

# North Sea saithe *Pollachius virens* growth in relation to food availability, density dependence and temperature

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**ABSTRACT:** North Sea saithe *Pollachius virens*, a major top predator in the area, supports the fishery economy of several European countries. However, recent stock assessments suggested a decrease in spawning stock biomass along with a decline in saithe mean weight-at-ages. In this context, we investigated North Sea saithe growth characteristics at the population level. First, saithe annual weight increments and age–length relationships were studied. Modelling of saithe age–length relationships was carried out using (1) the traditional von Bertalanffy growth function model, (2) the Verhulst logistic model and (3) an empirical linear model. Second, the effects of environmental factors on saithe growth were investigated. Explanatory environmental factors included food availability, represented by the total biomass of Norway pout *Trisopterus esmarkii*; intraspecific competition, i.e. density dependence, represented by saithe abundance; and temperature. This study revealed that the Verhulst logistic model was the best descriptor of saithe growth and that density dependence and food availability had significant effects on the saithe growth coefficient, while no effect of temperature was shown. We suggest that reduced food availability and increased competition may explain the recent decrease in the saithe growth coefficient.

**KEY WORDS:** Bottom-up processes · von Bertalanffy growth function · Logistic growth · Norway pout · Prey availability effects · Density-dependence · Predator–prey interactions · Resource limitation · Competition

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## INTRODUCTION

Understanding factors regulating population dynamics is a cornerstone in ecology, particularly in exploited ecosystems (Frederiksen et al. 2006, Laundré et al. 2014). The size of a population is strongly influenced by its position within the trophic network to which it belongs (Cury et al. 2003) and by the productivity of the ecosystem and its carrying capacity. In heavily exploited marine ecosystems, assessing the size (biomass and/or abundance) of commercial fish stocks with sufficient accuracy is of primary importance to support fisheries management.

In an ecosystem approach to fisheries management (FAO 2003), multi-species stock assessment tools have been developed to better integrate trophic interactions in fisheries diagnostics (ICES 2012). These tools generally allow the estimation of top-down effects, i.e. control exerted by predators on prey populations, through an estimation of predation mortalities; see Plaganyi (2007) for a review. However, the reverse effects (bottom-up), i.e. the potential regulation of predator populations through prey availability, are often not estimated despite their recognized importance (Frederiksen et al. 2006). Understanding these bottom-up processes is neces-

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sary to gain insights into interspecific competition, which involves relationships through shared preys in both directions (top-down and bottom-up).

Saithe *Pollachius virens* is a major top predator fish species in the North Sea, and it is commercially important for several European countries, i.e. Germany, France, the United Kingdom and Norway. Recent stock assessments suggest that North Sea saithe spawning stock biomass and mean weight-at-age (see Fig. 1) have decreased in recent years (ICES 2014a). This decrease might affect stock productivity and the sustainability of dependent fisheries (Brander 2007). Many factors related to genetic and/or phenotypic plasticity may affect fish growth (Sinclair et al. 2002). Genetic effects may be induced by fisheries (Stokes & Law 2000). The resulting changes on growth rate are supposedly slow, 0.1% per year according to Andersen & Brander (2009), and therefore might be highlighted only in long-term studies. In contrast, substantial changes related to phenotypic plasticity can be observed on shorter time scales.

Three environmental factors are commonly assumed to affect fish growth: density-dependence (Lorenzen & Enberg 2002, Sinclair et al. 2002), temperature (Brunel & Dickey-Collas 2010, Baudron et al. 2011) and food availability (Krohn et al. 1997, Gjøsaeter et al. 2009). Density-dependent regulation generally results from an increased intraspecific competition for food at large stock size (Sinclair et al. 2002, Brunel & Dickey-Collas 2010). Density-dependent growth was recognized as a common process for marine species (Lorenzen & Enberg 2002, Sinclair et al. 2002). Density-dependent effects need to be taken into account while managing species, as their removal and/or conservation might decrease or increase these effects (Lorenzen & Enberg 2002).

Changes in temperature might also affect food availability (Möllmann et al. 2005, Baudron et al. 2011) or have more direct effects on fish physiology. Indeed, there is an optimum temperature for growth (Jennings et al. 2001), which declines with decrease in food availability (Sinclair et al. 2002). In the theoretical case of unlimited food availability, growth would be determined by temperature only (Brett & Groves 1979). There is currently insufficient available information to relate saithe growth to environmental changes, and density-dependent effects are currently neglected (ICES 2014a). Hence, regulation through food availability, which is entangled with density-dependence and temperature, needs to be investigated.

Saithe growth may be controlled by food availability, resulting from changes in temperatures or intra- or interspecific competition, and thereby could be linked to densities of mid-trophic level species such as forage fishes (Frederiksen et al. 2006, Engelhard et al. 2014, Plaganyi & Essington 2014). These key species have been evidenced to either positively affect predator fish growth (Krohn et al. 1997, Huse et al. 2004, Gjøsaeter et al. 2009, Engelhard et al. 2014) or, on the contrary, negatively affect predator fish abundance through predation of the predators' eggs or larvae (Engelhard et al. 2014). Saithe diet is generally based on forage species, among which Norway pout *Trisopterus esmarkii* is of major importance (Bergstad 1991, Du Buit 1991, 1996, Engelhard et al. 2014).

