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Spatial differences in growth of lesser sandeel in the North Sea

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Abstract

Lesser sandeel, *Ammodytes marinus*, is a key prey to a variety of North Sea predators, including species such as single load seabirds which are highly sensitive to prey size and condition. While differences in weight at age across the North Sea have been investigated previously, the scale and cause of this variation as well as the potential link to spatial differences in predator performance remains unknown. This study presents an analysis of spatial patterns in length and condition of the lesser sandeel in the North Sea and the relationship of these with physical and biological factors. Both mean length at age and condition was found to be higher on warmer, deeper and central/north eastern fishing grounds. Sandeel in the water column exhibited large changes in condition over the season, having an initially low condition following spring emergence rising to a pronounced peak by June. Weight at age varied considerable both spatially and temporally, resulting in 4 fold and 1.9 fold variation in the number of sandeels required to obtain a specific weight, respectively. Hence, the value of sandeel as prey to single load predators varies considerably with values in central and northeastern North Sea being substantially higher than in northwestern and southern areas.

Highlights

- Spatial differences in growth resulted in 4-fold differences in weight at age 2
- Sandeel condition increased 1.5-fold over the season from early spring to June
- Spatio-temporal distribution of the fishery produced peaks in observed weight
- To obtain a kg of sandeel, the number of prey a predator must ingest varies 6-fold

Key words: Lesser sandeel, length, condition, temperature, spatial differences

1 Introduction

The lesser sandeel, *Ammodytes marinus* (L.), is a small elongate planktivorous fish which forms an important prey source for numerous fish, seabirds and mammals (Daan et al., 1990; Furness, 1990; Engelhard et al., 2014). Beyond their first year of life, their growth season spans only a few months in spring and early summer (Winslade, 1974a; Pedersen et al., 1999; Bergstad et al., 2002) and their spatial distribution is highly restricted (Wright et al., 2000; Jensen et al., 2011), making their importance particularly impressive. Outside these months, sandeel older than 1 year remain buried in the sediment, emerging only in mid-winter to spawn.

In their role as prey for numerous predators, weight and length at age is of great importance as the benefit of sandeel prey to predators depends on the ratio between handling time and prey energy content (Stephens and Krebs, 1986), a ratio to which single prey loading seabirds are particularly sensitive (Wanless et al., 2005). Predators targeting sandeel are likely to experience only minor changes in handling time but profound changes in the weight of prey items with differing prey size. Weight and length at age has been reported to differ across the North Sea, although the evidence for this is partially confounded by differences in the years and areas sampled and the studies cover only a small part of the total distribution area (Macer, 1966; Wright, 1996; Bergstad et al., 2002; Boulcott et al., 2007). If present, spatial differences may potentially explain why strong links between sandeel density and dependent predators such as seabirds have been reported for the north western North Sea (Monaghan, 1992; Rindorf et al., 2000) while further south the eastern English kittiwake populations apparently maintain high breeding success even in years of sandeel recruitment failure and low adult sandeel biomass (Frederiksen et al., 2005; ICES, 2014).

The factors that may affect length and condition include prey and competitor abundance as well as temperature. Temperature directly determines several vital physiological processes in fishes (Jobling, 1985), including food consumption and assimilation rate (Brett, 1979). Positive direct thermal effects on the rate of increase in length and condition will occur when food availability is not limiting and temperature is within the aerobic scope for growth (Pörtner and Rainer, 2007). Over the North Sea, surface and bottom temperatures generally vary by around 3 to 5 ^{o}C during summer (Elliot et al., 1991) and hence spatial differences in temperature could potentially introduce variability in scope for growth. Sandeel are visual feeders on zooplankton, particularly calanoid copepods (Macer, 1966; Winslade, 1974a; van Deurs et al., 2014) and if food is limiting, growth rate will reflect the temporally and spatially varying abundance of prey. Several authors have suggested that growth rate decreases late in the season when food is less abundant (Pedersen et al., 1999; Bergstad et al., 2002) and high local densities may inhibit growth rate through food competition (Bergstad et al., 2002).

Sandeels accumulate large amounts of lipids in their somatic tissue over the foraging season for somatic maintenance and secondary gonad development during the overwinter phase (Hislop et al., 1991; Boulcott and Wright, 2008). The onset of overwintering depends on the build-up of lipid reserves with long or high condition sandeel burying earlier than small individuals (Bergstad et al., 2002; Wanless et al., 2004, van Deurs et al., 2011). Therefore, both regional differences in growth rate and size-differentiated timing of emergence periods may lead to temporal changes in weight at age. Such changes appear in commercial catches where weight at age seems to peak mid-season (Pedersen et al., 1999). However, as there are likely to be regional differences in length and condition, the observed pattern in weight at age may be a sampling artefact caused by temporal changes in the areas fished by the commercial fishery.

This study presents an investigation of length and condition at age of sandeel with the aim to determine (1) whether there are spatial differences in length and condition at age, (2) whether such spatial differences can be explained by differences in biophysical conditions, (3) whether a decrease in weight at age late in the season as reported by Pedersen et al. (1999) is an artefact caused by spatially dependent length and a geographical change in fishing effort, (4) whether site specific decreases in length and condition at age occur late in the season indicating early burial of long or high condition fish and finally, (5) what are the consequences of spatiotemporal differences in weight at age on the number of sandeel required to obtain a kg by area.

2 Material and methods

Length and condition were analysed separately in this study. These two parameters differ in that length is generally monotonically increasing whereas condition may decrease and increase again over the course of the year. Hence, a decrease in length at age is likely to be caused by removal of large individuals from the population whereas this cannot be assumed for a decrease in condition or weight at age. Analysing length and condition rather than weight at age has the further advantage that they are statistically independent and can therefore be compared without the risk of spurious correlations arising. Variation in length and condition was analysed spatially, ignoring cohort and other temporal effects, as the data available were too unbalanced to allow a joint analysis of spatial and temporal variation.

2.1 Sandeel fishing ground definition

Fishing ground distribution was used to determine the distribution of foraging habitat (Jensen et al. 2011). Sandeels show extensive movements within fishing grounds but very limited movements between grounds (Kunzlik et al., 1986; Jensen et al. 2011). Therefore, all data on physical and biological conditions were averaged within fishing ground before further analyses. The only exception to this was the largest fishing ground, where analyses indicate that some spatial structure exists in length composition (Jensen et al. 2011).

2.2 Sandeel biological data

Sandeel data for the analyses were derived from a co-operation between the Danish Fishermens Association and the Technical University of Denmark that started in 1999. Samples of sandeel data up to 2010 were included in analyses, providing a full time span of 12 years. After 2010, the number of samples is lower and the spatio-temporal coverage changed in some years due to severe limitations on the fishery. The fishery targets several species of sandeel of which *A. marinus* is by far the most important and the focus of this study. Samples were collected by fishers directly from fishing vessels and the exact location and time of shooting and hauling of the trawl and the estimated total weight of the catch in the haul were recorded for each sample. Approximately 1 kg samples of sandeel were taken randomly from the catch. Bycatch of other species in the sandeel fishery consists of a very low percentage of gadoids and these were not included in the samples. In the laboratory, sandeel were sorted by species, and total length, L, in a subsample of *A. marinus* measured to the nearest half cm below. Comparison of the length distribution of these samples with randomly selected port samples taken from vessel landings indicated that there was no bias induced by fishermen's sampling. 5 to 10 sandeel per half cm group were randomly selected and age estimated using the sagitta otoliths. Age estimation was conducted by two readers following ICES protocols on the seasonal appearance of translucent and opaque zones in sandeel otoliths and the identification of secondary growth structures using daily increments (Wright, 1993; ICES, 1995). Reader agreement tested in workshops with other institutions was 83% for all ages (e.g. ICES, 2006). As age estimation agreement tends to decrease with age (ICES, 1995), fish of age 4 and older were grouped into a plus-group. Fishing ground was assigned to samples from the location of the midpoint of the haul.

Mean length at age was estimated by combining sampled length distributions with age-length keys. Age-length keys were produced separately for each fishing ground in each week and year using the method described by Rindorf and Lewy (2001) on all data available from the given fishing ground, week and year. Where possible, only data from the particular week in which a length sample was taken were used to estimate the age length key for the sample. If less than 50 sandeel were aged in a specific week or weekly data resulted in confidence intervals of the predicted proportion at age which were larger than 0.25, 2-week periods were used to estimate the age-length key. No further temporal aggregation of samples was conducted to ensure that no bias was introduced in length at age by using incorrect age-length keys. Each haul resulted in one mean length at age for each age group except if the predicted number at age was below 5. Mean lengths based on less than 5 fish were judged to be highly uncertain and excluded. Hence, number of mean lengths available differed between ages as not all ages were sufficiently represented in all samples. Age 0 sandeels were only partly selected by the fishing gear and hence were not included in analyses of length and condition. Due to uncertainty in the true age of 4+ sandeel, this age group was not included in the von Bertalanffy analyses. There was no subsequent weighting of the samples to reflect the catch in the haul from which the sample was taken or the number length measured in the sample.

Average condition *C* of fish of length *L* in each sample was estimated from the average weight *W* of fish of this length in the sample (Le Cren, 1951):

$$C = W/L^b \qquad (1)$$

The parameter *b* was the exponent estimated from the length-weight relationship derived from all samples together:

$$W = C_m L^b \qquad (2)$$

where C_m denotes the monthly average condition across all years and fishing grounds. The error around the relationship was assumed to be gamma distributed as the variation in weight increased with the mean. The average condition of each age group recorded in a sample was estimated as the average between half cm groups, weighted by the number of fish of the given age in the half cm group.

Catch in numbers per minute was assumed to be an index of density (Hilborn and Walters, 1992) and was estimated by combining catch in kg/minute haul time with the number of sandeel per kg in the particular haul. The geometric average catch in numbers per minute (all ages together) on each fishing ground in the particular week averaged over all years was used as an index of sandeel density.

2.3 Biophysical conditions

Average predicted biophysical conditions were derived from models as samples with sufficient spatio-temporal coverage were not available. The model predictions are average values based on information from a large number of individual samples whereas the sandeel mean length and condition are observations based on single samples. The sampling error in sandeel length and condition is therefore likely to be substantially larger than that of model predicted biophysical conditions, allowing the use of biophysical variables as independent factors in models without the use of methods, such as functional regression, to correct for variability in the independent factors.

