 1st of June the previous year to 1st of September in the current year. The estimates of average lifetime North Sea temperature were thus the average over all rectangles in 3, 9 and 15 months prior to the survey for cod of age 0.5, 1 and 1.5 years, respectively. Life-time average North Sea temperatures ($T_{L,NS,a,y,s}$) were estimated as the average temperature in this period for each age group and ambient life time temperatures ($T_{L,a,y,s}$) were estimated as the weighted average, weighting the temperature in each rectangle with the proportion of the age group caught in that rectangle (Appendix).

The half yearly North Sea average temperature, $T_{NS,y,s}$, was estimated as the average of the temperatures estimated in the 6 months prior to the survey in year *y* and season *s*. Ambient or cod-weighted temperature was estimated as the average ambient temperature in the period 0 to 3 months and 3 to 6 months prior to the survey. Average ambient temperature in the period 0 to 3 months prior to the survey was estimated by weighting the temperature rectangle *r* in that period by the proportion of cod of age *a* caught in rectangle *r* in year *y* and season *s*. Average ambient temperature in the period 3 to 6 months prior to the survey was estimated by weighting the temperature rectangle *r* in that period by the proportion of cod of the same cohort caught in the rectangle *r* in the previous survey (Appendix).

Measuring growth of fish

Growth of fish have been measured in several ways in the literature. Firstly, average length at age is a simple measure but has the disadvantage of measuring integrated growth over the entire life span of the fish. While this may not be a problem when examining growth of young individuals, average length of an older fish depends heavily on the conditions experienced earlier in life and little on recent growth. Average length is therefore suitable only for the detection of relationships between recent growth conditions and growth of young fish. Another measure frequently used is specific growth rate G (Jobling 1988; Björnsson and Steinarsson 2002):

$$G = 100\frac{\ln W_t - \ln W_{t-\Delta t}}{\Delta t}$$

where W_t is the weight of the fish at time t. This measure has the advantage of measuring growth in the period between two observations directly and hence is preferable if size of a fish is measured at more than one point in time. Unfortunately, G varies not only with recent growth conditions but also with size of the fish (Jobling 1988; Björnsson and Steinarsson 2002) and growth estimates can only be compared directly for a limited range of sizes. This is particularly inconvenient when growth conditions act in a comparable way on growth of several age groups (e.g. growth of all ages is enhanced at increased prey biomass). In this case, it is preferable to look at growth of all ages simultaneously and a model in which the parameters remain constant with size is needed. One model which fulfils this is the von Bertalanffy model. The von Bertalanffy equation describes length of a fish as a function of age and three constants:

(1) $$l_a = L_\infty \left(1 - e^{-K(a-a_0)}\right)$$

where l_a is average length of the fish at age a, L_∞ is the average maximum attainable length, K is instantaneous average growth rate and a_0 is a constant referring to the theoretical length at a=0. This model is clearly preferable if size at age of a cohort is estimated at several points in time. Note also that inserting length at age from the von Bertalanffy model to estimate of specific growth rate between age a and $a+\Delta a$ and rearranging, is it clear that G depends directly on age a, K, a_0 and the time elapsed between measurements (Δa) but is unaffected by L_∞. As the model includes three parameters, it can only be estimated if several age groups are included in the analyses.

Based on these considerations, it was decided to estimate growth of juvenile cod (cod younger than 18 months) by average length at age directly, growth of cod in the transition period between an invertebrate dominated diet and a piscivorous diet by specific growth rate G and growth of predominantly piscivorous cod by the parameters K and L_∞ from the von Bertalanffy equation.

To examine the likely effect of the observed temperatures on growth of cod, food unlimited growth rate *G* in the laboratory of cod of a particular size and ambient temperature was estimated from models given in two studies of temperature limited growth rate of cod fed to satiation: Jobling (1988) and Björnsson and Steinarsson (2002). Björnsson and Steinarsson used Icelandic cod whereas Jobling combined results from experiments with Scottish coastal cod, Norwegian coastal cod, North east arctic cod and North Sea cod (Edwards et al. 1972; Jones and Hislop 1978; Braaten 1984; Hawkins et al. 1985; Jobling 1988). Jobling described the relationship between growth rate *G*, *W* and temperature *T* as

$$\ln G = 0.216 + 0.297T - 0.000583T^3 - 0.441 \ln W$$

whereas Björnsson and Steinarsson described the relationship as

$$G = 0.5735TW^{-0.1934-0.02001T}$$

As potential growth rates are estimated from both temperature and weight of the fish, observed weight at age was estimated from the observed length at age as $W_{a,y,winter} = 0.0198\bar{l}_{a,y,winter}^{2.8571}$ and $W_{a,y,summer} = 0.0211\bar{l}_{a,y,summer}^{2.8571}$ for cod caught in the winter and summer surveys, respectively (Coull et al. 1989). This observed weight was used to predict potential growth at a range of temperatures for each age group.

Growth of cod feeding mainly on invertebrates

Average length of 0.5-, 1- and 1.5-year old cod was compared to life-time average ($T_{L,NS,a,y,s}$) and ambient ($T_{L,a,y,s}$) temperature, the index of density ($\ln(N_{a,y,s})$) and fishing mortality ($F_{1,y}$, 1.5-year olds only). The analyses were conducted using multiple linear regression models. The factors were tested for effect on the natural log of the average length, $\ln(\bar{l}_{a,y,s})$. To account for catchability changes due to changes in survey design, the intercept of the models for 0 and 1-year olds in summer was allowed to differ between the periods before and after 1991.

Growth in the transition period

Somatic growth in the transition period was examined by estimating the yearly growth rates from age 1 to age 2 and the half yearly growth rates from age 1.5 to age 2. Half-yearly ($g_{0.5,y}$) and yearly ($g_{1,y}$) growth rates were estimated as

$$g_{0.5,y} = \ln\bar{l}_{2,y,winter} - \ln\bar{l}_{1.5,y-1,summer}$$

and

$$g_{1,y} = \ln \bar{l}_{2,y,winter} - \ln \bar{l}_{1,y-1,winter}$$

These estimates are directly proportional to specific growth rate *G*. Growth in the transition period was investigated by fitting linear regression models where the independent variables were North Sea average and ambient temperature, average and ambient prey biomass index, log cod density index and fishing mortality of 1-year olds in the previous year. In the model of $g_{1,y}$, average values of the explanatory variable in the past year was used, except for the biomass index of demersal and clupeid prey where the values referred to the period between summer and winter in both cases, as the consumption of these prey types is low in the period before summer (Kikkert 1991). To account for changes catchability due to changes in survey design, the intercept of the model of $g_{0.5,y}$ was allowed to differ between the periods before and after 1991 as was the effect of the biomass index of clupeid and demersal fish in both models. All effects were assumed to be linear and the error around the relationship assumed to be normal distributed. The significance of explanatory variables was determined by forward elimination.