In the North Sea, the recent emergence of the highly piscivorous hake *Merluccius merluccius*, described by Baudron & Fernandes (2014) and Cormon et al. (2014), might have impacts on the North Sea ecosystem. These impacts could be direct, e.g. on prey species, or indirect, e.g. on other predator species feeding on similar prey assemblages. Saithe and hake have similar feeding habits, particularly concerning Norway pout (Bergstad 1991, Du Buit 1991, 1996). In addition, Cormon et al. (2014) showed an increasing spatial overlap between hake and saithe, correlated with Norway pout presence. Therefore, hake emergence might affect Norway pout biomass, which has been declining since 2009 (ICES 2014a), with a knock-on effect on saithe growth.

To understand the potential impacts of hake on saithe population in the North Sea, it appears necessary to first understand the potential relationships between Norway pout biomass and saithe growth characteristics that, to date, have not been investigated in this area. Norway pout is a short-lived species and its dynamics are driven by changes in recruitment and/or predation mortality rather than by fishing mortality, which is relatively low for this species (ICES 2014a). In addition, the environmental factors driving Norway pout recruitment are highly variable while predation mortalities are exerted on all ages by both saithe and hake (Lambert et al. 2009, ICES 2014a,b).

Both Norway pout and saithe are northern species with overlapping areas of distribution in the North Sea and Skagerrak (Lambert et al. 2009, ICES 2014a). However, only adult saithe show spatial overlap with Norway pout. Saithe juveniles are distributed inshore, where Norway pout (and adult saithe) are rarely present (ICES 2014a). Hence, high Norway

pout biomass (or saithe abundance) is expected to have little negative impact on saithe through predation (or cannibalism) on juveniles, which allows disentanglement of top-down and bottom-up effects. In addition, Cormon et al. (2014) showed a positive relationship between Norway pout and saithe probability of presence in the North Sea, while Lynam et al. (2015) showed a positive correlation between Norway pout and saithe biomass. For these reasons, it may be reasonable to assume that Norway pout biomass is a suitable descriptor of food available to saithe, particularly when investigating limitation of resources due to potential competition between saithe and hake. Evidencing resource limitation is a requirement to assume competitive interactions between 2 species (Link & Auster 2013). While difficult to highlight at large scale, this process may be evaluated through indirect methods such as the study of the relationship between prey availability and predator growth.

Growth characterisation generally involves the determination of the size of an organism (length or weight) in relation to time. Numerous models have been used to describe fish growth, of which the von Bertalanffy growth function (VBGF) model is probably the most common (Jennings et al. 2001, Katsanevakis 2006, Haddon 2011). However, the *a priori* use of the VBGF, even when providing a good description of growth for most fish species (Jennings et al. 2001), may be problematic (Katsanevakis 2006). Particularly, asymptotic length and age-at-size 0 estimations must be extrapolated and might lack biological meaning (Haddon 2011). Kienzle (2005) recognised the problems in using VBGF for the description of saithe growth, which does not show an asymptotic length. In this context, suitable growth model and biologically meaningful parameters must be selected to study the potential effects of the environment on growth of saithe species.

In this study, we investigated the interannual variability of North Sea saithe average growth in relation to different biotic and abiotic environmental factors. Saithe growth was first described using annual mean weight-at-age increments. Second, the relationship between saithe length and age was investigated. To this purpose, 3 models, describing saithe growth through either linear or asymptotic age-length relationships were considered. Environmental factors considered were (1) main prey availability, represented by the total biomass of Norway pout, a prey that also represents a major component of the hake diet; (2) density-dependence, represented by saithe abundance; and (3) temperature.

## MATERIALS AND METHODS

### Data

#### Saithe size-at-age characteristics

Saithe *Pollachius virens* mean weight-at-age (kg), from age 3 to age 10 (yr), was extracted from ICES (2014a) over the period 1987 to 2012 (Fig. 1). Age-length keys (ALKs) were compiled on the basis of length measurements and age reading on otoliths, using both survey and commercial data sources. ALK survey data were collected during the ICES North Sea International Bottom Trawl Survey and subsequently extracted from the ICES online database of trawling surveys for the period 1991 to 2012 (except for 2006, for which data were missing). Data were explored by age for length values, and outliers (extreme values considered biologically meaningless) were ignored in subsequent analyses. The final survey database included ALKs from ages 2 to 10 yr (Table 1).

#### Environmental factors

Annual Norway pout *Trisopterus esmarkii* total stock biomass (TSB, t) and saithe abundance (total no. of ind.) were extracted from the ICES (2014a) assessment report for the period 1987 to 2012. Seabottom temperatures (°C), measured using sonde devices (CTD), were extracted from the ICES oceanographic online database (<http://ocean.ices.dk/HydChem>) at quarter and statistical rectangle (1° longitude × 0.5° latitude) resolution. Bottom temperatures were averaged annually from 1987 to 2012 over the Northern North Sea and Skagerrak. Spatial coverage is shown in Fig. 2.