Average predicted bottom and surface temperatures at each fishing ground across all years was taken from a 3 dimensional finite difference hydrodynamic model set up in spherical coordinates (She et al., 2007). Temperature within each fishing ground was estimated as the average temperature of locations within the fishing ground, averaged over the months March to June, since this is considered to be the period of most active feeding and growth (Macer, 1966; Bergstad et al., 2002; van der Kooij et al., 2008), and the years from 1999 to 2008.

Data on protozooplankton and copepods were generated by a 3D circulation model (She et al., 2007) coupled to the Ecological ReGional Ocean Model (ERGOM) for the years 2004-2006 (Maar et al., 2011). The version used contains 11 pelagic state variables describing nitrogen cycling through 3 groups of phytoplankton (diatoms, flagellates and blue-green algae), microzooplankton, mesozooplankton, and detritus and sea water concentrations of nutrients (NO_3, NH_4, PO_4, SiO_2) and dissolved O_2. Model data of both zooplankton groups is summed, vertically integrated and the ground specific average over the months March to June estimated over all three years. The accuracy of model predictions for mesozooplankton biomass has been verified by comparison with field samples by Gürkan et al. (2013) and Maar et al. (2014). Plankton data were only available for the years 2004 to 2006 and temperature data from 1999 to 2008. Maps of the biophysical input variables can be seen in fig. 1.

3 Calculation

3.1 Estimating growth age

As sandeels feed and grow in a limited period during spring and summer, the growth function used to describe length at age should take account of this rather than assume constant length growth over the year. A solution to this is to estimate the 'growth age', t_g, as the difference between true age (in decimal years) t_a and the time spent buried, the product of the length of the buried season t_b, and the age in years, t_y, equal to 0, 1, 2 or 3:

$$t_g = t_a - t_y t_b \qquad (3)$$

By subtracting buried periods, length becomes a smooth function of time for fish caught during the growth period. The duration of the length growth period was estimated to be 15.0 weeks (Supplementary material). Age 0 was set to week 12 of the year of hatching as this was the first week where samples were available. The choice of start week is relevant in combination with the estimated t_0 (see below) to determine length at the first occurrence in the samples. For subsequent ages, the choice of week 12 does not imply that length growth must start in week 12. It only implies that the number of weeks from the cessation of length growth in one year to the onset of length growth in the next year is 37 weeks (=52 weeks-15 weeks). Hence, length growth may start earlier than week 12 and cease earlier than week 27 without affecting the analyses.

3.2 Identifying the effects of long term average biophysical conditions on length at age and condition

The effect of biophysical conditions on length at age was estimated through analyses of the parameters of the von Bertalanffy growth equation based on data from the entire North Sea and ignoring any cohort effects. This method is suitable for revealing the effect of average conditions at the fishing ground (e.g. average bottom temperature at the fishing ground during the growth season) on growth in length. The relationship was analysed by first estimating a common von Bertalanffy equation for all samples (eq. 4) by minimizing the squared deviation between observed and predicted length, $\hat{l}$, from the model:

$$\hat{l} = L_\infty\left(1-\exp\left(-K(t_g-t_0)\right)\right) = L_\infty\left(1-\exp\left(-K(t_a-t_y t_b-t_0)\right)\right) \qquad (4)$$

where L_∞, *K* and t_0 are the parameters of the von Bertalanffy equation describing asymptotic length, intrinsic somatic length growth rate and the theoretical age at length 0, respectively. A second von Bertalanffy relationship was then constructed where one of the parameters L_∞, *K* and t_0 was a second degree polynomial in one of the explanatory variables. The decrease in variation (sum of squares) incurred by including the effect of the explanatory variable was then evaluated with an F-test. This was performed for the following explanatory variables; surface temperature, bottom temperature, copepod biomass, proto-zooplankton biomass, depth, latitude, longitude and average density at the given fishing ground. All variables were normalized to range between -1 and 1 before estimating the parameters to facilitate the optimisation of the model parameters in the non-linear model (Zuur et al., 2009). The correlation between explanatory variables was investigated to determine whether any combinations of variables exhibited high collinearity. One model was then fitted for each of the combinations of a 2nd degree polynomial effect of the factors surface temperature, bottom temperature, copepod biomass, proto-zooplankton biomass, depth, latitude, longitude and average density on each of the parameters L_∞, K and t_0, a total of 24 model fits. The model with the highest probability of improving the description of mean length at age was then chosen (F-test) and the procedure repeated using this model as the new basic model and comparing this to models adding all remaining combinations of effects one at a time. Once a second degree polynomial of a particular factor had been found significant, higher degree polynomials of the particular factor were also tested. Cross effects between the explanatory variables were not tested with the exception of those between latitude and longitude. As the objective of this analysis was to identify major sources of variation rather than all sources of variation, only factors explaining more than 1% of the residual variation in mean length from a common von Bertalanffy were included in the final model.

In addition to the analyses of length at age, the relationship between average condition at each fishing ground and the long term average biophysical conditions surface temperature, bottom temperature, copepod biomass, proto-zooplankton biomass, depth and average density at the given fishing ground was analysed. To describe a relationship where condition increases with time but possibly decreases in the end, a second degree polynomial effect of the different variables was added to the model of condition as a function of week:

$$C = pol_3(week) + pol_2(x) \qquad (5)$$

Where x denotes the variable investigated and $pol_i(x)$ is a i^{th} degree polynomial in x. The relationship between average condition at age and week was analysed by fitting a 3rd degree polynomial as preliminary investigations showed a plateau in this state which was poorly fitted by a 2nd degree polynomial.

A joint model for all ages with a separate polynomial for the effect of week for each age group was used whereas the effect of the biophysical variable tested was the same for all ages. Similarly to the analyses of the von Bertalanffy parameters, the variable with the highest F-value was added to the model and the process rerun to examine the effect of the remaining variables (Forward elimination). Only weeks with at least 100 observations were used to assure that the effect of week was not affected by poorly sampled weeks outside the main season.

Finally, to investigate whether the samples are unbalanced with respect to the spatial distribution of samples in different weeks, the average latitude and longitude of samples were estimated and the presence or absence of trends in these were derived by estimating the Pearson correlation between week and latitude and longitude, respectively.

3.3 Changes in length and condition of sandeels accessible to the fishery

As the emergence behaviour of sandeels can affect the length and condition of individuals in the catch, changes in length at age were examined at grounds where fishing took place over at least 5 weeks in a season. A second degree polynomial was fitted to length at age, $\hat{l}$, as a function of week (t) at fishing grounds where at least 3 samples were taken in each of at least 5 weeks during a season. If the second degree term of the polynomial was significantly negative, the predicted length in the last week sampled was compared to the confidence interval of the predicted length in the week where length was predicted to be greatest. If the predicted length in the last week fell below this confidence interval, a significant decrease in length late in the season was recorded. This method was used rather than a non-linear model, as the non-linear model was unable to estimate the saturation level. In addition to this, the residual length at age from the von Bertalanffy model as a function of week of the season was investigated for trends.

Even if there is no difference in the fraction buried at length early and late in the season, higher conditioned sandeels may have buried earlier leading to a decline in the average condition of sandeels accessible to the fishery late in the season. Therefore, seasonal changes in average condition were modelled using the same methodology used to consider length changes. To investigate the change in condition over the course of a season, condition of 1- and 2-year olds in samples from fishing grounds were examined to detect decreases in length at age. Due to limited spatial coverage late in the season, samples taken later than week 22 were excluded from the analysis.

3.4 Spatio-temporal differences in weight at age

Weight at age was predicted for each bank and week by estimating length and age and condition from the reduced models of length at age and condition, respectively.

4 Results

4.1 Data and initial analyses

A total of 478 702 sandeel were length measured in the samples taken. Of these, age was estimated in 228 668. After eliminating samples from fishing grounds where <5 hauls were taken, samples from outside the main fishing season, samples from fishing grounds and weeks where age-length keys were not available as well as samples taken outside the area covered by the zooplankton data, 384 175 length measurements were used to calculate a total of 3 856 estimates of length at age originating from 68 fishing grounds (fig. 2, fig. 3). Of these, 54% were length at age 1, 34% age at length 2 and 11% length at age 3.

The length - weight relationship had the exponent b=3.060 (standard deviation=0.005) and the monthly average condition factors are given in table 1. A total of 38 425 observations were included in the analyses and length explained 93% of the total deviance in weight and monthly differences in average condition explained another 1.0%. There was an initial increase in average condition followed by a significant decrease in July (table 1).

4.2 Identifying the effects of long term average biophysical conditions on length at age

By far the largest part of the variation in length was explained by the effects of latitude and longitude on L_∞ and K, respectively. These factors together explained 41% of the variation in mean length at age (table 2). The final model based on the normalised variables was

$$\hat{l} = L_\infty\left(1-\exp\left(-K(t_g - t_0)\right)\right) = L_\infty\left(1-\exp\left(-K(t_a - t_y t_b - t_0)\right)\right)$$

where

$$K = 0.609^{(0.032)} + 0.152^{(0.014)}Lon - 0.086^{(0.012)}Lon^2 + 0.308^{(0.028)}T_S + 0.274^{(0.033)}T_S^2$$
$$+ 0.073^{(0.010)}D - 0.072^{(0.012)}D^2$$

$$L_\infty = 17.6^{(0.22)} - 0.44^{(0.23)}Lat - 10.3^{(0.57)}Lat^2 + 11.9^{(1.0)}Lat^3 + 19.5^{(1.3)}Lat^4$$

$$t_0 = -0.734^{(0.061)}$$

and *Lon* is longitude, T_S is surface temperature, *Lat* is latitude, *D* is depth and values in parentheses denote standard error of the estimates. The response of L_∞ and *K* to latitude, longitude, surface temperature and depth is shown in Fig. 4. The polynomial in latitude was weakly determined at the extremes and fixing normalised latitudes to >56.6 °N or <52.7 °N improved the fit significantly and resulted in the parameters shown here. The final model explained 46.9% of the total variation around a common von Bertalanffy relationship. Fish were larger in the northeast North Sea and had a higher intrinsic somatic length growth rate in warm areas and areas which were not too shallow (fig. 4, fig. 5). Variation in von Bertalanffy parameters associated with the minimum, median and maximum observed values of the contributing factors is given in Fig. 5. Location had a large effect on length at age and condition even after accounting for temperature. This can be illustrated from predicted length and condition at the different sandeel grounds as a function of local latitude, longitude, surface temperature and depth, with a 10.1 cm range in length at age 1 across the grounds (fig. 6).