Growth of cod older than 2 years

Growth of cod older than 2 years was examined through an analysis of the relationship between the parameters in the von Bertalanffy model and temperature, density index, prey fish biomass indices and fishing mortality. To facilitate the analyses, Eq. 1 was rearranged to describe the relationship between length at age a, l_a, and length at age $a+\Delta a$, $l_{a+\Delta a}$. $l_{a+\Delta a}$ can be rearranged to $l_{a+\Delta a} = L_\infty\left(1-e^{-K(a+\Delta a-a_0)}\right) = L_\infty\left(1-e^{-K\Delta a}\right)+e^{-K\Delta a}L_\infty\left(1-e^{-K(a-a_0)}\right)$. Inserting $l_a = L_\infty\left(1-e^{-K(a-a_0)}\right)$ (Eq. 1), we obtain

$$l_{a+\Delta a} = L_\infty\left(1-e^{-\Delta a K}\right)+e^{-\Delta a K}l_a \qquad (2)$$

If age is measured in years and the time elapsed between the two measurements of average length (Δa) is 0.5 year, Eq. 2 corresponds to comparing the length of a given cohort with that 6 months earlier. We examined the length of fish of age 2.5 years up to age 5.5, avoiding the oldest groups which contain both 6-year olds and older fish. If it is assumed that L_∞ remains constant while K varies between years and ages, and that $\bar{l}_{a,y,s}$ derived from surveys provides an unbiased estimate of l_a, Eq. 2 becomes

$$\bar{l}_{a,y,winter} = L_{\infty}\left(1 - e^{-0.5K_{a,y,s}}\right) + e^{-0.5K_{a,y,s}}\,\bar{l}_{a-0.5,y-1,summer}$$

$$\bar{l}_{a,y,summer} = L_{\infty}\left(1 - e^{-0.5K_{a,y,summer}}\right) + e^{-0.5K_{a,y,summer}}\,\bar{l}_{a-0.5,y,winter}$$

in winter and summer, respectively. This is a standard autoregressive model of order 1. L_{∞} was assumed to remain constant over the period while K was a linear function of the explanatory variables. An F-test of the significance of each explanatory variable was conducted by comparing the residual variation to that of a model where growth rate was constant for the same time range (the period included depends on the explanatory variables as not all variables were known in all years). The significance of explanatory variables was determined by forward elimination. The explanatory variables tested were season (s), average ($T_{NS,y,s}$) and ambient ($T_{a,y,s}$) temperature, average ($B_{j,NS,y,s}$) and ambient ($B_{j,a,y,s}$) prey biomass indices, fishing mortality ($F_{a-1,y-1}$ in winter and $F_{a-0.5,y}$ in summer) and the density index ($\ln N_{a,y,s}$). As density decreases with age, including the density index directly would provide a measure of the combined effect of age and density rather than the effect of density alone. To avoid this, $\ln N_{a,y,s}$ was expressed in units of standard deviations from the mean of the given age group and this standardised measure denoted $\ln N^{*}_{a,y,s}$. The parameters were estimated using the NLIN procedure in SAS® (SAS Institute Inc. 2001). Variance in length at age increased with the mean (correlation=0.69) whereas there was no correlation between average $\ln \bar{l}_{a,y}$ and the variance of this (correlation=0.02). The model was therefore fitted assuming the residuals of $\ln \bar{l}_{a,y}$ to be normal distributed.

Examination of residuals

All residuals were tested from significant deviations from a normal distribution (Shapiro-Wilks test), trends and autocorrelations (Pearson correlation coefficients).

Results

Less than 10 fish of an age group were caught on two occasions: 6+-year olds in the 3rd quarter of 1986 and 4-year olds in the 3rd quarter of 1988. Average length was not estimated in these cases.

Average length of age 0.5 cod increased significantly in the period before 1991 (correlation=0.84, P=0.0088, Fig. 3a). Though average length also increased after 1991, no significant change was seen for cod of age 0.5 in this period, in age 1 over the entire period or in age 1.5 in the period before and after 1991(correlations=0.16, 0.09, 0.71 and -0.07, for age 0.5 after 1991, age 1 in the entire period and age 1.5 before and after 1991, respectively). In contrast to this, average length of cod older than 18 months decreased over the period (correlations ranging from -0.30 to -0.62, ages 2 years and above, significant for all ages except age 6+, Fig. 3). From 1983 to the end of the time series, this corresponded to a decrease in length at age of 10% and 13%, on average, in the first and third quarter, respectively.

Trends in North Sea average and ambient values

There was no significant trend in the biomass indices for either North Sea average clupeid, demersal or sandeel fish prey (All correlations with year>-0.63 and <0.16, P>0.05, Fig. 4). However, there has been a drastic decrease in the biomass of demersal fish from 2000 to 2005, reaching all time lows in 2004 and 2005 (Fig. 4). Changes in distribution of cod into areas of unknown (presumably low) and low sandeel biomass led to a negative trend in the ambient biomass of sandeel of all age groups (correlation between year and $B_{s2,a,y,summer}$ ranged from -0.31 to -0.61,

$P<0.05$ for all ages but age 2.5 and between year and $B_{s3,a,y,summer}$ from -0.15 to -0.58, $P<0.05$ for all ages above 3.5).

The average North Sea temperature increased significantly in the 6 months before and after the 1st quarter survey (correlations=0.53 and 0.48, P=0.0127 and 0.0235, respectively). With the exception of cod younger than 2.5 years, half-yearly ambient temperatures were significantly colder than the average (Table 1) and the differences amounted to as much as 1°C for some ages. Further, though both average and ambient temperature increased for all ages except age 1 in summer, the increase in ambient temperature was only significant for ages 0.5, 1 and 4.

The potential growth rate estimated by Jobling's method reaches its maximum at a higher temperature than growth rate estimated by Björnsson and Steinarsson's method, and as a result of this, the two models predict markedly different effects of temperature (Fig. 5). Whereas temperature is predicted to account for less than 10% changes in growth of North Sea cod older than 1 year using Björnsson and Steinarsson's model, Joblings method predicts a decrease of up to 50% within the temperature range experienced (between 6 to 12°C, Fig. 5). Both models predict a large effect on temperature on growth of the youngest age group (0.5-year olds).

Growth within the first 18 months

Average length of juvenile cod was highly correlated to average lifetime temperature (Fig. 6; Table 2) while the effect of fishing mortality was insignificant. The correlations with North Sea average temperature and the density index were always less significant than that with average ambient temperature (Table 2). After including the effect of ambient life time temperature ($T_{L,a,y,s}$), the final models of average length became

$$\ln \hat{\bar{l}}_{0.5,y<1991,summer} = 1.99^{(0.14)} + 0.032^{(0.012)} T_{L,0.5,y,summer}$$

$$\ln \hat{\bar{l}}_{0.5,y\geq 1991,summer} = 1.85^{(0.12)} + 0.032^{(0.012)} T_{L,0.5,y,summer}$$

$$\ln \hat{\bar{l}}_{1,y,winter} = 1.78^{(0.24)} + 0.108^{(0.023)} T_{L,1,y,winter}$$

$$\ln \hat{\bar{l}}_{1.5,y<1991,summer} = 2.70^{(0.17)} + 0.065^{(0.017)} T_{L,1.5,y,summer}$$

$$\ln \hat{\bar{l}}_{1.5,y\geq 1991,summer} = 2.66^{(0.17)} + 0.065^{(0.017)} T_{L,1.5,y,summer}$$

where values in parentheses denotes standard error of the estimates (r^2=0.48, 0.53 and 0.53 for ages 0.5, 1 and 1.5, respectively). The effect of the index of density on length of 1 and 1.5-year olds was no longer significant after the effect of ambient temperature was included in the model (P=0.3409 and 0.1148, respectively). The effect of temperature in the model of 0.5 year olds was significantly lower than that in the model of 1-year olds (P=0.0034), whereas the difference between 1.5-year olds and the other age groups was not significant (P=0.1128 and 0.1327, for age 0.5 and 1, respectively). Inspecting the residuals, the relationship between log length and lifetime ambient temperature appeared to decelerate. This was modelled by letting log length be a second degree polynomial in temperature. The second degree term was significantly different from zero (P=0.0173) and the resulting model became:

$$\ln \hat{\bar{l}}_{1,y,winter} = -4.38^{(2.36)} + 1.34^{(0.47)} T_{L,1,y,winter} - 0.061^{(0.023)} T_{L,1,y,winter}^{2}$$

(r^2=0.66). The distribution of the residuals was not significantly different from a normal distribution for any of the ages and no significant trends or autocorrelations in residuals were found.