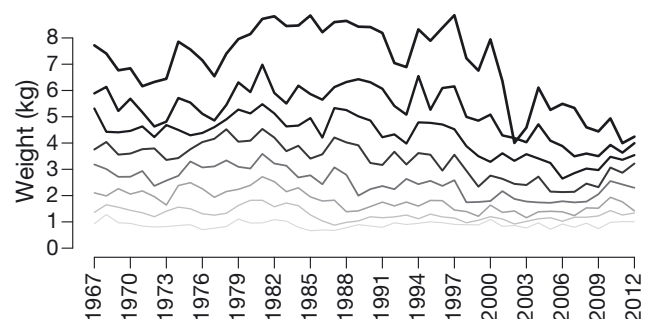


Fig. 1. Saithe mean weight-at-age trends from 1967 to 2012, from 3 yr old (light grey thin line) to 10+ yr (thick black line). Source: ICES (2014a)

Table 1. Overview of North Sea saithe population size characteristics data, their units and their age and time coverage

Data	Unit	Age (yr)	Years
Mean weight-at-age	kg	3–10	1987–2012
Annual mean weight increment	kg	4–9	1988–2012
Length-at-age	cm	2–10	1991–2012 <sup>a</sup>

<sup>a</sup>Year 2006 is missing

### Saithe growth characteristics

#### Annual mean weight increments

Saithe annual mean weight increments were calculated (Eq. 1) for each age using mean weight-at-age data described previously (Fig. 1, Table 1). Because there were no age 2 saithe individuals in the North Sea (ICES 2014a), we did not calculate the annual weight increment between ages 2 and 3. Age 10 is considered as a plus group (age 10 and older) by ICES (2014a). Therefore, the calculation of an annual weight increment between ages 9 and 10 was not possible (Table 1).

$$\delta w_{a_t} = w_{a_t} - w_{a-t-1} \quad (1)$$

where  $\delta w$  is the annual average weight ( $w$ ) increment (kg),  $a$  is age (yr) and  $t$  is time (yr).

#### Age-length relationship

Three candidate growth models were fitted to the saithe age-length data: the traditional VBGF, a Verhulst logistic growth model, and a (more empirical) linear model.

The VBGF (VB) model (Eq. 2) assumes an asymptotic relationship between length,  $l$  (cm), and age,  $a$ , depending on 3 parameters: an asymptotic length,  $l_\infty$  (cm), a growth coefficient,  $K_{VB}$  ( $\text{yr}^{-1}$ ), which determines how swiftly length,  $l$ , converges towards its asymptotic value; and  $a_0$  (yr), which represents the theoretical age at which individuals are of size 0.

$$l_a = l_\infty \times (1 - e^{-K_{VB} \times (a - a_0)}) \quad (2)$$

The logistic (LG) model (Eq. 3) assumes a sigmoidal relationship between  $l$  and  $a$ , depending on 3 parameters:  $l_\infty$ , a relative growth coefficient,  $K_{LG}$  ( $\text{yr}^{-1}$ ), and a sigmoidal curve inflection point,  $a_1$  (yr), which represents the theoretical age at which individual growth trajectory changes.

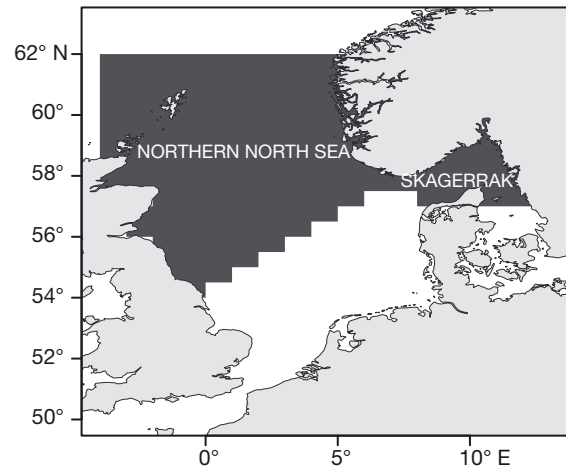


Fig. 2. Spatial coverage of sea bottom temperatures used in the study

$$l_a = l_\infty \times \frac{1}{(1 + e^{-K_{LG} \times (a - a_1)})} \quad (3)$$

The linear (LM) model (Eq. 4) assumes that, within the range of data available,  $l$  is linearly related to  $a$ , depending on an intercept,  $l_0$ , which represents the length at age 0, and a regression coefficient,  $K_{LM}$  ( $\text{cm yr}^{-1}$ ), here representing growth.

$$l_a = l_0 + K_{LM} \times a \quad (4)$$

Age proportions within each year were checked to ensure sufficient and similar representation of the different ages. As different ages represented within a year belong to different cohorts, and to reduce the cohort-related correlation, the 3 models were fitted for each year separately (ICES 1991). Therefore, each year was considered as an independent subpopulation, allowing us to identify potential short-term variations by representing saithe annual average growth (Haddon 2011) rather than to focus on cohort average growth, which may involve longer-term effects. Linear models (Eq. 4) were fitted using linear regression, while asymptotic models (Eqs. 2 & 3) were fitted using non-linear least squares (NLS) regression. NLS iterations were optimized using Marquadt's algorithm and starting values set as follows:  $K = 0.07 \text{ yr}^{-1}$  (Jennings et al. 1998),  $l_\infty = 177.1 \text{ cm}$  (Jennings et al. 1998),  $a_0 = -0.8 \text{ yr}$  (Froese & Pauly 2014) and  $a_1 = 5 \text{ yr}$  based on saithe age at first maturity (Froese & Pauly 2014, ICES 2014a). NLS regressions were optimized using R 2.15.3 and an  $nls$  function of  $\{nlmrt\}$  (Nash 2013). The 3 candidate models were evaluated based on comparison of their corrected Akaike's information criterion (AICc), which is used to compare goodness of fit (GoF) in non-nested models (Burnham &

Anderson 2002). Differences between all models ( $\Delta AIC_c$ ) were calculated, and the model with smallest AICc was selected.