Among the explanatory variables, 3 pairs showed high correlation (Pearson correlation>0.8): copepod biomass and proto-zooplankton biomass (correlation=0.81), bottom temperature and latitude (correlation=0.89) and bottom temperature and depth (correlation=-0.80). Among these factors, only latitude was included in the final model. Surface temperature, longitude and sandeel density were not highly correlated to any of the other variables.

The factors having the greatest effect on average condition at a fishing ground were almost identical to those affecting the parameters in the von Bertalanffy model of growth in length. The final model of condition included effects of week, age, latitude and sea surface temperature. Week and age explained 42% of the total variation and condition increased with latitude and sea surface temperature (latitude r^2=0.054 and sea surface temperature r^2=0.037). The r^2 increased by less than 1% by adding further variables. The reduced model of condition in mg/cm$^{3.06}$ was

$$C = pol_3(week|age) - 2.56^{(0.43)}Lat + 0.0240^{(0.0039)}Lat^2 + 0.104^{(0.012)}T_S$$

Where

$$\begin{aligned} pol_3(week|age) = {} & 8.2^{(1.6)} - 0.339^{(0.053)}age \\ & + \left(-1.38^{(0.28)} + 0.0193^{(0.0029)}age\right)week \quad + 0.102^{(0.016)}week^2 \\ & - 0.00228^{(0.00030)}week^3 \end{aligned}$$

Condition of all ages peaked in week 20 and condition of age 1 sandeel was slightly higher than that of older sandeel.

Average longitude of the samples showed a clear temporal pattern with a significant decrease in longitude over the season (correlation= -0.59, *P*=0.0197). The trend appeared to be dome shaped rather than linear, and estimating a second degree polynomial relationship between week and average longitude resulted in an r^2 of 0.82. There was no trend in average latitude of the samples over the weeks (correlation= -0.22, *P*=0.4203). The trend in longitude combined with the almost monotonically increasing relationship between longitude and *K* resulted in a clear dome shaped relationship between predicted length in the samples and week of the season and hence a relationship between age and length which appears to fluctuate around a von Bertalanffy relationship (fig. 7). Mean length at age in the samples peaked around midway through the season, with decreases of 1.4 and 0.9 cm thereafter, corresponding to 11 and 7% for ages 1 and 2, respectively. This corresponds to an apparent decrease in mean weight from the maximum observed of 23% and 38%, respectively, at the end of the season. As the model of length at age did not include any decrease in length growth late in the season, this effect was entirely caused by the unbalanced sampling design of the fishery, which started at higher longitudes.

4.3 Changes in length and condition of sandeels accessible to the fishery

Only four fishing grounds were sampled sufficiently in any one year to be included in the analyses of a late season decrease in length, and each of them only in one year (fig. 8). Of these, the concave second degree polynomial fitted the data significantly better than a linear relationship only at Berwick Bank ($P<0.02$ for both ages). This fishing ground was sampled markedly later in the season than the others, and this could be the reason for the absence of an effect at the other grounds. Length at age was significantly lower than the observed maximum for weeks greater than 24 for age 1 and weeks greater than 23 for age 2. The decrease observed up to the last sampling week was 0.8 cm for 1-year olds and 1.7 cm for 2-year olds, corresponding to 6 and 13%, respectively (fig. 8).

Condition was a significantly concave function of week ($P<0.05$) for all ages at all banks except for age 1 at Southernmost Rough and age 2 at Berwick Bank and Stendysse ($P>0.25$)(fig. 9). The condition at age 2 on N. W. Rough reached a plateau from which it did not decrease significantly while condition at age 1 decreased significantly from week 21 onwards, in total exhibiting a decrease in condition of 15%. The samples in which the decrease in condition at Berwick Bank was recorded were obtained after week 22 exhibiting a decrease in condition of 12 and 13%, for ages 1 and 2 respectively. Condition in the remaining cases increased monotonically with week until week 21 (fig. 9). Across the four banks, condition appeared to increase from values as low as 2.0 $\mathrm{mg}\bullet\mathrm{cm}^{-3.06}$ until a peak value of 3.2-3.5 $\mathrm{mg}\bullet\mathrm{cm}^{-3.06}$ was attained around week 20-22 (late May – early June), corresponding to more than 160% of that recorded at the beginning of the season.

Together with the observed decrease in mean length late in the season, the decrease in condition of individuals accessible to the fishery resulted in a predicted decrease in mean weight of 34% and 15% in age 1 sandeel at Berwick bank and N. W. Rough, respectively and of 64% in age 2 sandeel at Berwick Bank, corresponding to 4.9% per week and 3.8% per week in age 1 sandeel at Berwick bank and N. W. Rough, respectively and 9.1% per week in age 2 sandeel. The remaining 5 combinations of fishing ground and age showed no significant decrease in mean length or condition late in the season and hence no decrease in mean weight at age.

4.4 Spatio-temporal differences in weight at age

Weight at age varied considerable both spatially and temporally. Weight at age 2 in week 21 varied 4-fold between locations in the North Sea (4.6 to 19.0 g), corresponding to 216 to 53 age 2 sandeel per kg. Within a specific location, weight at age varied from the beginning to the end of the season, but the variation was substantially less than the spatial variation. For example, mean weight at age 1 and 2 increased by 90% and 65%, respectively, from week 13 to 20 at N. W. Rough, corresponding to 264 1-year olds sandeel in week 13 compared to 139 in week 20.

5 Discussion

Whilst the existence of spatial differences in growth rate of lesser sandeel within the North Sea has been reported previously (Macer, 1966; Bergstad et al., 2002; Wanless et al., 2004; Boulcott et al., 2007), the present study provides the most comprehensive view of regional variability in any sandeel species. Sandeel grew faster at eastern locations, at high temperatures and at greater depths and the asymptotic length and condition both increased towards northern sandeel banks. Further, condition was higher at warmer fishing grounds. While a few instances of lower length or condition at age late in the season were recorded, the regional differences in length at age combined with the spatio-temporal distribution of the fishery were sufficient to explain the dome-shaped relationship between length and week of the year. No further sign of dome shaped patterns could be seen in the residuals from the model. Weight at age varied considerably and spatial and temporal differences resulted in 4 fold and 1.9 fold variation in the number of sandeels required to obtain a specific weight, respectively. Hence, unless handling time differs substantially between sandeel size groups, the energy value of sandeel as prey to predators varies considerably.

Temperature had a large positive effect on *K* while there was no effect on asymptotic length or t_0. *K* in the original theoretical foundation of the von Bertalanffy equation is directly proportional to standard metabolic rate, a factor known to increase exponentially with temperature (Behrens et al., 2007). As temperature influences the emergence of sandeels (Winslade, 1974b; van der Kooij et al., 2008), feeding activity (Winslade, 1974b) and the scope for growth, this factor may be expected to explain a large component of length-at-age variability. Average copepod and proto-zooplankton biomass and average density at the given fishing ground did not affect length or condition at age. However, this may reflect the fact that standing biomass alone is not the determining factor, as also duration, production and timing of the feeding period relative to peak zooplankton abundance plays a role. For example, copepod biomass tends to peak later and for a shorter period in the north western North Sea than in the north east North Sea (Fransz et al. 1991), corresponding with the low and high growth areas for sandeel. Condition of age 1 sandeel was slightly higher than that of older sandeel. This matches their higher energy requirements during the overwintering phase (van der Kooij et al. 2008, van Deurs et al. 2011).

There was little evidence of length-related differences in the onset of winter burying through to week 22 as only 25% and 33% of the relationships between week and length and week and condition, respectively, were significantly decelerating. The decrease in mean length and weight at age over the season observed here and in

Pedersen et al. 1999 was therefore largely a result of changes in the distribution of the fishery from the early exploitation of the central and eastern banks, where mean length is large, to the later fishery on western grounds, where mean length is smaller (fig. 6). The low occurrence of decreases in mean condition late in the season is in contrast with results on mean weights on some grounds reported by Bergstad et al. (2002) and Wanless et al. (2004). However, these studies reported the decrease to commence around midsummer, which approximately marks the end of the sampling period in this study. The decrease in length and condition observed at Berwick Bank after week 22 and the lack of any increase in length of age 2 sandeels at 2 of the 4 grounds examined could be consistent with these local studies. Hence, it is possible that size differentiated burying takes place after mid-summer.

The length of the growth season for the three grounds with sufficient data yielded a combined average of 15 weeks, although this may be linked to their close geographic proximity. If length of the season varies geographically, it is possible that part of the effect recorded on the von Bertalanffy parameters is caused by effects on the length of the growth season rather than effects on K and L_∞. Estimation of season length at other fishing grounds would provide information on the range of values exhibited by this parameter and would improve the estimates of local parameters.

The von Bertalanffy parameters reported here are determined from average length in the catches at consecutive points in time and therefore are only estimates of the actual length growth rate of individual sandeel if catchability is independent of length and mortality is not size related within a given age group, time and place. Catchability of sandeel is determined by the selectivity of the gear and the coincidence between sandeels in the water column and the path of the gear (Hilborn and Walters 1992). Sandeel fisheries operate with very small mesh sizes and it seems unlikely that there will be major length differences in catchability within the path of the gear. However, there is a possibility for mean lengths to be affected by length differences in horizontal distribution. If the sandeel move into the fishing ground as they grow, this will tend to depress length growth rates estimated from mean lengths (Jensen et al., 2011). However, such a depression should be evident by a mismatch between the length of individuals at the end of a season and the length of individuals of the same age in years at the beginning of the subsequent season as large fish will be overrepresented in the beginning of the season. This was not observed here and there was generally a good agreement between length at age 1 in the end of the growth season and length at age 2 in the beginning of the season the subsequent year, as demonstrated by the estimated season length which depended on the close correspondence between length at the end of the seasons and in the beginning of the subsequent season (supplementary material).

Mortality of fish prey is often reported to be size dependent (Ursin, 1973; Cook, 2004). However, though such size dependence would affect the parameters estimated, it is unlikely to explain the differences in length at age between north and south and low and high temperature areas reported in this study. For this to be the case, the predation on large sandeel should be lower in the northern-eastern North Sea and in areas of high surface temperature. This seems unlikely as the abundance of both gadoids and mackerel is highest in the northern North Sea (Cunningham et al., 2007; Lewy and Kristensen, 2009) and consumption by predatory fish should be positively related to temperature within the range observed here.