Growth in the transition period

Growth in the transition period was significantly positively related to the index of cod density and the sandeel biomass index in the 2nd or 3rd quarter (table 3, fig. 7). The correlation with ambient sandeel biomass index was higher than that with North Sea average sandeel biomass index for both quarters and growth rates, indicating that the change in overlap with sandeel was important. After including the effect which had the highest correlation with growth rate in the models, the remaining effects (including temperature) became insignificant and the resulting models were

$$g_{0.5,y} = 0.12^{(0.02)} + 0.0025^{(0.0008)} B_{s2,1,y-1,summer}$$

$$g_{1,y} = 0.51^{(0.04)} + 0.052^{0.019} \ln N_{2,y,winter}$$

(r^2= 0.34 and 0.26, respectively). The distribution of the residuals did not differ significantly from a normal distribution and no significant trends or autocorrelations in residuals were found. The effects of cod density and sandeel 3rd quarter biomass indices became insignificant when the other parameters were added (P=0.6288 and 0.9034, respectively) as did the difference between the period before and after 1991 (P=0.5341). Unfortunately, the cod density index was positively correlated to all sandeel biomass indices (table 3), which renders it difficult to determine which of the two factors is the most important one.

Von Bertalanffy growth analyses

After including the highly significant (P=0.0007) seasonal change in *K* in the model, the effect of the ambient demersal fish biomass index had the most significant effect (P=0.0039). Including this factor, no other variables maintained a significant effect. However, the cod density index was only marginally significant (P=0.0977) and inspecting the residuals, there appeared to be an effect of the density index in winter whereas no effect was seen in summer. Restricting the effect of density to affect only growth from summer to winter, the effect passed the significance level (P=0.0331). After including this parameter, none of the remaining variables retained a significant effect (P>0.15). The model of *K* became

$$\hat{K}_{a,y<1991,winter} = 0.142^{(0.037)} + 0.59^{(0.28)} B_{demersal,a,y,winter} - 0.020^{(0.011)} \left(\ln N^{*}_{a,y,winter}\right)$$

$$\hat{K}_{a,y\geq 1991,winter} = 0.142^{(0.037)} + 0.18^{(0.07)} B_{demersal,a,y,winter} - 0.020^{(0.011)} \left(\ln N^{*}_{a,y,winter}\right)$$

$$\hat{K}_{a,y<1991,summer} = 0.104^{(0.025)} + 0.59^{(0.28)} B_{demersal,a,y,summer}$$

$$\hat{K}_{a,y\geq 1991,summer} = 0.104^{(0.025)} + 0.18^{(0.07)} B_{demersal,a,y,summer}$$

$$L_{\infty} = 151^{(25)}$$

($r^2=0.16$). Though the effects of season, the biomass index of demersal fish and the density index were significant, the proportion of the variation which could be attributed to these factors was small, each explaining only 7.1%, 6.4% and 2.5% of the unexplained variation, respectively. There was no trend in the residuals and the distribution of the residuals did not deviate significantly from a normal distribution. The residuals were neither significantly autocorrelated for a given age and a lag of 1 year nor for a given cohort and a lag of 1 year. However, the residuals within a year of adjacent age groups were significantly positively correlated (correlation=0.23, P=0.0152) and residuals of a given cohort was significantly negatively correlated to that of the same cohort 6 months earlier (correlation=-0.35, P<0.0001). Residuals were not correlated to age (correlation=0.01, P=0.8675) which should have been the case if length at age of older ages was biased due to decreasing catchability of very large fish (Godø et al. 1999).

Discussion

Growth of cod within their first 1.5 years of life was highly dependent on temperature. Though the increase in average temperature seen over the period could therefore potentially have increased growth rates, this effect was abated by a change in the distribution of juveniles, and no increase in ambient temperatures or growth of cod of age 1 and 1.5 could be detected. Growth of older ages was not related to temperature. Instead, growth in the transition period between a diet dominated by invertebrates and a diet dominated by fish was positively related to cod density and sandeel biomass whereas growth of older cod was positively related to biomass of demersal fish prey and negatively related to cod density. Both growth of juveniles, transition cod and cod older than 2 years showed higher correlations with ambient estimates of temperature and prey biomass than North Sea average values, demonstrating the importance of including the effect of changes in distribution of prey and predator.

The increase in juvenile length with increasing temperature appeared to be caused by an effect on growth during at least the first 12 months. Had growth been affected only up to age 0.5, the effect of life time temperature should have decreased as age increased. In contrast to this, the effect of temperature increased significantly from age 0.5 to age 1 indicating that the positive effect persisted in the second half year of life. Similar positive relationships between growth of juveniles and temperature have been found in Irish cod, Northeast Arctic cod and Placentia Bay cod (Michalsen et al. 1998; Armstrong et al. 2004; Mello and Rose 2005), perhaps indicating that temperature dependent growth of immature fish is the cause of the high correlation between ambient temperature and length at age 4 detected by Brander (1995). The negative effect of density on length of 1.5-year olds did not persist after the effect of temperature was taken into account. This confirms the earlier results by van Alphen and Heesen (1984) and Rijnsdorp et al. (1991) who detected no link between length at age 1 and density based on data from1968 to 1989.

Growth of cod in the transition phase was significantly correlated to both ambient sandeel biomass and cod density, but as the two time series were highly correlated, it is difficult to determine which of the two had the most important effect. The positive effect of increasing density on growth could seem counterintuitive and may lead to the conclusion that ambient sandeel biomass was the causal factor. However, positive relationships between density and feeding success have been recorded in other fish feeding on schooling or patchy prey (Major 1978; Pitcher et al. 1982). If cod switch from feeding on invertebrates to feeding on patchily distributed tightly schooling sandeel, it may be an advantage to forage in groups. Hence the explanation for the similarity of the two effects may be that they work together to produce changes in growth.

Growth of cod older than 2 years showed clear seasonal differences with the autumn estimate of *K* being 50% higher than the spring estimate. A similar seasonal pattern was seen in cod off Newfoundland (Mello and Rose 2005). The difference in growth in the study of Newfoundland cod was linked to temperature and the seasonally variable predation on capelin (*Mallotus villosus*). In the current study, no effect of temperature could be found and the demersal fish biomass index could not explain the difference between seasons. As the spring period encompasses the spawning period of North Sea cod (Daan et al. 1990), the seasonal difference may be linked to a trade off between using the available energy for reproduction or for growth. Growth in both seasons was positively related to increasing biomass of demersal fish but independent of the biomass of sandeel or clupeids. As sandeels constitute less than 8% of the diet of these age groups (Fig. 2), the lack of effect on growth of old cod is not unexpected. However, the same argument cannot be made for clupeids. Though they generally contribute less to the diet than demersal fish, their contribution is as high as 30% in some age groups (Fig. 2). Possibly, the catchability of pelagic fish to the demersal trawl used in the surveys varies to an extent where any underlying relationship becomes undetectable. Alternatively, the changes in clupeid biomass over the period have been too small for any serious effects on growth to occur. Growth of cod and prey fish abundance is significantly correlated in both Icelandic cod (Steinarsson and Stefánsson 1996), Northeast Arctic cod (Jørgensen 1992) and cod on the Newfoundland and Labrador shelves (Krohn et al. 1997; Mello and Rose 2005). However, the proportion of the variation in growth which can be explained by temperature and prey abundance is often low (24% and 23% in Northeast Arctic cod and cod off Newfoundland, respectively (Jørgensen 1992; Krohn et al. 1997)). These figures include a substantial effect of temperature and hence the proportion which can be attributed to prey biomass is only a fraction of this. Hence the 6.4% of the variation in growth which could be attributed to demersal fish biomass would appear to be a level comparable to that seen in other stocks, in spite of the fact that the diet of

North Sea cod differs from that of these stocks. North Sea cod consumes a variety of fish prey and only occasionally does a single prey species account for more than 30% of the weight of the stomach content (Kikkert 1993), whereas capelin accounts for up to 50%, 69% and 85% of the stomach content in the Icelandic, North East Arctic and Newfoundland stocks, respectively (Pálsson 1983; Mehl 1989; Lilly 1991).