### Effect of the environment

#### Annual mean weight increment analysis

Generalized least squares were used to fit the relationships between the saithe annual mean weight-at-age increment,  $\delta w_{a,t}$ , and environmental factors prevailing during the year of the increment ( $t - 1$ ) as described by Eq. (5):

$$\delta w_{a,t} \sim \mu + \beta_1 \cdot n_{\text{TSB}_{t-1}} + \beta_2 \cdot s_{\text{NB}_{t-1}} + \beta_3 \cdot \Theta_{t-1} + \epsilon_t \quad (5)$$

where  $\mu$  is the intercept,  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are the coefficients associated with Norway pout TSB ( $n_{\text{TSB}}$ ) representing food availability, saithe abundance in numbers (NB) of individuals ( $s_{\text{NB}}$ ) representing density-dependence and mean bottom temperature ( $\Theta$ ), and  $\epsilon$  is the residual error. Residuals were checked for time autocorrelation using correlograms.

When significantly autocorrelated, the residuals' error structure could be described by either an autoregressive model (AR), where residuals ( $\epsilon_t$ ) depend on lagged ( $z$ ) residuals ( $\epsilon_{t-z}$ ); a moving average model (MA), where  $\epsilon_t$  depends on both random noise indexed at time  $t$  ( $v_t$ ) and its lagged value ( $v_{t-z}$ ); or an autoregressive moving average model (ARMA), combining both (Zuur et al. 2009). The error structure was determined by examining the autocorrelation and partial autocorrelation functions (Zuur et al. 2009, Gröger et al. 2014). The regression described by Eq. (5) was modified to include the suitable time correlation structure chosen among the previously mentioned ones in  $\epsilon_t$ . The GoF of the error-structured model was compared to original models based on AIC. Eq. (6) describes a first-order (1,1) ARMA process.

$$\epsilon_t = \phi \cdot \epsilon_{t-1} + v_t + \theta \cdot v_{t-1} \quad (6)$$

where  $\phi$  is the AR parameter,  $v$  is the random noise and  $\theta$  is the MA parameter. When residuals were not autocorrelated, the regression was equivalent to an ordinary least squares regression. Least-squares optimisation was made using the Nelder & Mead (1965) algorithm.

Contribution of the different descriptors was tested using either the  $F$ -test, when residual errors were not significantly autocorrelated, or the Wald test, when residuals autocorrelation was taken into account. Variables with the highest  $p$ -values were dropped

one by one to select significant variables by backward elimination ( $\alpha < 0.05$ ). As multiple tests were carried out (1 test per mean weight-at-age increment),  $p$ -values were adjusted using the Holm correction (Wright 1992) to keep the familywise type I error rate at level  $\alpha = 0.05$ . In total, 6 regression models, from age increments 3–4 ( $\delta w_4$ ) to 8–9 ( $\delta w_9$ ), with different descriptor coefficients and descriptor significance per model, were fitted. Regression residuals, after autocorrelation was taken into account if necessary, were tested for trends, normality and homoscedasticity.

#### Growth coefficient analysis

The study of environmental effects focused on temporal variations of the saithe growth coefficient,  $K$ , as other growth parameters might result from extrapolation or are biologically meaningless (Kienzle 2005, Haddon 2011). First, the trends of the 3 environmental variables ( $n_{\text{TSB}}$ ,  $s_{\text{NB}}$  and  $\Theta$ ) were compared to annual  $K$  trends estimated with selected growth models. Pearson correlation coefficients ( $r$ ) between  $K$  and environmental time series were calculated. To study the short-term variations of growth, we used a 1 yr time lag for the exploration of environmental effects. Thus, we focused on short-term environmental effects (conditions prevailing the year before) on saithe annual average growth. Next, the relationships between  $K$  and the environment were investigated with regression techniques similarly to annual mean weight-at-age increments (see previous subsection). Regression residuals were checked for autocorrelation, resulting in the error term potentially including the adequate autoregressive model, e.g. the ARMA model (Eq. 6). Contribution of the different descriptors was tested using either the  $F$ -test when no significant time autocorrelation was found or otherwise the Wald test. Significant variables were selected by backward elimination ( $\alpha < 0.05$ ). Regression residuals, after autocorrelation was taken into account if necessary, were tested for trends, normality and homoscedasticity.

## RESULTS

### Saithe growth characteristics

Trends in mean weight-at-age annual increments showed a general decrease for saithe *Pollachius virens* of all ages between 1988 and 2000 (Fig. 3). In addition, weight-at-age increments of the older fish were subject to large interannual variations.