The spatial differences in length and condition at age have important implications to local productivity, as fecundity is related to weight at age (Gauld and Hutcheon, 1990; Boulcott and Wright, 2008; Boulcott and Wright, 2011) and fast growing *A. marinus* can mature a year earlier (Boulcott et al., 2007). Sandeel near the UK coast, such as at Berwick Bank, were shorter at age than other aggregations and this partly explains why few age 2 were found to mature in this area (Boulcott et al., 2007). Conversely, sandeel at banks in the north eastern North Sea appear to grow rapidly and some are able to mature as young as age 1 (Boulcott et al., 2007).

Sandeel grew to a larger asymptotic length in the central and north-eastern North Sea than in north-western areas. Weight at age 2 in week 21 varied 4-fold between locations in the North Sea. The variation in temporal weight was substantially less than the spatial variation. For example, mean weight at age 1 and 2 increased by 90% and 65%, respectively, from week 13 to 20 at N. W. Rough. A predator which captures each sandeel individually therefore experiences poorer energetic returns in the north-western North Sea than in other areas, an effect that may be aggravated by higher energy density of high condition fish. This is likely to make predators in the north-western North Sea particularly sensitivity to changes in sandeel abundance. This is in accordance with both the general level and the annual variation of kittiwake breeding success, which is high and stable in eastern English colonies but low and highly variable in eastern Scottish colonies (Frederiksen et al., 2005). If this relationship is extrapolated, single load predators of sandeel may be expected to experience problems in the far south part of the North Sea as well.

6 Conclusions

Whilst the existence of spatial differences in growth rate of lesser sandeel within the North Sea has been reported previously (Macer, 1966; Bergstad et al., 2002; Wanless et al., 2004; Boulcott et al., 2007), the present study provides the most comprehensive view of regional variability in any sandeel species. Sandeel grew faster at north-eastern and central locations, at high temperatures and at greater depths and the asymptotic length and condition both increased towards northern sandeel banks. Further, condition was higher at warmer fishing grounds. While a few instances of lower length or condition at age late in the season were recorded, the regional differences in length at age combined with the spatio-temporal distribution of the fishery were sufficient to explain the dome-shaped relationship between length and week of the year. Hence, the results clearly show the danger of making assumptions on the biology of a species based on a biased sampling design. Weight at age varied considerable and spatial and temporal differences resulted in 4 fold and 1.9 fold variation in the number of sandeels required to obtain a specific weight, respectively. Hence, the value of sandeel as prey to single load predators varies considerably with values in central and north-eastern North Sea being substantially higher than in north-western and southern areas.

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Marine Life, Impact on Economic Sectors (VECTORS). P. Wright was supported by the Scottish Government project ST007. We are deeply grateful to the fishing skippers who collected the data and placed them at our disposal, to Stina B. S. Hansen, Nina Fuglsang and the laboratory assistants who worked up the thousands of length samples and age determined an immense number of otoliths and to Josefine Egekvist for mapping.

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Tables

Table 1. Monthly average condition (only months with more than 1000 observations included).

Month	$10^3 * C_m$ (g/cm$^{3.06}$)
March	2.32 (2.25-2.39)
April	2.71 (2.65-2.76)
May	3.10 (3.03-3.17)
June	3.04 (2.98-3.11)
July	2.83 (2.74-2.92)

Table 2. Effects of local average factors on von Bertalanffy parameters. Proportion of residual variation in mean length explained by each factor (forward selection). Only factors explaining at least 1% of the residual variation were included. All factors were highly significant ($P<0.0001$).

Variable	Effect on parameter	F(df1,df2)	r^r	Cummulated r^r
Longitude	K	570(2, 3854)	0.228	0.228
Latitude	L_∞	597(6, 3848)	0.183	0.411
Surface temperature	K	95(2, 3846)	0.028	0.439
Depth	K	109(2, 3844)	0.030	0.469

Figure captions

Fig. 1. Maps of biophysical variables used in spatial analyses. Depth (A), sea surface temperature (B), proto-zooplankton (C) and copepods (D).

Fig. 2. Sampling locations (x), fishing grounds (grey polygons) and named fishing grounds (text) referred to in the study.

Fig. 3. Length as a function of growth age.

Fig. 4. Predicted effect of latitude on L_∞ (A), longitude on K (B), sea surface temperature on K (C) and depth on K (D).

Fig. 5. Effect of longitude (A, effect on K), latitude (B, effect on L_∞), sea surface temperature (C, effect on K) and depth (D, effect on K) on length at age. Length at age predicted at maximum (solid), minimum (hatched) and at midways between maximum and minimum (at a value of (maximum-minimum)/2, hatch-dot). Black lines refer to the estimated length, grey lines to the 95% confidence interval of the estimate.

Fig. 6. Maps of predicted length at each ground in week 21 at age 1 (A), 2 (B) and 3 (C) and predicted condition at age 1 in week 21 (D). Shading indicates mean length and condition, respectively, white indicating the lowest level and black the highest. Minimum length at age 1, 2 and 3: 7.0, 12.1 and 13.1 cm, respectively. Maximum length at age 1, 2 and 3: 17.1, 19.5 and 21.2 cm, respectively.

Fig. 7. Predicted length as a function of growth age estimated from the final von Bertalanffy model (A) and residual from predicted length as a function of growth age (B). The von Bertalanffy model used to predict length does not include a decrease in length growth rate over the season and the apparent drop in length from the middle of the

season is entirely driven by changes in spatial distribution of the fishery. Line indicates average predicted length per week over the entire data set (A) and a second degree polynomial (B).

Fig. 8. Development in length at age as a function of week at N. W. Rough in 2006 (A), Berwick Bank in 2003 (B), Southernmost Rough in 2006 (C) and Stendysse in 2003 (D). Age 1 (solid diamonds) and 2 (open triangles). Solid line is a second degree polynomial, hatched lines are 95% confidence limits of the mean.

Fig. 9. Development in average condition factor over the season. Condition at age 1 (solid diamonds) and 2 (open triangles) as a function of week at N. W. Rough in 2006 (A), Berwick Bank in 2003 (B), Southernmost Rough in 2006 (C) and Stendysse in 2003 (D). Solid line is a 2nd degree polynomial of age 1, long dash a 2nd degree polynomial of age 2 and hatched lines are 95% confidence limits of the mean.

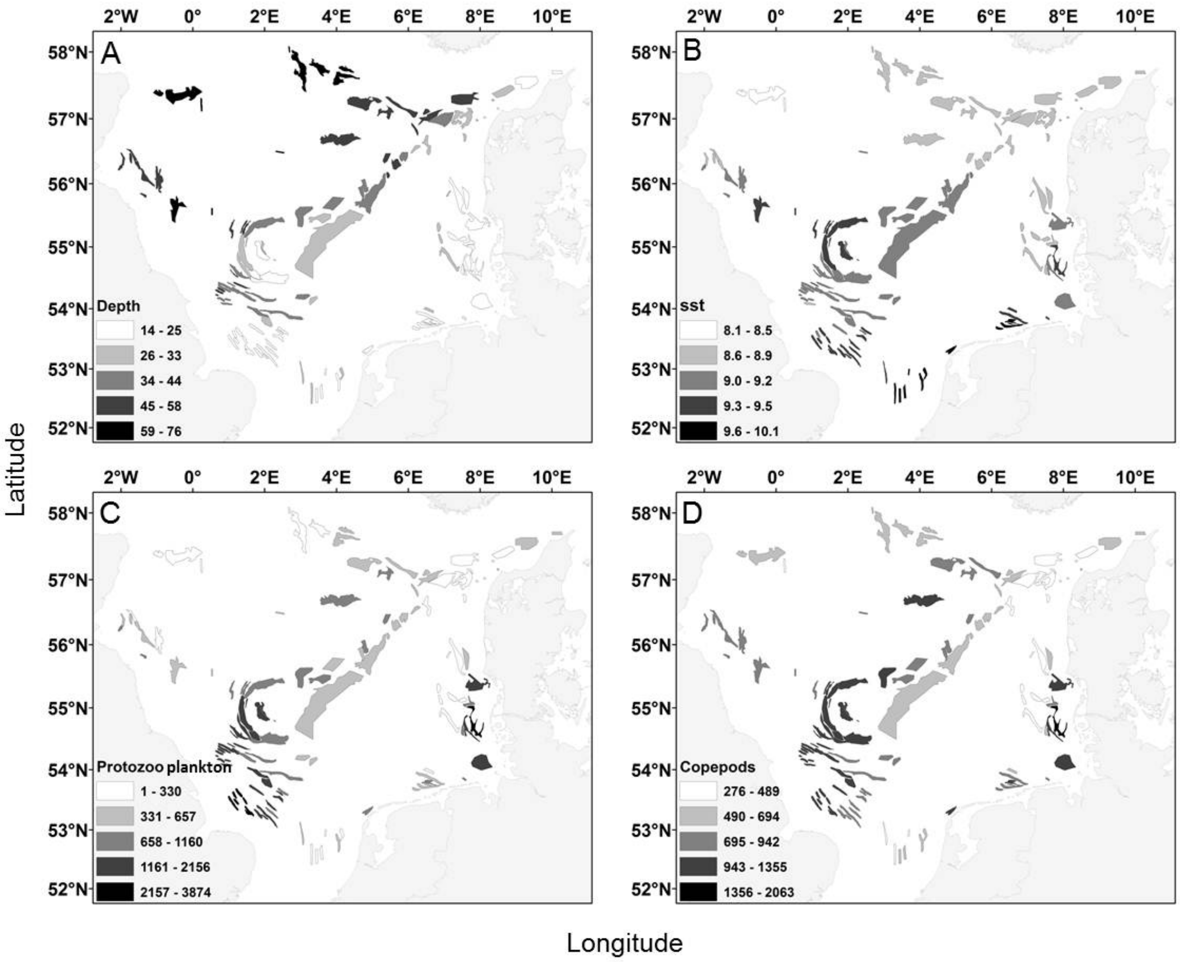

A
B
C
D
2°W
0°
2°E
4°E
6°E
8°E
10°E
58°N
57°N
56°N
55°N
54°N
53°N
52°N
Depth
14 - 25
26 - 33
34 - 44
45 - 58
59 - 76
sst
8.1 - 8.5
8.6 - 8.9
9.0 - 9.2
9.3 - 9.5
9.6 - 10.1
Protozoo plankton
1 - 330
331 - 657
658 - 1160
1161 - 2156
2157 - 3874
Copepods
276 - 489
490 - 694
695 - 942
943 - 1355
1356 - 2063
Latitude
Longitude