Though temperature has increased over the period, there was no evidence of an increase in growth of cod older than 2 years as predicted by the relationship between temperature and food unlimited growth given by Jobling (1988). A similar lack of effect of temperature on growth of older cod was seen in the Northeast Arctic where average length at age 7 decreased as temperature increased (Michalsen et al. 1998) and in Plactentia Bay, where growth of cod age 8 and 9 decreased with temperature (Mello and Rose 2005). In contrast to this, there was a positive effect of temperature on growth of Northwest Atlantic cod stocks experiencing average temperatures between 0^{o}C and 3^{o}C (Krohn et al. 1997; Riget and Engelstoft 1998; Swain et al. 2003). No effect of temperature was found on growth of the 4X stock on the Scotian shelf, where average temperature (6.8^{o}C) approached that in the North Sea. Assuming that the relationship between food unlimited growth and temperature estimated for Icelandic cod by Björnsson and Steinarsson (2002) can be generalised to all cod stocks, an increase in temperature from 8 to 9^{o}C should result in a change in growth rate of less than 6% (Fig. 5). In comparison, an increase in temperature from 2 to 3^{o}C should result in an increase in growth rate of more than 25%. Hence, the discrepancy between the conclusions on the effect of temperature in cold and warm water stocks is not surprising.

Increased density was followed by decreased autumn growth of North Sea cod older than 2 years. The results confirm earlier results by Macer (1983) and van Alphen and Heesen (1984), who found density dependent growth in cod of age 3 and ages 2, 3 and 4, respectively. The fact that the effect could only be detected in the second half of the year may indicate that intra-specific competition for prey or habitat acts mainly within the autumn period. Houghton and Flatman (1980) found decreased growth rate of cod in the west central North Sea at high densities based on weight at age in commercial catches, but growth within this and other areas was later examined by Bromley (1989), who concluded that no evidence of density dependent growth could be detected within local areas. He suggested that the causal relationship between density and growth in the North Sea could be acting through changes in distribution. If this is the case, the coinciding decrease in abundance and shift in distribution into slow growth areas seen in later years (Perry et al. 2005; Andrews et al. 2006; Rindorf and Lewy 2006) should result in a positive correlation between density and growth in contrast to the negative correlation found in cod older than 2 years. Decreased growth at high densities has been found in the Southern Gulf of St. Lawrence cod (Sinclair et al. 2002*b*), in two out of four stocks on the Labrador and Newfoundland shelves (Swain et al. 2003), Irish Sea cod (Armstrong et al. 2004) and North east Arctic cod (Michalsen et al. 1998). Though an affect appeared to be present in Irish Sea cod, temperature and recruitment is highly correlated in this stock, and it remains unclear whether the results are caused by the combined links between density and temperature and temperature and growth (Armstrong et al. 2004). The density dependent decrease in growth rate of juvenile Northeast Arctic cod occurs through changes in distribution as large yearclasses experience lower ambient temperatures and hence achieve lower growth rates (Michalsen et al. 1998). Hence, there does not appear to be a general presence or absence of density dependence in all stocks, and the presence of similar or opposing trends stress the need to examine several variables when attempting to determine the effects on growth of cod.

Negative correlations between size selective fishing mortality and size at age exist in Southern Gulf of St. Lawrence cod (Sinclair et al. 2002*a*) and the West Greenland stock (Riget and Engelstoft 1998), but no such effect was seen in the North Sea. However, the number of partially recruited age groups is higher in the Southern Gulf of St. Lawrence than in the North Sea (Pinhorn and Halliday 2001) leaving a greater time span for effects to occur. In the North Sea, size selective fishing has the potential to affect mainly cod at age 1.5 (the only partially recruited age group (Pinhorn and Halliday 2001)). Even so, length at this age was uncorrelated to fishing mortality. Though there is always a possibility that this result is caused by poor quality of the assessment of the stock, we also investigated the correlation between length at age and the minimum mesh size regulations and obtained the same result (results not shown). As natural mortality of this age group is about four times the fishing mortality (ICES 2006), the effect of size selective fishing mortality may be masked by the much larger effect of size selective predation mortality. Further, results in the literature of investigations of the effect of fishing mortality are not unanimous. Size at age in the stock in the Northern Gulf of St. Lawrence appears to be unaffected by fishing mortality (Dutil et al. 1999), in spite of the significant relationships seen in the adjacent Southern Gulf of St. Lawrence stock (Hanson and Chouinard 1992; Sinclair et al. 2002*a*). However, of the 12 stocks examined by Pinhorn and Halliday (2001), only the southern Gulf of St. Lawrence stock, the Northeast Arctic stock, the Iceland stock and the Labrador stock are partially recruited to the fishery for more than 5 years (Pinhorn and Halliday 2001), and hence have potential to exhibit severely decreased size at age as a result of size selective fishing mortality. Of these stocks, the Northeast Arctic stock shows no evidence of a decrease in length at high fishing mortalities. Rather, high fishing mortality seems to be accompanied by large size at age, perhaps due to density dependent effects on both (Marshall et al. 2004). Another stock experiencing high fishing mortalities, the Irish cod stock, showed a similar lack of relationship between size at age and fishing mortality (Armstrong et al. 2004) and hence the lack of effect in the North Sea does not appear to be unique.

The positive correlation between residuals from the von Bertalanffy model within a given year indicates that yearly changes in growth conditions affect all age groups similarly. However, the result may also be caused by the statistical correlation introduced by the sampling procedure which combines age-length keys with length distributions. This appeared to be the more likely reason as correlations between residuals were only significant for ages 4.5 and 5.5 when age groups were analysed separately and the problem of statistical correlation increases with increasing length overlap of the age groups. The negative correlation between the residuals and those of the same cohort 6 months earlier indicates that a larger than expected size in a given survey is generally followed by smaller than expected size in the subsequent survey. This could be a result of sampling errors if an estimate of large size at one age is in some cases caused by sampling errors alone. The subsequent survey will then tend to find fish that are smaller than expected. When analysed for each age separately, the correlations were significant only for fish of age 3, 5 and 5.5, two of which are hampered by low catch rates (5 and 5.5 year olds). This may indicate that the problem is linked to the higher sampling error of these ages. The residuals were not significantly correlated with those from the same cohort 1 year earlier, indicating that between cohort differences in growth rates were either small or swamped by yearly differences. Autocorrelation in the residuals results in a lower number of degrees of freedom than the number of observations and as reducing the number of degrees of freedom results in higher probability estimates, the probability levels given here should be taken as minimum estimates. The r^2 values are, however, unaffected by this problem.