Based on AICc metrics, the saithe age–length relationship was generally best described by a logistic growth model (see Table 3). The 3 candidate models, LM, LG and VB, after being adjusted to our range of data, were not equally meaningful in biological terms. The empirical LM model, which assumed an infinite growth (no asymptote), estimated growth parameters in a biologically meaningful range, with length at age 0,  $l_0$ , ranging from 16.41 to 30.41 cm and  $K_{LM}$  ranging from a length increase per year of 4.73 to 8.12 cm (Table 2). By contrast, the VB model, which builds on ecological theory, led to biologically meaningless estimations of  $l_\infty$  (median  $l_\infty > 80\,000$  m). In comparison,  $l_\infty$  values estimated using the LG model were more realistic (median  $l_\infty = 165$  cm) even if estimates for 5 yr (1998 to 2000, 2003, 2004) were also meaningless (maximum  $l_\infty > 260\,000$  m). These extreme values of  $l_\infty$  must have been caused by the age range of our data, which does not completely cover saithe lifespan (Cohen et al. 1990, 25 yr old), thus not allowing estimation of the asymptotic plateau.

Comparison of the GoF of the 3 models highlighted a better fit of LG models that had the smallest AICc for all years except 2010, for which the VB model had the best fit (Table 3). The LM and VB models had a similar GoF, except for years 2008, 2010 and 2011. To model saithe growth consistently over years, and based on the models' biological meaningfulness and GoF, the LG model was selected as the best descriptor of saithe growth (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m542p141\\_supp.pdf](http://www.int-res.com/articles/suppl/m542p141_supp.pdf)). The saithe growth coefficient ( $K_{LG}$ ) globally decreased from 1991 to 2004. At a finer scale,  $K_{LG}$  decreased (1991 to 1992, 1996 to 2000, 2002 to 2004) and increased (1992 to 1996, 2000 to 2002) alternately (Fig. 4). From 2004 to 2011, there was a general increase in  $K_{LG}$ , except in 2009. The increase in

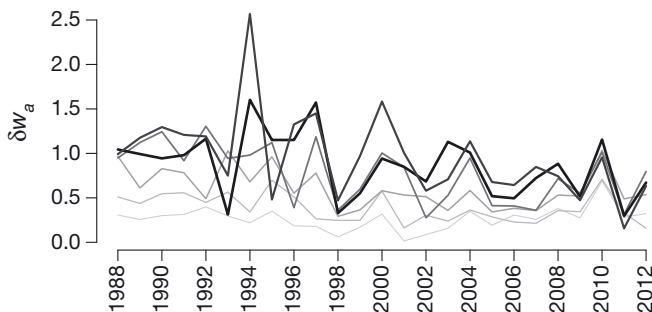


Fig. 3. Temporal trends in North Sea saithe annual mean weight-at-age increment ( $\delta w_a$ ) over the 1988–2012 period, showing increments between ages 3 and 4 ( $\delta w_4$ , light grey thin line) to increments between ages 8 and 9 ( $\delta w_9$ , thick black line).  $w$ : weight (kg);  $a$ : age (yr)

$K_{LG}$  observed from 2009 until 2010 was similar to that of  $K_{VB}$ , which also showed a better fit for this particular year, thereby confirming that the use of the LG model in 2010 did not affect general trends of the annual saithe growth coefficient. Finally,  $K_{LG}$  started to decrease again from 2011 to 2012. General trends were consistent between all 3  $K$  estimates (Fig. 4), which confirms our observations (Fig. 4).

Table 2. Parameter estimate distribution depending on growth model used.  $l_0$ : length at age 0 (cm);  $K_{LM}$ : linear model growth coefficient (cm yr<sup>-1</sup>);  $a_i$ : sigmoidal curve inflection point (yr);  $K_{LG}$ : logistic model growth coefficient (yr<sup>-1</sup>);  $l_\infty$ : asymptotic length (cm);  $a_0$ : age at size 0 (yr);  $K_{VB}$ : von Bertalanffy growth function model growth coefficient (yr<sup>-1</sup>)

Estimate parameter	Minimum	Median	Maximum
Linear model, Eq. (4)			
$l_0$	16.41	22.40	30.41
$K_{LM}$	4.73	6.47	8.12
Logistic model, Eq. (3)			
$a_i$	2.62	8.88	138.40
$K_{LG}$	0.10	0.18	0.39
$l_\infty$	82	165	26.7E6
von Bertalanffy growth function model, Eq. (2)			
$a_0$	-6.10	-3.14	-0.93
$K_{VB}$	3.7E-7	7.6E-7	0.16
$l_\infty$	95.00	8.4E6	17.6E6

Table 3. Differences in corrected Akaike's information criterion ( $\Delta AIC_c$ ) by model pair (between brackets).  $\Delta AIC_c(1/2) = AIC_c(\text{model 1}) - AIC_c(\text{model 2})$ . LM: linear model; LG: logistic model; VB: von Bertalanffy growth function model

Year	$\Delta AIC_c(\text{LM/LG})$	$\Delta AIC_c(\text{LM/VB})$	$\Delta AIC_c(\text{LG/VB})$
1991	100.17	5.70	-94.47
1992	281.86	-1.00	-282.86
1993	111.92	-1.01	-112.92
1994	143.85	-1.00	-144.85
1995	-5.51	-0.67	4.83
1996	121.04	-1.00	-122.04
1997	247.85	-1.01	-248.85
1998	348.21	-1.00	-349.22
1999	560.41	-1.00	-561.42
2000	239.14	-1.00	-240.15
2001	212.69	-1.00	-213.70
2002	122.59	-1.00	-123.60
2003	533.72	-1.01	-534.73
2004	615.62	-1.00	-616.62
2005	7.16	-1.00	-8.17
2007	97.05	-1.00	-98.06
2008	71.49	74.55	3.05
2009	31.93	3.45	-28.49
2010	989.94	1222.62	232.68
2011	1304.48	672.73	-631.74
2012	358.49	2.41	-356.08