Fig 1

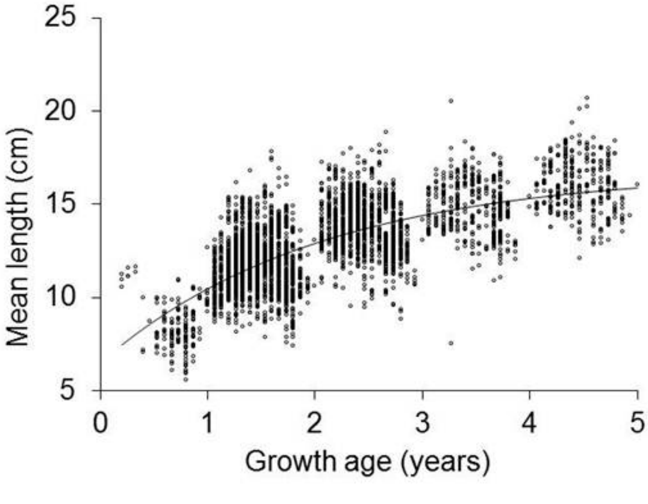

25
20
15
10
5
0
1
2
3
4
5
Mean length (cm)
Growth age (years)

Fig. 2

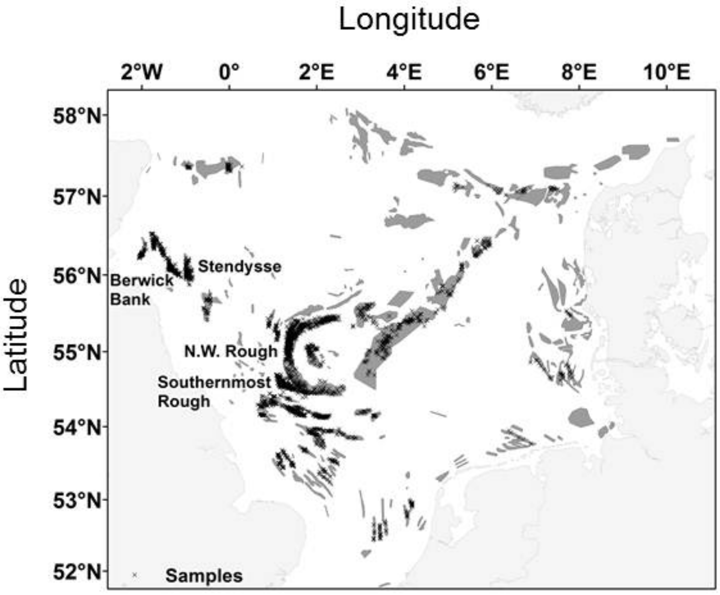

Longitude
2°W
0°
2°E
4°E
6°E
8°E
10°E
58°N
57°N
56°N
55°N
54°N
53°N
52°N
Latitude
Berwick Bank
Stendysse
N.W. Rough
Southernmost Rough
× Samples

Fig. 3

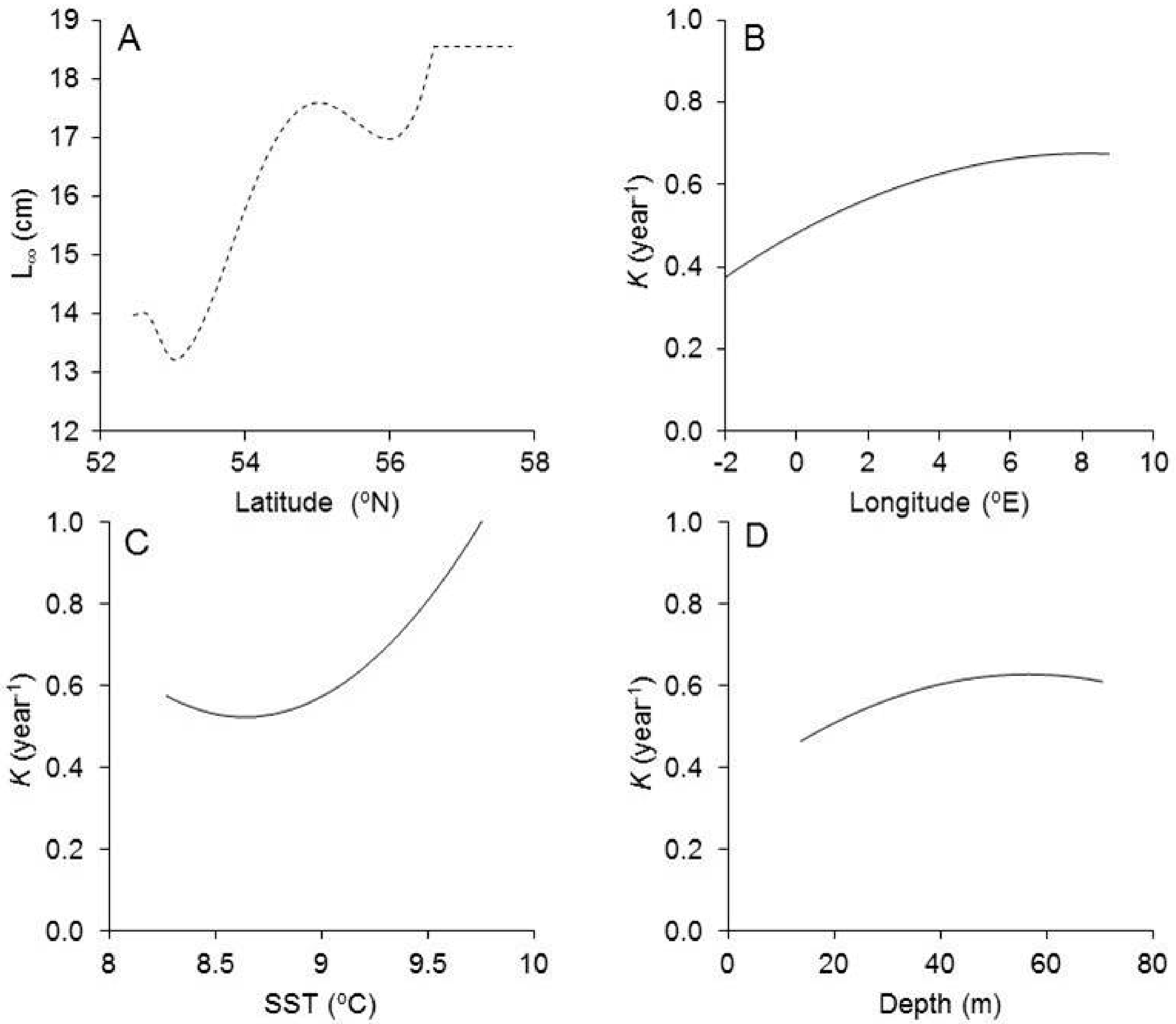

A
L∞ (cm)
19
18
17
16
15
14
13
12
52
54
56
58
Latitude (°N)
B
K (year^{-1})
1.0
0.8
0.6
0.4
0.2
0.0
-2
0
2
4
6
8
10
Longitude (°E)
C
K (year^{-1})
1.0
0.8
0.6
0.4
0.2
0.0
8
8.5
9
9.5
10
SST (°C)
D
K (year^{-1})
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
Depth (m)

Fig. 4

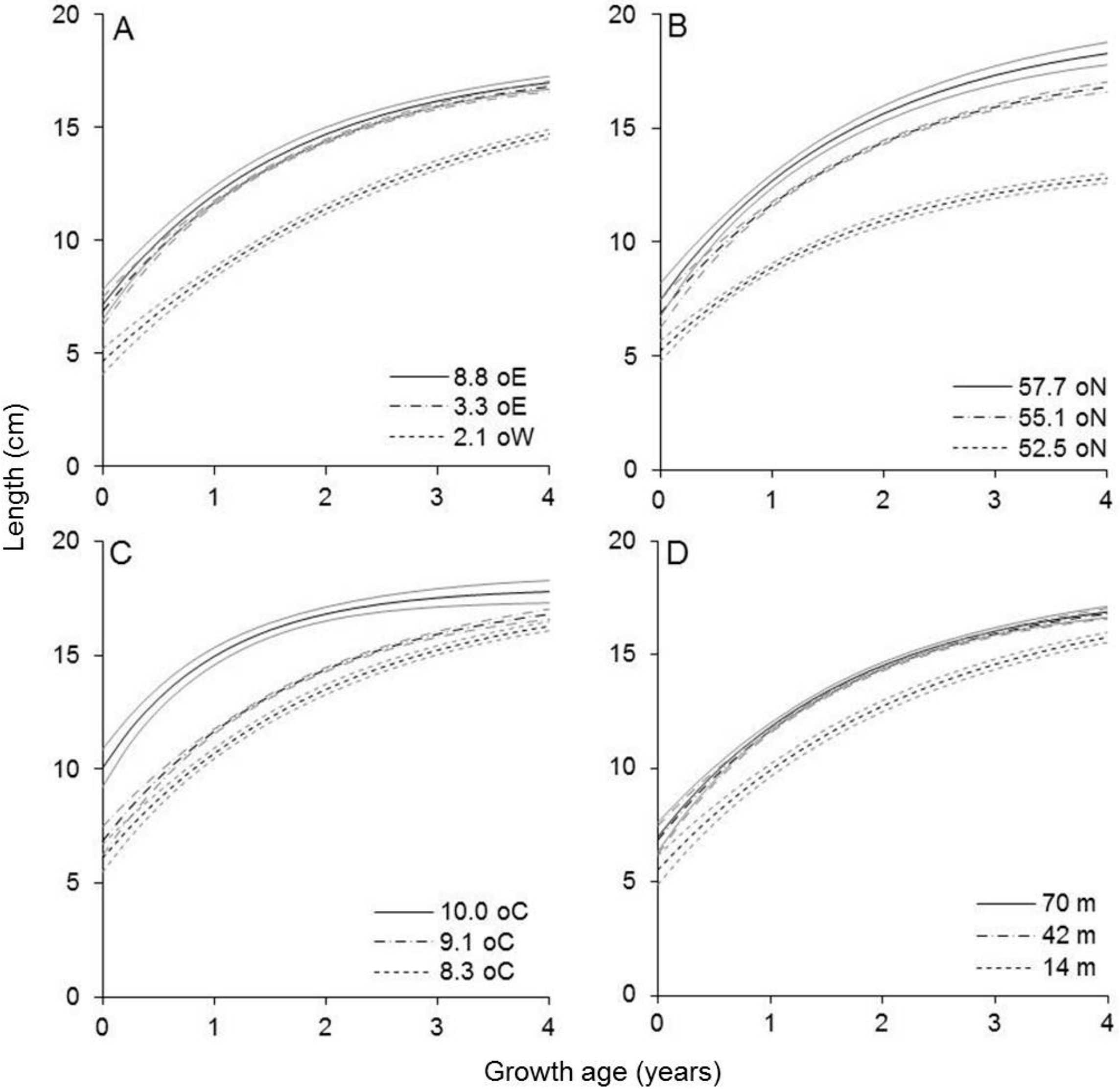

A
8.8 oE
3.3 oE
2.1 oW
B
57.7 oN
55.1 oN
52.5 oN
C
10.0 oC
9.1 oC
8.3 oC
D
70 m
42 m
14 m
0
5
10
15
20
0
1
2
3
4
Length (cm)
Growth age (years)

Fig. 5.