Though the von Bertalanffy growth parameters did not exhibit any trend over the past 20 years, this does not rule out growth changes in a longer time perspective. The confidence limit of the estimate of L_∞ obtained here were wide and included the estimates of $110.8^{(2.8)}$ and $118.7^{(5.6)}$ cm presented by Daan (1974) for southern and northern North Sea cod, respectively, in the period 1968 to 1972. Reanalysing his data using model (2), the difference between the northern and southern parts in L_∞ and K are insignificant (P=0.2374 and 0.1654, respectively) and a fit using data from both areas results in the estimates $L_\infty=113.6^{(4.7)}$ cm and $K=0.300^{(0.033)}$. Fixing L_∞ at this value and using the present data results in an estimate of K of $0.241^{(0.010)}$ which is not significantly different from the value estimated from Daans data (P=0.0871). Even earlier than the investigation by Daan are the data from Graham on length of cod in the southeastern North Sea (Graham 1934). Using his estimates of length at ages 1.5 to 6.5 in March and September of 1991 to 1927 and fixing L_∞ to 113.6 cm results in an estimate of $K=0.219^{(0.020)}$. This value is significantly different from that obtained from Daans data (P=0.0358) but not from the estimate derived in the present study (P=0.3252). Hence there may have been an increase in growth rate from the early 20th century to the 1970s, but the current growth rate seems to have decreased to a value between the two historical estimates.

This study has shown a decrease in length at age of fish older than 1.5 years over the past 23 years. This appeared to be caused by a decrease in growth of cod in the transition phase as length at age of cod younger than 2 years has increased slightly with increasing temperatures and growth rates of fish older than 2 years showed no trend over the period. The decreased growth in the transition phase appeared to be linked either to decreasing ambient sandeel biomass, decreasing cod density or both. However, as ambient sandeel biomass is highly dependent on the distribution of cod the coinciding trends may be also be caused by a shift in the dominance of southern aggregations towards a dominance of northern aggregations. Cod aggregations within the central North Sea do not differ genetically (Hutchinson et al. 2001), but this does not necessarily imply that northern and southern aggregations do not have individual characteristics. As cod in different areas have different scopes for growth (Andrews et al. 2006), the change in growth rate could be the result of a change either in the proportion of the stock which reside in fast-growth areas or in the proportion of the number of cod recruited in a number of relatively stationary sub-stocks in fast-growth areas. If the latter situation occurs, temporal changes in growth caused by changes in distribution may not be reversible unless the relative importance of the different aggregations is restored. In conclusion, there does not appear to be scope for increased growth of cod older than 2 years with increasing temperatures. Rather, as increasing temperatures tend to lead to a more northerly distribution (Perry et al. 2005; Rindorf and Lewy 2006), growth rate of North Sea cod may further decrease if temperatures continue to be above the long term average as ambient sandeel biomass and cod density are both negatively related to this factor (O'Brien et al. 2000; Rindorf and Lewy 2006). Furthermore, increased growth of juveniles as temperatures increase may lead to a higher fishing mortality on age 1 cod (Pinhorn and Halliday 2001) and hence further aggravate the severe decrease in recruitment to the North Sea cod stock due to the combined effects of poor recruitment success and a severe decrease in spawner biomass.

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Appendix

Estimation of age-length keys

Age-length keys were estimated by the method described by Rindorf and Lewy (2001). This method utilises the smoothness of length at age distributions to provide more accurate estimates of age at length than traditional methods. The number of fish observed of a given age in a sample is assumed to be multinomial distributed, but the variance may exceed that of this distribution. In the present study, length at age was assumed to be normal distributed. Analyses were also performed based on the assumption of gamma distributed length at age, but these analyses provided poorer fits to the observed age at length.

Age at length is analysed by comparing the proportion of fish at length l which are of age a, $p_{a,l}$, with the proportion of fish which are of age a or older, $p_{a+,l}$. This is equivalent to estimating the probability that a fish of a given length is of age a given that the fish is of age a or older. The variable analysed is the continuation ratio logit:

$$\log\left(\frac{p_{a,l}}{p_{a+,l}}\right)$$

The continuation logit can be used to estimate the probability of being of age group a at length l, $\hat{p}_{a,l}$, (Rindorf and Lewy 2001):

$$\hat{p}_{1,l} = \left(\frac{\hat{p}_{1,l}}{p_{1+,l}} \right)$$

$$\hat{p}_{a,l} = \left(\frac{\hat{p}_{a,l}}{p_{a+,l}} \right) * \left(1 - \sum_{j=1}^{a-1} \hat{p}_j \right) \quad , \quad a > 1$$

The model analysed in this study was that appropriate for individuals with normal distributed length at age (Rindorf and Lewy 2001):

$$\log\left(\frac{p_a}{p_{a+}} \right) = b_{a,y,q,ro} + c_{a,y,q,ro} l + d_{a,y,q,ro} l^2$$

where *b*, *c* and *d* are parameters to be estimated in the model and indices *y*, *q* and *ro* denotes year, quarter and each of 8 ICES roundfish areas (Fig. 1), respectively. Overdispersion was allowed by estimating scale by the Pearson statistic. The number of parameters estimated varies as the number of roundfish area-year-quarter combinations which fulfil the data requirement varies between ages.

The model was used to predict the proportion of fish of each age at a given length, year, quarter and roundfish area. The proportion of fish which were age *a* was set to zero outside the length range in which age *a* was observed to avoid extrapolating small probabilities outside the realistic length span of the age group. Fish larger than the maximum size aged were assigned to the plus group. Combinations of age, year, quarter and roundfish area where less than 5 fish of that age or older, on average, were aged in each length group were not used to predict the proportion at age. In these roundfish areas, a regional model was used to predict the proportion at age. This model analysed the age at length of regions based on two adjacent roundfish areas (areas 1 and 3, 2 and 4, 5 and 6 or 7 and 8, ICES 1996). The parameters *b*, *c* and *d* were estimated using all data (i.e. both data from the sparsely sampled roundfish areas and from other areas) and were allowed to vary with age, year, quarter and region. If the regional data did not fulfil the data requirements, the parameters estimated for the entire North Sea were used to estimate the proportion at age:

$$\log\left(\frac{p_a}{p_{a+}}\right) = b_{a,y,q} + c_{a,y,q} l + d_{a,y,q} l^2$$

The resulting age-length key is a result of the combined proportions at age from these different spatial scales. Hence, the age-length key for a given location may be based on roundfish area data for the youngest age groups whereas North Sea scale data are used for the older age groups.

Estimation of sandeel biomass indices

The biomass of sandeel caught per day in a statistical rectangle *r* in a given year *y* and quarter *q* increases with size of the fishing vessel (ICES 1995), and the biomass available to a vessel of gross tonnage *GT*, $\hat{CPUE}_{GT,y,q,r}$, was modelled as

$$\ln(\hat{CPUE}_{GT,y,q,r}) = \alpha_{q,r} + \beta_{y,q} + \gamma_q \ln(GT)$$

The parameters α, β and γ were estimated using general linear models assuming a normal error distribution of $\ln(CPUE_{GT,y,q,r})$. A total of more than 100 000 Danish logbook records of catches of sandeel per day were used. A standard vessel size of 200 GT was used to estimate and index of the sandeel biomass in a given square and year in the second ($B_{s2,y,r}$) and third ($B_{s3,y,r}$) quarter:

$$B_{s2,y,r} = \exp(\alpha_{2,r} + \beta_{y,2})200^{\gamma_2}$$

$$B_{s3,y,r} = \exp(\alpha_{3,r} + \beta_{y,3})200^{\gamma_3}$$

This model was used to estimate sandeel biomass indices in the years 1983 to 2005 in the 2nd quarter and 1983 and 2004 in the 3rd quarter. Due to catch restrictions, the number of logbook records in the 3rd quarter of 2005 was too low to allow the estimation of reliable sandeel biomass indices. Note that if survey changes in 1991 bias all catches by a common factor, the estimated ambient sandeel biomass index is unaffected by changes in gear:

$$B_{s2,a,y,s} = \frac{1}{\sum_r ca_{a,1} n_{a,y,q,r}} \sum_r ca_{a,1} n_{a,y,s,r} B_{s2,y,r} = \frac{1}{\sum_r ca_{a,2} n_{a,y,s,r}} \sum_r ca_{a,2} n_{a,y,s,r} B_{s2,y,r}$$

where $ca_{a,1}$ and $ca_{a,2}$ is the catchability of cod age a to the survey before and after 1991, respectively and $n_{a,y,s,r}$ is the number of cod of age a caught in an average haul in rectangle r in year y and quarter q.