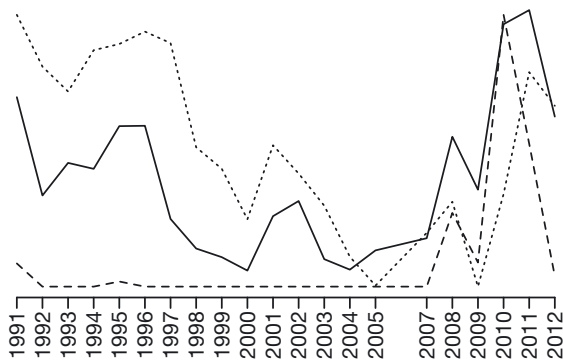


Fig. 4. Growth coefficients,  $K$ , estimated for period covering 1991 to 2012 using the linear model, the Verhulst logistic growth model and the von Bertalanffy growth function (VGBF). The dotted line shows the linear model growth coefficient estimates,  $K_{LM}$  (Eq. 4); the solid line shows the Verhulst logistic model growth estimates,  $K_{LG}$  (Eq. 3); and the dashed line shows the VGBF model estimates,  $K_{VB}$  (Eq. 2).  $y$ -axes are not plotted, as absolute values of the different growth coefficients are not of interest

## Environmental effects

There was evidence that environmental factors, particularly Norway pout *Trisopterus esmarkii* biomass and saithe abundance, affected annual average growth of saithe. Indeed,  $K_{LG}$  was found to be negatively correlated (with a 1 yr time lag) with saithe total abundance ( $s_{NB}$ ,  $r = -0.67$ , Fig. 5a) and, to a smaller extent, with temperature ( $\Theta$ ,  $r = -0.13$ , Fig. 5c). The correlation was positive with Norway pout biomass ( $n_{TSB}$ ,  $r = 0.41$ , Fig. 5b). These effects were confirmed by regression analyses of  $K_{LG}$  against the environment, which highlighted negative density-dependent effects and positive food availability effects on saithe annual average growth with a time lag of 1 yr (Table 4). Temperature, which showed little variation over the studied time period (Fig. 5c), was not significantly related to  $K_{LG}$  ( $\alpha = 5\%$ ). In addition, the  $K_{LG}$  observed time series comparison with the fitted time series, i.e. predicted from models including significant environmental factors, indicated a relatively smoother estimation of  $K_{LG}$ , particularly after 2003 (Fig. 6).

Density-dependence and prey availability together explained 46.79% of the model deviance (not shown). When saithe abundance increased by 659 000 individuals, saithe annual average growth,  $K_{LG}$ , dropped by 0.01 in the following year. Likewise, a 503 000 t increase of Norway pout total biomass led to a  $K_{LG}$  increase of 0.001 in the following year. Density-dependent effects on saithe annual average growth were strong and were the main driver of  $K_{LG}$  trends, explaining 29.67% of deviance against 17.12% deviance explained by food availability. Graphical observations of different effects may suggest that food availability becomes a limiting factor only when density-dependence is reduced (Fig. 7).

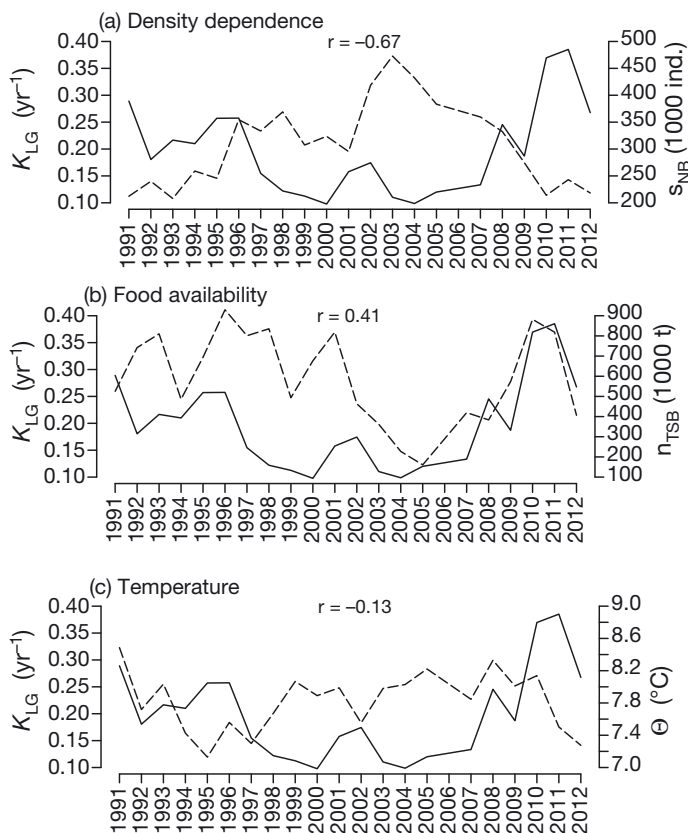


Fig. 5. Environmental factors time series from 1991 to 2012 compared to saithe growth coefficient estimates and the corresponding Pearson correlation coefficient ( $r$ ). Solid lines represent the growth coefficient from the logistic growth model,  $K_{LG}$ , and dashed lines represent the environmental variables of the year before. (a) Saithe abundance ( $s_{NB}$ ), (b) Norway pout total stock biomass ( $n_{TSB}$ ) and (c) temperature ( $\Theta$ )