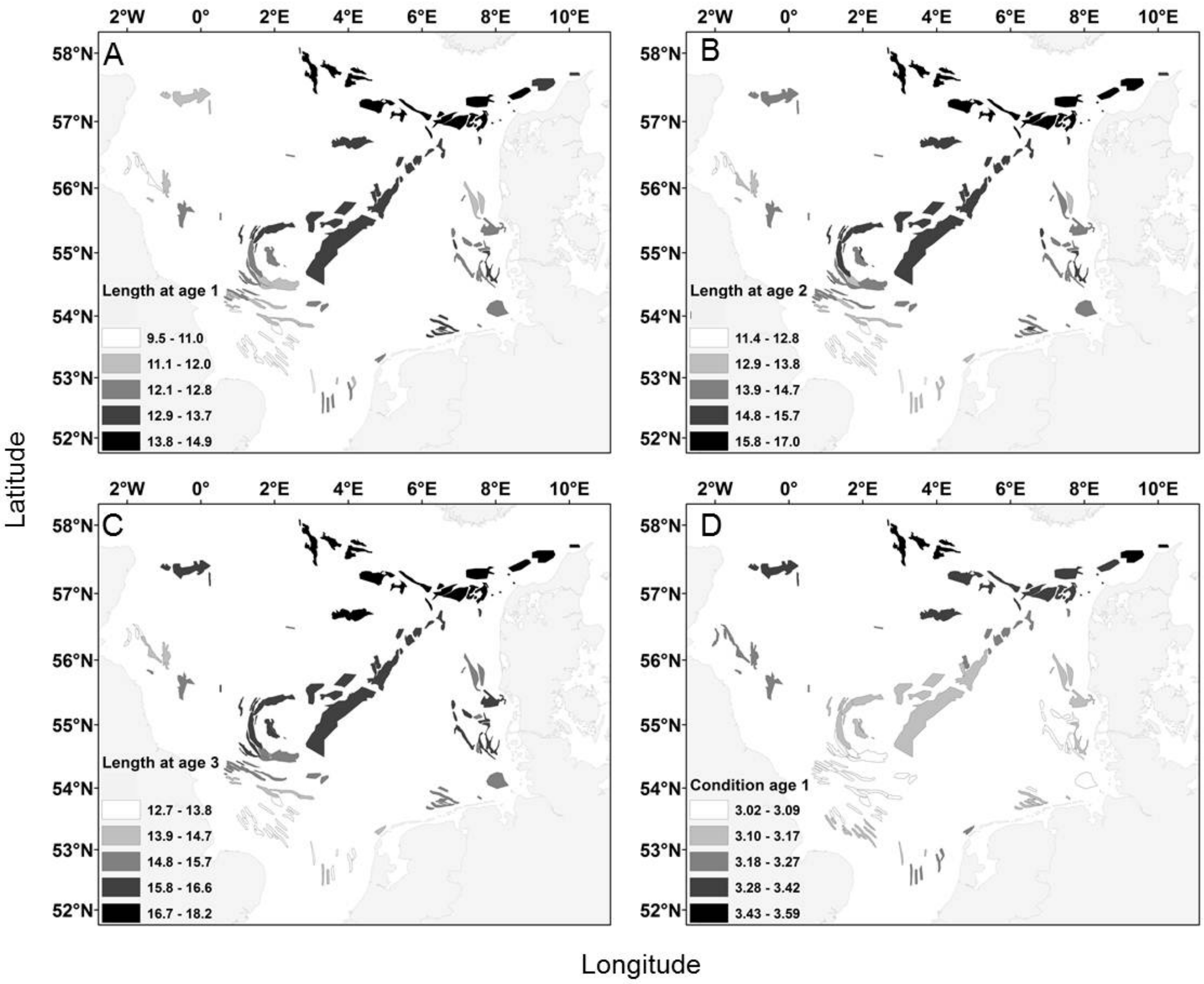

A
Length at age 1
9.5 - 11.0
11.1 - 12.0
12.1 - 12.8
12.9 - 13.7
13.8 - 14.9
B
Length at age 2
11.4 - 12.8
12.9 - 13.8
13.9 - 14.7
14.8 - 15.7
15.8 - 17.0
C
Length at age 3
12.7 - 13.8
13.9 - 14.7
14.8 - 15.7
15.8 - 16.6
16.7 - 18.2
D
Condition age 1
3.02 - 3.09
3.10 - 3.17
3.18 - 3.27
3.28 - 3.42
3.43 - 3.59
2°W
0°
2°E
4°E
6°E
8°E
10°E
58°N
57°N
56°N
55°N
54°N
53°N
52°N
Latitude
Longitude

Fig. 6.

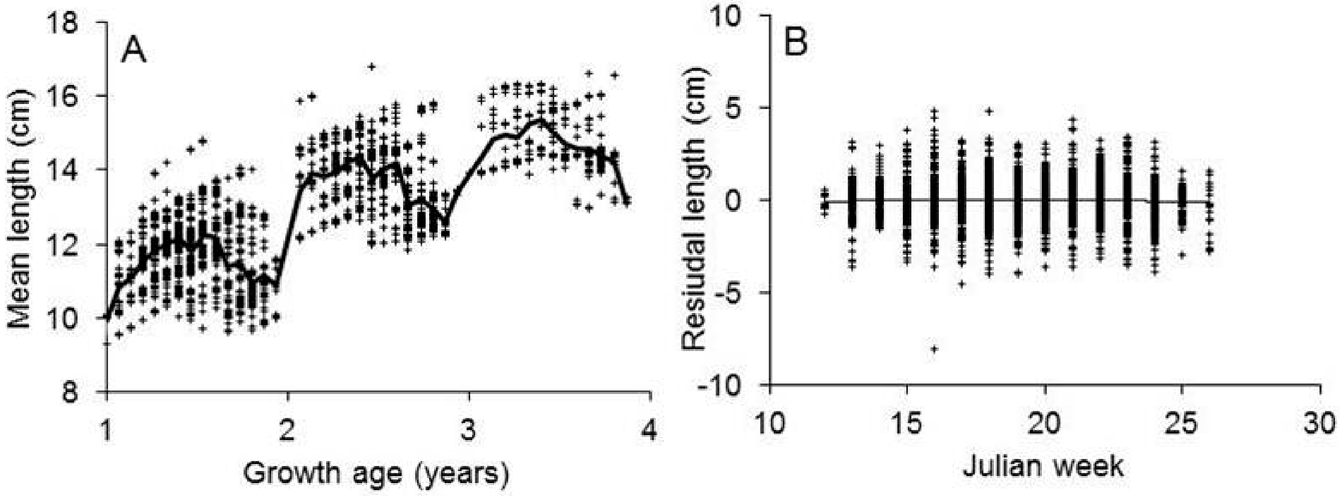
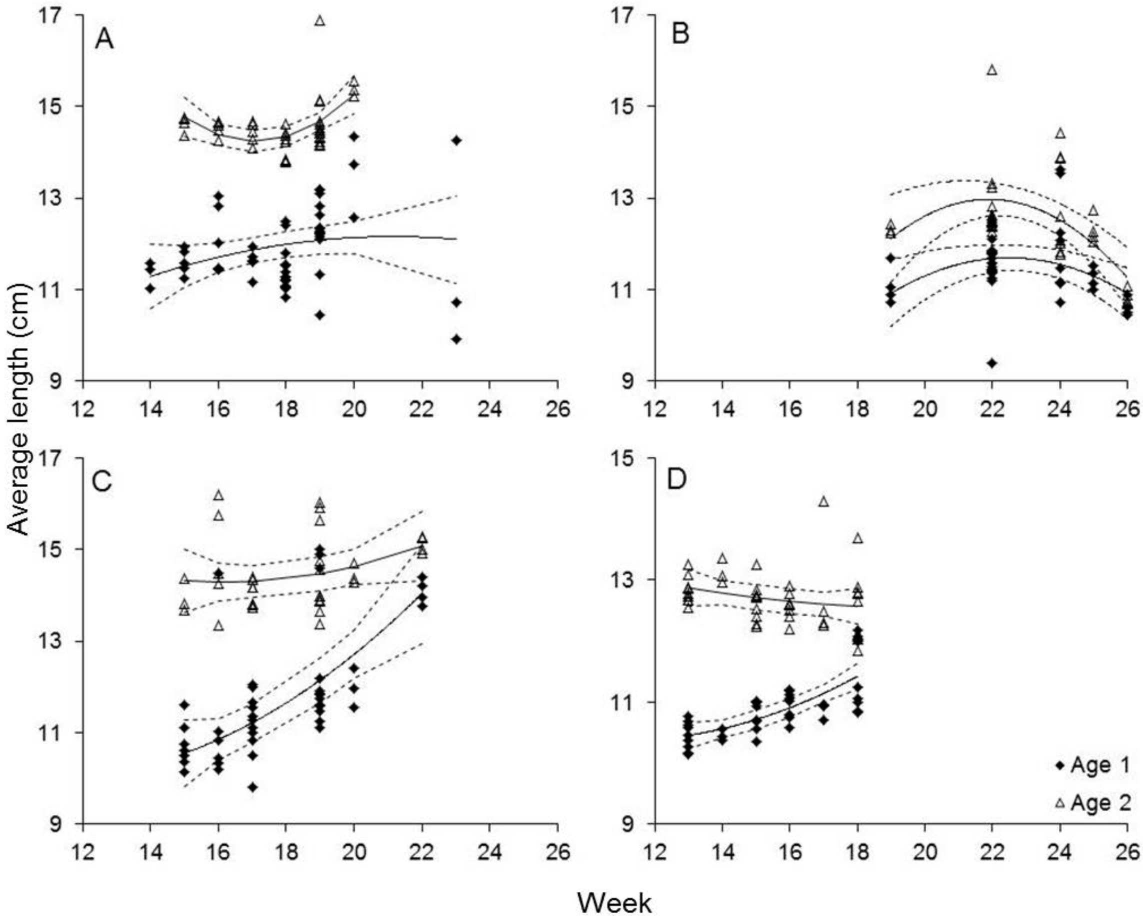

A
Mean length (cm)
18
16
14
12
10
8
1
2
3
4
Growth age (years)
B
Resiudal length (cm)
10
5
0
-5
-10
10
15
20
25
30
Julian week

Fig. 7



A
B
C
D
Average length (cm)
Week
17
15
13
11
9
12
14
16
18
20
22
24
26
◆ Age 1
△ Age 2

Fig. 8.