Estimation of average life time ambient temperature

The estimation of average life time ambient temperature posed a special problem as the distribution of fish younger than 1 year is not necessarily well reflected by the distribution of 0.5-year olds in the 3rd quarter survey. It was therefore decided to assume that the distribution of 1-year olds in the 1st quarter survey reflected that of the cohort up to age 1 for fish of age 1 and 1.5. The estimates of average lifetime ambient temperatures were therefore:

$$T_{L,0.5,y} = \frac{1}{\sum_r n_{0.5,y,s,r}} \sum_r n_{0.5,y,s,r} T_{6-8,y,r}$$

$$T_{L,1,y} = \frac{1}{3\sum_r n_{1,y,s,r}} \sum_r n_{1,y,s,r} \left(T_{6-8,y-1,r} + T_{9-11,y-1,r} + T_{12-2,y,r} \right)$$

$$T_{L,1.5,y} = \frac{1}{5\sum_r n_{1,y,s,r}} \sum_r n_{1,y,s,r} \left(T_{6-8,y-1,r} + T_{9-11,y-1,r} + T_{12-2,y,r} + T_{3-5,y,r} \right) + \frac{1}{5\sum_r n_{1.5,y,s,r}} \sum_r n_{1.5,y,s,r} T_{6-8,y,r}$$

where $T_{6-8,y,r}$ $T_{9-11,y,r}$ $T_{12-2,y,r}$ and $T_{3-5,y,r}$ denotes the average temperature in year *y* in rectangle *sq* in the months June to August, September to November, December the previous year to February the current year and March to May, respectively and $n_{a,y,s,r}$ is the number of cod of age *a* caught in an average haul in rectangle *r* in year *y* and quarter *q*. The estimates of ambient temperature are unaffected by the changes in survey gear as is ambient sandeel biomass index.

Ambient temperature within the last 6 months was estimated as

$$T_{a,y,winter} = \frac{1}{2\sum_r n_{a-0.5,y-1,summer,r}} \sum_r n_{a-0.5,y-1,summer,r} T_{9-11,y-1,r} + \frac{1}{2\sum_r n_{a,y,winter,r}} \sum_r n_{a,y,winter,r} T_{12-2,y,r}$$

$$T_{a,y,summer} = \frac{1}{2\sum_r n_{a-0.5,y,winter,r}} \sum_r n_{a-0.5,y,winter,r} T_{3-5,y,r} + \frac{1}{2\sum_r n_{a,y,summer,r}} \sum_r n_{a,y,summer,r} T_{6-8,y,r}$$

Tables

Table 1. Relationship between halfyearly average North Sea temperature ($T_{NS,y,s}$) and ambient temperatures ($T_{a,y,s}$). Values in bold are significantly different from 0 at the 5% (*), 1% (**) or 0.1% (***) level.

	September to February			March to August	
Age	Correlation[1]	Difference[2]		Correlation[1]	Difference[2]
1	**0.73*** **	-0.07		**0.63** **	-0.03
2	**0.76*** **	**0.29* **		**0.90*** **	**-0.41*** **
3	**0.94*** **	**-0.26*** **		**0.90*** **	**-0.49*** **
4	**0.91*** **	**-0.37*** **		**0.86*** **	**-0.73*** **
5	**0.78*** **	**-0.54*** **		**0.83*** **	**-0.97*** **
6+	**0.81*** **	**-0.69*** **		**0.79*** **	**-1.14*** **

[1] Correlation between ambient temperature and North Sea average temperature

[2] Average difference between ambient temperature and North Sea average temperature ($T_{a,y,s}$ - $T_{NS,y,s}$)

Table 2. Correlation between ln(average length at age of juveniles) and half yearly average North Sea temperature ($T_{NS,y,s}$), ambient temperatures ($T_{a,y,s}$), log density ($\ln\left(N_{a,y,s}\right)$) and fishing mortality ($F_{a,y}$). Values in bold are significant at the 5% level

Age	0.5	1	1.5
$T_{L,a,y,s}$	**0.60****	**0.73*****	**0.63****
$T_{L,NS,a,y,s}$	**0.47***	0.35	0.24
$\ln\left(N_{a,y,s}\right)$	0.20	**-0.41***	**-0.41***
$F_{a,y}$			-0.06

Table 3. Correlation between North Sea average and ambient sandeel biomass in the second and third quarter ($B_{s2,NS,y-1,summer}$, $B_{s2,1.5,y-1,summer}$, $B_{s3,NS,y-1,summer}$ and $B_{s3,1.5,y-1,summer}$, respectively), cod density ($\ln\left(N_{2,y,winter}\right)$) and half yearly ($g_{0.5,y}$) and yearly ($g_{1,y}$) growth rate of cod and between explanatory values and density in the transition period. Explanatory values which were not significantly correlated to one of the two measures of growth rate as either ambient or North Sea average values are not listed. Values in bold are significant at the 5% level.

Age	$\ln\left(N_{2,y,winter}\right)$	$B_{s2,NS,y-1,summer}$	$B_{s2,1.5,y-1,summer}$	$B_{s3,NS,y-1,summer}$	$B_{s3,1.5,y-1,summer}$
$g_{0.5,y}$	**0.49***	**0.58****	**0.50***	0.24	0.09
$g_{1,y}$	**0.51***	0.38	0.30	**0.43***	0.31
$\ln\left(N_{2,y,winter}\right)$		**0.75*****	**0.62****	**0.65****	**0.53***

Figure captions

Fig. 1. Map of the study area. Small rectangles indicates ICES statistical rectangles, Black lines indicate areas used to estimate age-length keys (ICES Roundfish areas).

Fig. 2. Food composition in cod stomachs (data from Kikkert (1993)). Herring and Sprat (white), gadoids (grey) and sandeel (black). Left column within tick marks represents winter (4th and 1st quarter) values, right column represents summer (2nd and 3rd quarter) values.

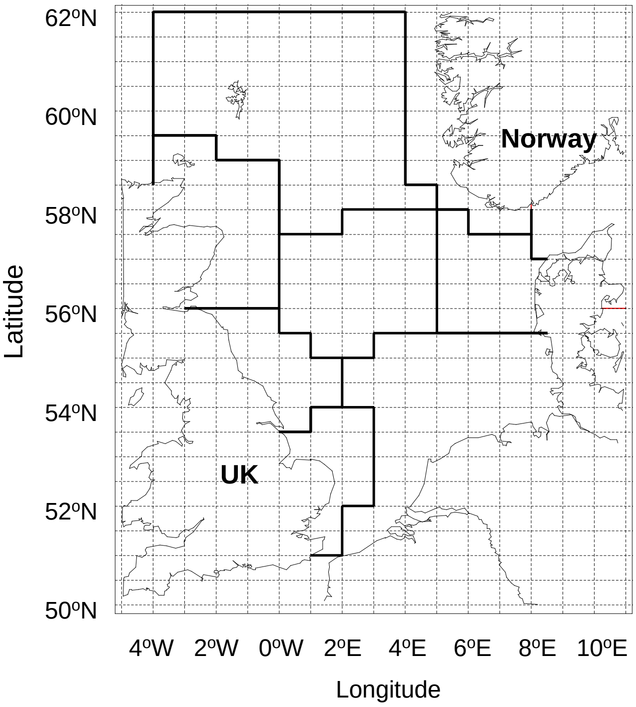
Fig. 3. Average length of selected age groups of cod. a: 0-groups in the 3rd quarter (▲) and 1-groups in the 1st (◇) and 3rd quarter (◆). Symbols not connected indicate change of survey design. b and c: Cod age 2 (×), 3 (□), 4 (△), 5 (+) and 6 (∗) in the 1st (b) and 3rd quarter (c).