Table 4. Significant relationships of North Sea saithe growth characteristics with environmental variables. Descriptor variables are  $n_{TSB}$ , for Norway pout total biomass;  $s_{NB}$ , for saithe abundance; and  $\Theta$ , for temperature. ACF indicates the autocorrelation structure.  $p$ -values were obtained after Holm adjustment concerning weight at age ( $w_a$ ) (yr)

Response	Descriptor	ACF	Coefficient	$p$ -value
Annual mean weight-at-age increment ( $\delta w_a$ )				
$\delta w_6$	$s_{NB}$	None	$-1.57E-6$	<0.05
$\delta w_7$	$s_{NB}$	None	$-2.21E-6$	<0.05
Logistic model growth coefficient ( $K_{LG}$ )				
	$s_{NB}$	None	$-6.59E-7$	<0.01
	$n_{TSB}$	None	$5.03E-8$	<0.05

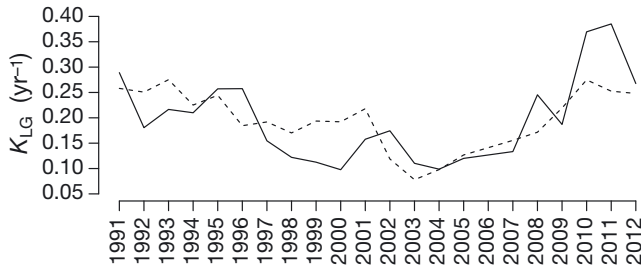


Fig. 6. Observed saithe growth coefficient,  $K_{LG}$  (solid line), and  $K_{LG}$  fitted with models including significant environmental factors (dashed line)

To summarise, saithe grew slower when density-dependence was higher independently of Norway pout availability. However, when density dependence was reduced ( $s_{NB} < 200\,000\ t$ ), saithe tended to grow faster when more Norway pout was available.

Density-dependence was the only environmental factor which had a significant effect on the saithe annual mean weight-at-age increment (Table 4). In addition, this negative effect was limited to annual weight increments between ages 5 to 6 ( $\delta w_6$ ) and 6 to 7 ( $\delta w_7$ ).

## DISCUSSION

In this study, we found that given the limitations of our data (older ages missing), saithe *Pollachius virens* growth is best described by a logistic relationship between age and length. In addition, density-dependence and food availability had negative and positive significant effects on saithe growth, respectively, while temperature was in no cases significant.

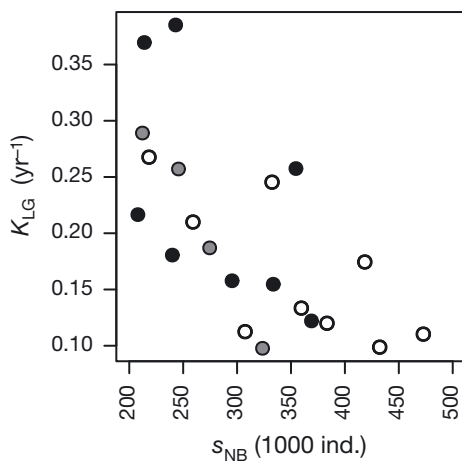


Fig. 7. Saithe average growth ( $K_{LG}$ ) as function of saithe total abundance ( $s_{NB}$ ). Circles represent Norway pout availability ( $n_{TSB}$ )—white: low availability ( $n_{TSB} < 500\,000\ t$ ); grey: medium availability ( $500\,000\ t < n_{TSB} < 700\,000\ t$ ); black: high availability ( $n_{TSB} > 700\,000\ t$ )

The generally poor performance of the VBGF to model saithe annual growth in terms of GoF, as well as the lack of biological meaning of some of the growth parameters estimated, confirms the unsuitability of the VBGF to model saithe growth when the range of age-length data is generally located well away from the asymptotic plateau (Kienzle 2005). The non-asymptotic behaviour of the saithe growth curve, within our observation window, is confirmed by the suitability of the linear model, which globally performed similarly to the VBGF model, to model saithe growth. The difficulties in estimating  $L_\infty$  may also question the suitability of the logistic model, which is also asymptotic. However, the high GoF of the logistic model when fitted to the saithe age-length data used and the reasonable range of the estimated parameters confirm its suitability. The yearly based estimation, instead of the cohort-based estimation often used in growth studies, held down temporal correlation (ICES 1991), thus allowing consideration of each year's populations as independent. This reduces the age-related correlation (different ages represented within a year belong to different cohorts) and enhances the focus on the short-term environmental effect by averaging saithe growth for each year.