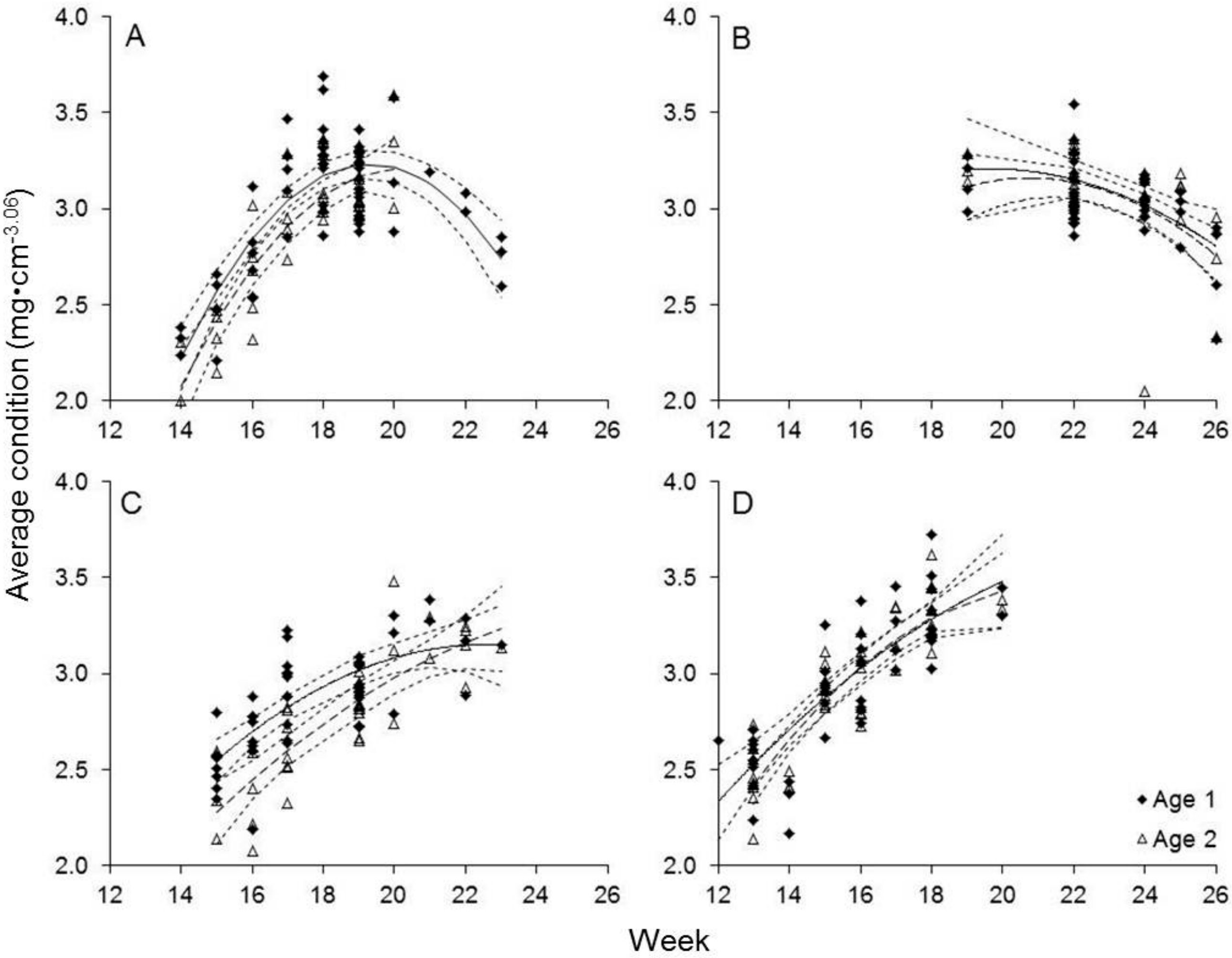

A
B
C
D
Average condition (mg•cm$^{-3.06}$)
Week
4.0
3.5
3.0
2.5
2.0
12
14
16
18
20
22
24
26
◆ Age 1
△ Age 2

Fig. 9.

Supplementary material

Estimating season length

Unfortunately, estimating season length while also estimating the von Bertalanffy growth parameters is not straight forward. Instead, we estimated season length using only data from cohorts sampled in two consecutive years with at least 5 weeks of sampling in each year. For these cohorts, time spend buried between the first and second growth season was estimated by minimizing the squared deviation between observed and predicted length, $\hat{l}$:

$$\hat{l} = L_\infty\left(1 - \exp\left(-K(t_g - t_0)\right)\right) = L_\infty\left(1 - \exp\left(-K(t_a - t_y t_b - t_0)\right)\right)$$

where L_∞, K and t_0 are the parameters of the von Bertalanffy growth equation describing maximum length, intrinsic growth rate and the theoretical age at length 0, respectively. As the fishing grounds fulfilling the requirement for number of samples were all situated in the Dogger Bank complex, the parameters were assumed to be the same for all grounds and estimated in a common model using PROC NLIN in SAS version 9.2 for Windows. To avoid including cohorts which did not add information to the relationship, the model was initially fitted for each cohort and fishing ground separately. Fishing ground/cohort combinations for which the model failed to converge were eliminated from further analyses.

Six cohorts were sampled in 5 weeks in each of two consecutive years: N. W. Rough, 2004, 2005, 2006 and 2007 cohorts, Southernmost Rough, 2004 cohort and Stenkanten, 2005 cohort. Of these, the model failed to converge for N.W. Rough 2005 and 2007 and these cohorts were excluded from further analyses. The length of the growth season estimated in common for all cohorts and fishing grounds was 15.0 weeks (standard error 4.2). The data used are seen in fig. S1.

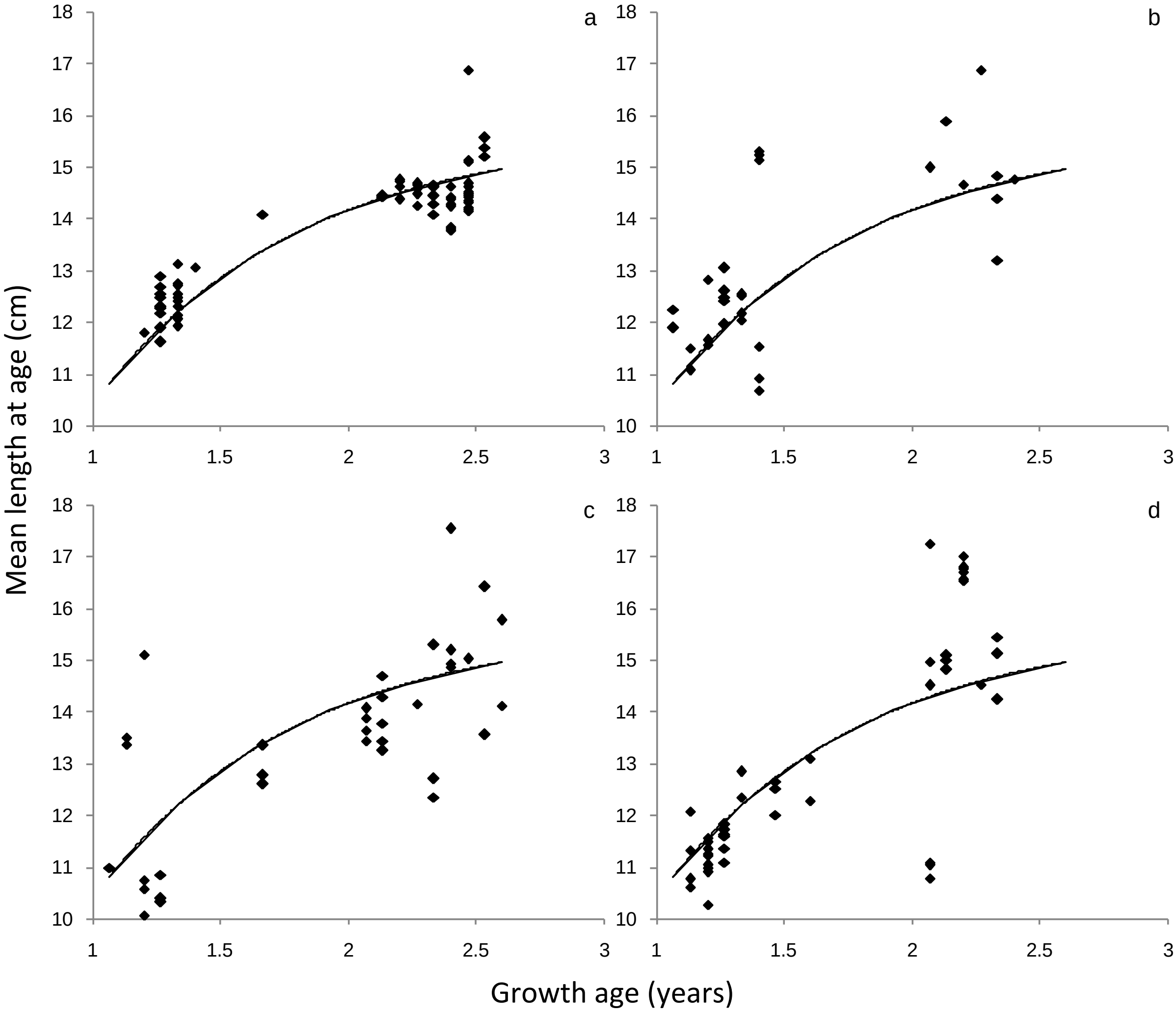


Fig. S1. Length as a function of estimated growth age (growth season length=15 weeks, age 0= week 12 of the year of hatching). N. W. Rough 2004 and 2006 cohorts (a and b, respectively), Southernmost Rough 2007 cohort (c) and Stenkanten 2005 cohort (d). Line is estimated common von Bertalanffy growth curve.