Fig. 4. Temporal development in prey biomass indices and density index of cod. Sandeel in the 2nd quarter (a), clupeid fish prey in the 1st (b) quarter, other fish prey in the 1st (c) quarter and density index of cod (d). Average in the North Sea (×) and ambient prey biomass of cod age 2 (□) and 4 (△) (a, b and c) and density of age 2 (□) and 4 (△)(d).

Fig. 5. Temperature and growth according to the model suggested by Björnsson and Steinarsson (2002)(a) and Jobling (1988)(b). a: Growth relative to maximum for the given age. Black indicates 95-100% of max growth, grey shades represent 5% levels of deteriorating growth. Area within white lines represents temperatures experienced in the period from 1983 to 2005. b: Temperature and growth relative to maximum. Note that all size groups exhibit the same relationship between temperature and relative growth in this model.

Fig. 6. Average ln(length) of cod age 0.5 year (a), 1 year (b) and 1.5 (c) years as a function of average life time ambient temperature. Period before (◇) and after (×) 1991 (a and c) and entire periods (◇)(b). Broken lines are regressions for the period before 1991. Lines are linear regressions for the period after 1991 (a and c) and the entire period (b).

Fig. 7. Growth rate during the transition period as a function of density (a) and residuals around a linear relationship between density and growth rate as a function of ambient sandeel biomass (b). Half yearly growth rate $g_{0.5,y}$ (◇) and yearly growth rate $g_{1,y}$ (□). Ambient sandeel biomass are values taken for the 2nd ($B_{s2,1,y-1,summer}$) and 3rd ($B_{s3,1,y-1,summer}$) quarter for $g_{0.5,y}$ and $g_{1,y}$, respectively. Lines are linear regressions for $g_{0.5,y}$ (solid) and $g_{1,y}$ (broken).



1025

1026 Fig. 1

1027

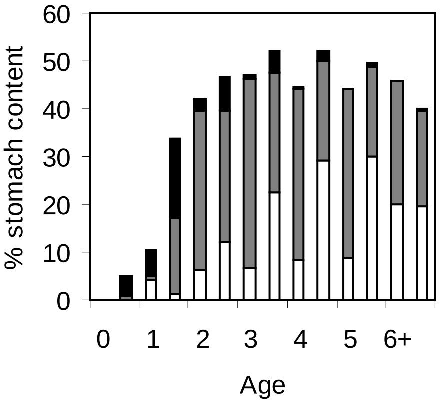
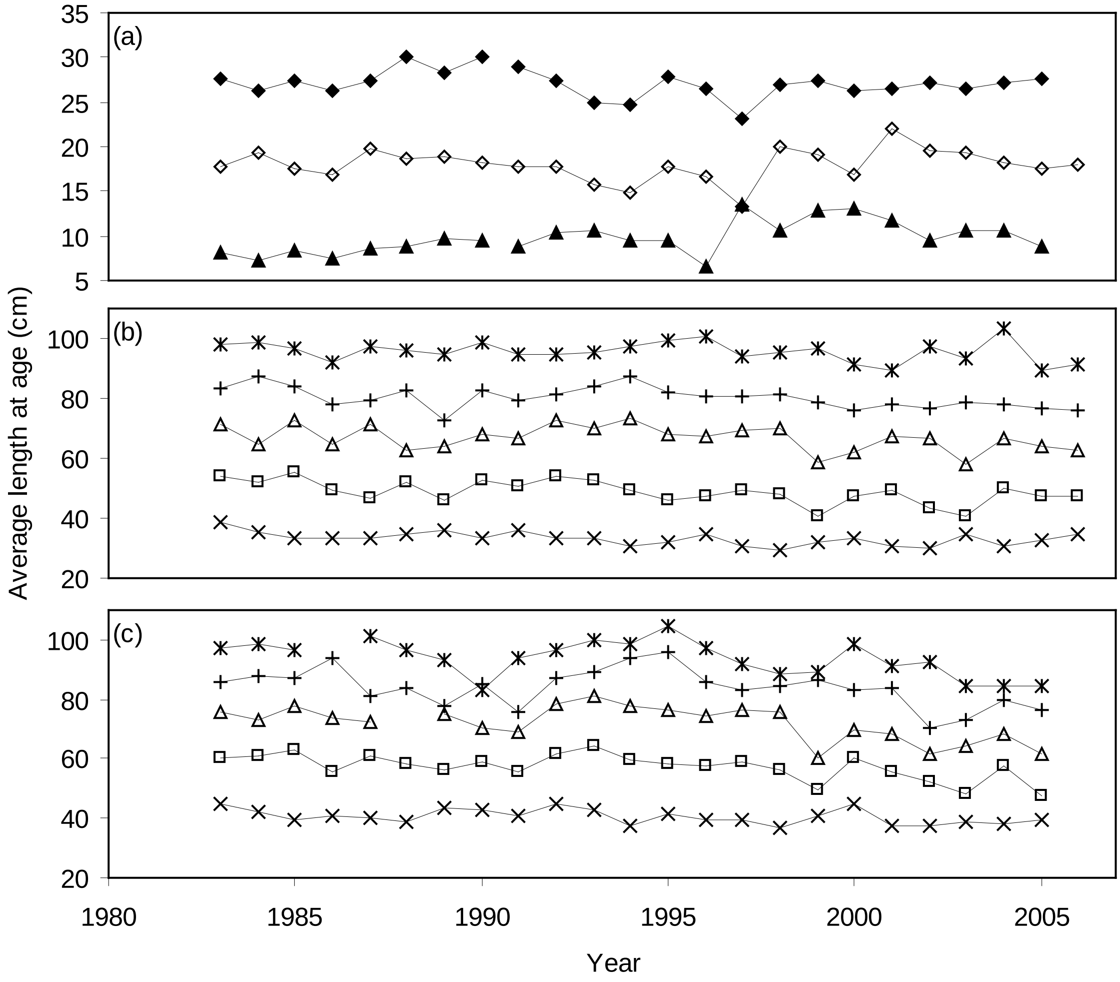