Tests of effect on von Bertalanffy parameters

Forward elimination tests of effect on von Bertalanffy parameters. Models selected are marked in bold. The total number of observations is 3856.

Model parameters included together with tested effect: K, L_∞, t_0,	DF model addition	Residual sum of squares			F			Probability of effect being 0			R^2			Cummulated R^2
Tested effect on		K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	
Tested effect of second degree polynomial in:														
Density	2	7903	7819	8095	224	247	173	<0.0001	<0.0001	<0.0001	0.104	0.114	0.082	
Bottom temperature	2	7976	7901	7974	204	225	205	<0.0001	<0.0001	<0.0001	0.096	0.104	0.096	
SST	2	7936	8453	8096	215	84	173	<0.0001	<0.0001	<0.0001	0.100	0.042	0.082	
Copepods	2	7856	8112	8028	6883	169	191	<0.0001	<0.0001	<0.0001	0.110	0.081	0.09	
Protozoo	2	8318	8246	8339	117	135	112	<0.0001	<0.0001	<0.0001	0.057	0.065	0.055	

Latitude	2	8319	8161	8312	116	156	118	<0.0001	<0.0001	<0.0001	0.057	0.075	0.058	
longitude	2	**6808**	7081	7096	**570**	473	468	**<0.0001**	<0.0001	<0.0001	**0.228**	0.197	0.196	0.228
Depth	2	8701	8743	8659	27	17	36	<0.0001	<0.0001	<0.0001	0.014	0.009	0.019	

Model parameters included together with tested effect: K, L_∞, t_0, K 2^{nd} degree polynomial in longitude	DF model addition	Residual sum of squares			F			Probability of effect being 0			R^2			Cummulated R^2
Tested effect on		K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	
Tested effect of second degree polynomial in Density	2	6660	6651	6737	43	45	20	<0.0001	<0.0001	<0.0001	0.017	0.018	0.008	
Bottom temperature	2	5960	5916	6156	274	290	204	<0.0001	<0.0001	<0.0001	0.096	0.101	0.074	
SST	2	6636	6789	6725	5956	5	24	<0.0001	0.0045	<0.0001	0.019	0.002	0.009	
copepods	2	6677	6720	6685	38	25	35	<0.0001	<0.0001	<0.0001	0.015	0.01	0.014	

protozoo	2	6602	6641	6638	60	48	49	<0.0001	<0.0001	<0.0001	0.023	0.019	0.019	
latitude	2	5720	**5616**	5874	366	**409**	306	<0.0001	**<0.0001**	<0.0001	0.123	**0.135**	0.106	0.364
longitude	2		6628	6682		52	36		<0.0001	<0.0001		0.02	0.014	
Depth	2	6204	6078	6322	187	231	148	<0.0001	<0.0001	<0.0001	0.068	0.083	0.055	
longitude^3+longitude^4	2	6528	6778	6762	83	9	13	<0.0001	0.0002	<0.0001	0.032	0.003	0.005	

Model parameters included together with tested effect: K, L_∞, t_0, K 2nd degree polynomial in longitude, L_∞ 2nd degree polynomial in latitude	DF model addition	Residual sum of squares			F			Probability of effect being 0			R^2			Cummulated R^2
Tested effect on		K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	
Tested effect of second degree polynomial in Density	2	5603	5579	5612	4	13	1	0.0132	<0.0001	0.2994	0.001	0.004	0	
Bottom temperature	2	5544	5588	5552	25	9	22	<0.0001	<0.0001	<0.0001	0.008	0.003	0.007	

SST	2	5254	5252	5273	132	133	125	<0.0001	<0.0001	<0.0001	0.041	0.041	0.039	
copepods	2	5546	5553	5538	24	22	27	<0.0001	<0.0001	<0.0001	0.008	0.007	0.009	
protozoo	2	5518	5567	5552	34	17	22	<0.0001	<0.0001	<0.0001	0.011	0.005	0.007	
latitude	2	5574		5578	14		13	<0.0001		<0.0001	0.005		0.004	
longitude	2		5591	5381		9	84		0.0002	<0.0001		0.003	0.027	
Depth	2	5475	5476	5454	49	49	57	<0.0001	<0.0001	<0.0001	0.016	0.016	0.018	
longitude^3 +longitude^4	2	5429	5423	5603	66	68	4	<0.0001	<0.0001	0.0117	0.021	0.022	0.001	
latitude^3 +latitude^4	2	5580	**5235**	5527	12	**140**	31	<0.0001	<0.0001	<0.0001	0.004	**0.043**	0.01	0.407
Latitude*longitude	2	5565	5477	5590	18	49	9	<0.0001	<0.0001	0.0001	0.006	0.016	0.003	

Model parameters included together with tested effect: K, L_∞, t_0, K 2nd degree polynomial in longitude, L_∞ 4th degree polynomial in latitude	DF model addition	Residual sum of squares			F			Probability of effect being 0			R^2			Cummulated R^2

Tested effect on		K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	
Tested effect of second degree polynomial in														
Density	2	5224	5201	5195	8	25	30	0.003696	5.67E-07	4.77E-08	0.001	0.004	0.005	
Bottom temperature	2	5101	5100	5146	51	51	33	<0.0001	<0.0001	<0.0001	0.015	0.015	0.01	
SST	2	**5041**	5084	5075	**74**	57	61	**<0.0001**	<0.0001	<0.0001	**0.022**	0.017	0.018	**0.429**
copepods	2	5194	5231	5186	15	1	18	<0.0001	0.2522	<0.0001	0.005	0	0.006	
protozoo	2	5168	5193	5189	25	15	17	<0.0001	<0.0001	<0.0001	0.008	0.005	0.005	
latitude	2	5176		5231	22		1	<0.0001		0.2309	0.007		0	
longitude	2		5187	5078		18	59		<0.0001	<0.0001		0.005	0.018	
Depth	2	5060	5051	5070	67	70	63	<0.0001	<0.0001	<0.0001	0.02	0.021	0.019	
longitude^3 +longitude^4	2	5079	5139	5226	59	36	3	<0.0001	<0.0001	0.0374	0.018	0.011	0.001	

latitude^3 +latitude^4	2	5190	5235	5235	17		0	<0.0001		0.9224	0.005	0	0	
Latitude*longitude	2	5098	5105	5208	52	49	10	<0.0001	<0.0001	<0.0001	0.016	0.015	0.003	
latitude^5 +latitude^6	2	5191	5167	5230	16	25	2	<0.0001	<0.0001	0.1292	0.005	0.008	0.001	

Model parameters included together with tested effect: K, L$_\infty$, t$_0$, K 2nd degree polynomial in longitude and SST, L$_\infty$ 4th degree polynomial in latitude	DF model addition	Residual sum of squares			F			Probability of effect being 0			R^2			Cummulated R^2
Tested effect on		K	L$_\infty$	t$_0$	K	L$_\infty$	t$_0$	K	L$_\infty$	t$_0$	K	L$_\infty$	t$_0$	
Tested effect of second degree polynomial in Density	2	5024	5017	5004	7	9	14	0.0014	<0.0001	<0.0001	0.002	0.003	0.004	
Bottom temperature	2	4785	4802	4870	103	0	0	<0.0001	1	1	0.029	0.027	0.019	
SST	2		5016	5033		10	3		<0.0001	0.0400		0.003	0.001	
copepods	2	4985	5019	4987	22	8	21	<0.0001	0.0002	<0.0001	0.006	0.003	0.006	

protozoo	2	4963	4986	4986	30	21	21	<0.0001	<0.0001	<0.0001	0.009	0.006	0.006	
Latitude	2	4959		5040	32	0	1	<0.0001		0.5776	0.009		0.00	
Longitude	2		5027	4969	0	5	28		0.0053	<0.0001		0.002	0.008	
Depth	2	**4763**	4770	4824	**112**	1	87	<0.0001	0.3680	<0.0001	**0.032**	0.031	0.025	0.46
latitude^3 +latitude^4	2	4937		5037	41		2	<0.0001		0.2031	0.012		0	
longitude^3 +longitude^4	2	5004	4995	5034	14	3	3	<0.0001	0.0499	0.0551	0.004	0.005	0.001	
SST^3 +SST^4	2	5015	5017	5041	10	4	0	<0.0001	0.0184	0.9962	0.003	0.003	0	
Latitude*longitude	2	4928	4965	5023	44	5	7	<0.0001	0.0068	0.0012	0.013	0.009	0.002	
latitude^5 +latitude^6	2	4959	4943	5039	32	5	1	<0.0001	0.0067	0.4225	0.009	0.011	0	

Model parameters included together with tested effect: K, L_∞, t_0, K 2nd degree polynomial in longitude, SST and depth, L_∞ 4th degree polynomial in latitude	DF model addition	Residual sum of squares	F	Probability of effect being 0	R^2	Cummulated R^2

Tested effect on		K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	K	L_∞	t_0	
Tested effect of second degree polynomial in Density	2	4760	4757	4752	1	2	4	0.3939	0.1109	0.0115	0.000	0.001	0.001	
Bottom temperature	2	4754	4740	4763	4	9	0	0.0245	<0.0001	0.9722	0.001	0.003	0	
SST	2		4738	4752		10	4		<0.0001	0.0130	0	0.003	0.001	
copepods	2	4744	4760	4735	8	1	11	0.0005	0.4118	<0.0001	0.002	0.000	0.003	
protozoo	2	4708	4736	4718	22	11	18	<0.0001	<0.0001	<0.0001	0.006	0.003	0.005	
latitude	2	4727		4759	14		2	<0.0001		0.1928	0.004	0	0.001	
Longitude	2		4742	4710		8	21		0.00021	<0.0001		0.002	0.006	
Depth	2		4746	4738		7	10		0.0013	<0.0001		0.002	0.003	
latitude^3 +latitude^4	2	4717		4757	19		2	<0.0001		0.0829	0.005		0.001	
longitude^3 +longitude^4	2	4728	4734	4754	14	12	4	<0.0001	<0.0001	0.0249	0.004	0.003	0.001	

SST^3 +SST^4	2	4754	4741	4759	3	9	1	0.0321	0.0002	0.2739	0.001	0.002	0.000	
Depth^3 +Depth^4	2	4761	4745	4758	1	7	2	0.4742	0.0008	0.1252	0.000	0.002	0.001	
latitude^5 +latitude^6	2	4722	4695	4756	16	28	3	<0.0001	<0.0001	0.0813	0.005	0.008	0.001	
Latitude*longitude	2	4722	4707	4730	4754	23	13	<0.0001	<0.0001	<0.0001	0.005	0.006	0.004	