Fig. 2



1031

1032 Fig. 3

1033

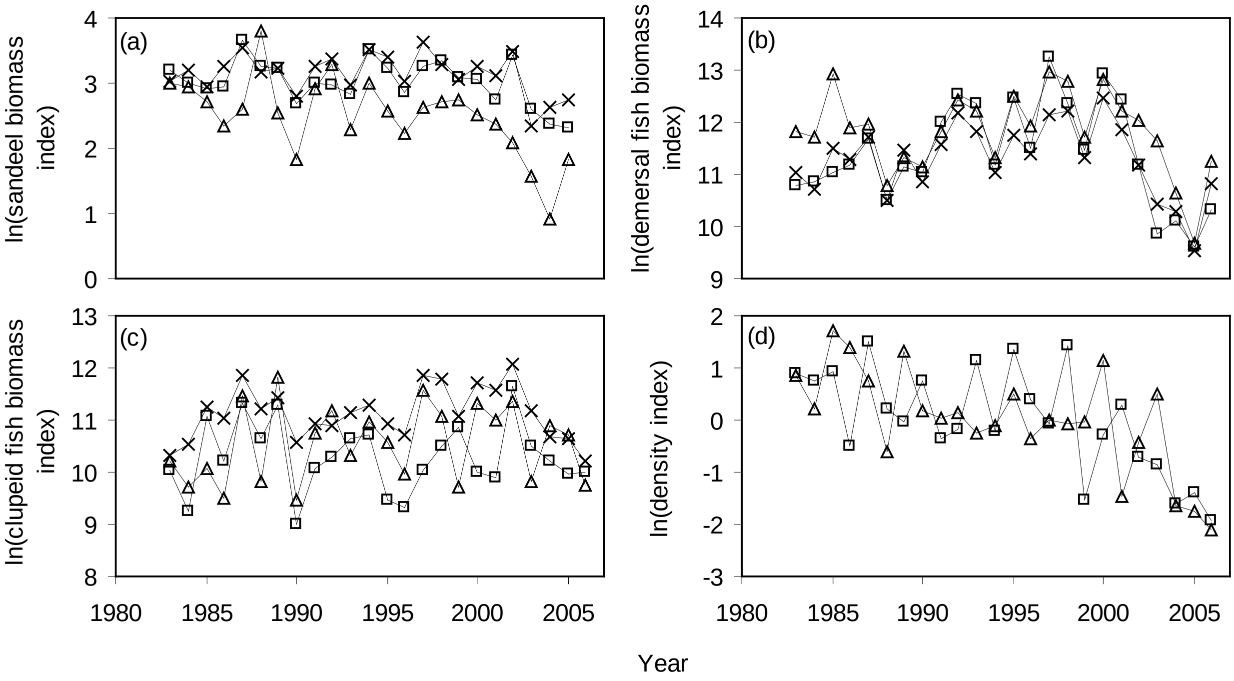

(a)
(b)
(c)
(d)
ln(sandeel biomass index)
ln(demersal fish biomass index)
ln(clupeid fish biomass index)
ln(density index)
0
1
2
3
4
9
10
11
12
13
14
8
9
10
11
12
13
-3
-2
-1
0
1
2
1980
1985
1990
1995
2000
2005
Year

Fig. 4

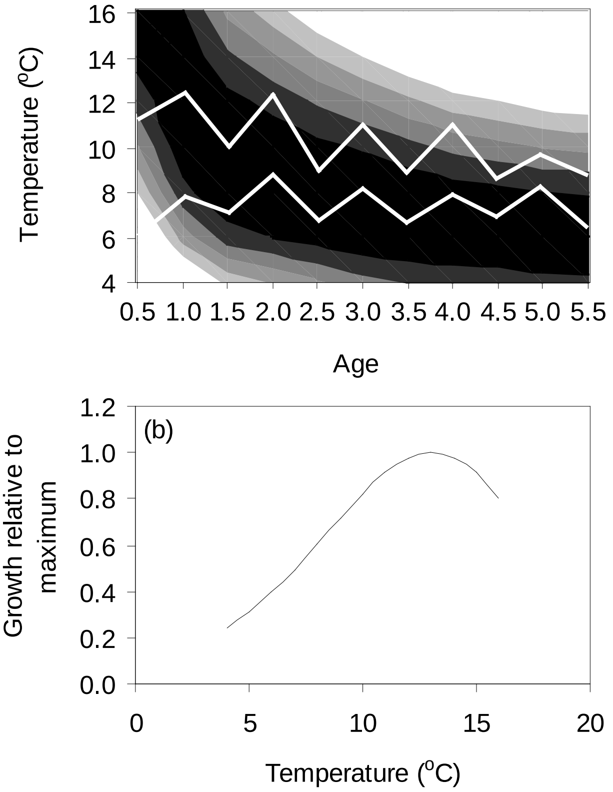

Temperature (^oC)
16
14
12
10
8
6
4
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0 5.5
Age
(b)
Growth relative to maximum
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Temperature (^oC)

Fig. 5

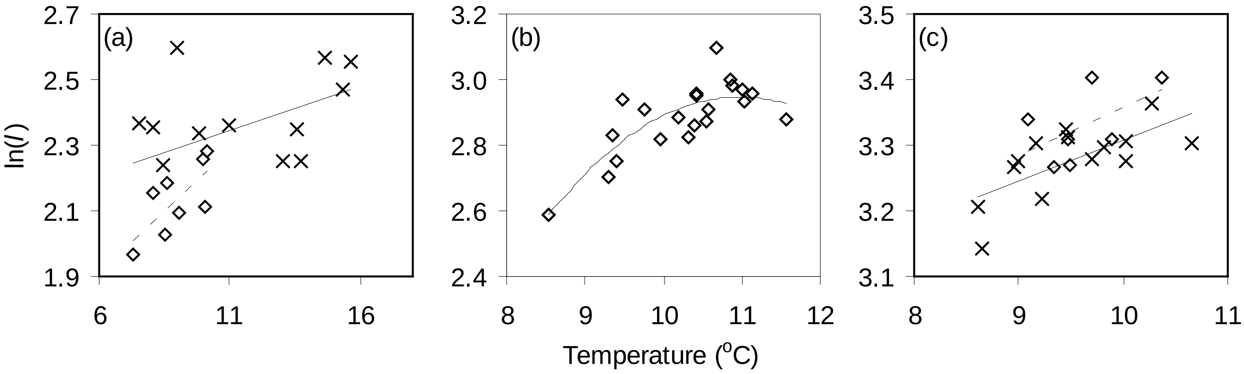

(a)
(b)
(c)
ln(I)
2.7
2.5
2.3
2.1
1.9
6
11
16
3.2
3.0
2.8
2.6
2.4
8
9
10
11
12
3.5
3.4
3.3
3.2
3.1
8
9
10
11
Temperature (^{o}C)

Fig. 6

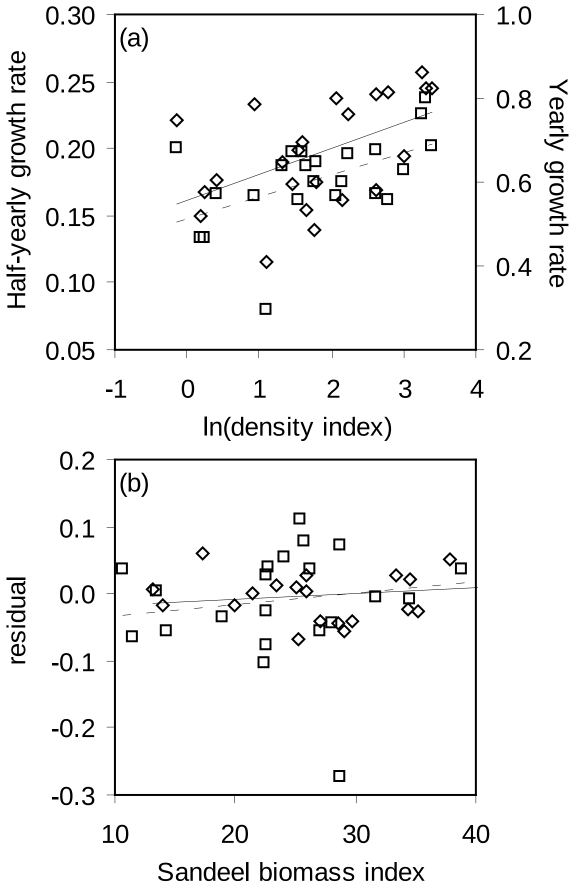

(a)
Half-yearly growth rate
0.30
0.25
0.20
0.15
0.10
0.05
Yearly growth rate
1.0
0.8
0.6
0.4
0.2
-1
0
1
2
3
4
ln(density index)
(b)
residual
0.2
0.1
0.0
-0.1
-0.2
-0.3
10
20
30
40
Sandeel biomass index

Fig. 7