Even if the absolute values of the estimated growth coefficients,  $K$ , cannot be directly compared, as not representing growth in the same way (see Eqs. 2–4), the comparison of their time trends is possible. This comparison reveals consistent trends independently of the model used to describe saithe growth. Particularly, a growth increase beginning in 2004 can be observed in the 3  $K$  time series resulting from linear, logistic and VBGF estimation as well as in the mean weight increments of the younger ages ( $\delta w_4$ ,  $\delta w_5$ ,  $\delta w_6$ ).  $K_{LG}$  was estimated using a logistic model, selected as the best model to describe saithe annual average growth.  $K_{LG}$  shifted in 2004 from a decreasing to an increasing trend. This trend shift coincides with the inception of 3 species management plans within the European Union–Norway agreement: North Sea saithe, Northern hake *Merluccius merluccius* and North Sea cod *Gadus morhua*.

This coincidence might result from fishing pressure reduction (Engelhard et al. 2015), although the link is not straightforward. The different management plans, when successful, must result in an abundance and/or biomass increase of the targeted species (saithe, hake and cod). In this context, significance of the negative density-dependent effects would suggest that the increase in saithe biomass (due to a decrease in fishing mortality) should, according to



our result, lead to a decrease in saithe growth, which is opposite to the observed trend. There are 2 explanations for this apparent paradox. First, the effects of management plans on fishing mortality and stock abundance are unlikely to be instantaneous, particularly in a changing environment context, leading to a more or less fast actual abundance and/or biomass increase depending on species resilience (Miller et al. 2010). Second, management plans may first have an impact on young individuals which will increase the average growth rate of saithe in the first years before leading to decline. These mid-term effects may be confirmed by the  $K_{LG}$  decreasing trend starting in 2010. However, fishing mortality alone is not always sufficient to explain growth, as environmental factors might influence recruitment and dynamics as well as growth in shorter terms.

Considering short-term effects (1 yr), almost half of the  $K_{LG}$  temporal variation was significantly explained by density-dependence, represented by saithe abundance, and by food availability, represented by Norway pout *Trisopterus esmarkii* total biomass. The contrasting direction of density-dependent and food availability effects is consistent with ecological theory (Jennings et al. 2001, Cury et al. 2003) and confirms the entanglement of these 2 variables (Lorenzen & Enberg 2002, Sinclair et al. 2002). The significance of density-dependent effects on age 5–6 increments ( $\delta w_6$ ) and age 6–7 increments ( $\delta w_7$ ) may be related to changes in the amount of energy allocated to somatic growth caused by maturation (Brett & Groves 1979, Day & Taylor 1997), which occurs between ages 4 and 5 for saithe (ICES 2014a). In this case, we would have expected older age increments to have a significant relationship with density-dependence as well. The lack of observable density-dependent effects could result from the high variability of the older age annual mean weight increments and suggests that annual mean weight-at-age increments, particularly for the older ages, were too variable to be a good descriptor of saithe growth.

The negative correlation between temperature and  $K_{LG}$  may suggest that annual mean temperatures are above the growth optimum (Brett & Groves 1979). The absence of significant effects of temperature on saithe growth might be explained by the narrow range of temperature variations experienced by the North Sea saithe population in the last 20 yr. Because of the limited length of the time series available and the fact that we study effects at the large scale of the whole North Sea, the best way to investigate temperature effects on saithe growth would be to conduct a study of spatial variation in growth characteristics at

a broader geographical scale, e.g. across the North Sea, the northeastern Arctic and the Faroe Islands populations. Such comparisons would be of great interest, as these saithe populations all overlap with Norway pout distribution (Lambert et al. 2009). Larger coverage might allow study of the interactions between temperature, density-dependence and food availability, which are particularly meaningful when studying growth (Brett & Groves 1979, Sinclair et al. 2002, Brunel & Dickey-Collas 2010). Also, a study of saithe growth based on cohorts instead of years, as was done for haddock *Melanogrammus aeglefinus* in the North Sea (Baudron et al. 2011), or using asymptotic/maximum body size (Baudron et al. 2014) might highlight temperature effects.

The greater effect of density-dependence relative to food availability may indicate that Norway pout alone is not a sufficient descriptor of food availability and that other forage species may be of importance. For instance, euphausiids, which are a high energetic value prey (Pedersen & Hislop 2001) and which were recorded as an important prey for saithe in the North Sea (Bergstad 1991, Du Buit 1991), may have an impact on saithe growth (Carruthers et al. 2005). However, the significant effect of Norway pout biomass, which increased from 2004 and decreased from 2009 (ICES 2014a), on saithe growth indicates that Norway pout is a key species for saithe, and confirms previous study results (Cormon et al. 2014, Lynam et al. 2015). This reinforces the assumption of bottom-up processes regulating the growth of North Sea saithe and, combined with density-dependent effects, might confirm an increasing (intra- or interspecific) competition for food resources.

This study shows that forage fish availability has an effect on predator growth. Similar results were obtained in past studies investigating the interactions between capelin *Mallotus villosus* and cod (North-west Atlantic cod, Krohn et al. [1997]; Barent Sea cod, Gjøsaeter et al. [2009]) or sandeel *Ammodytes* sp. and their predators in the North Sea (Engelhard et al. 2013). Regarding North Sea saithe, no evidence of its dependency on its main fish prey was reported before the present study. However, Carruthers et al. (2005) showed a relationship between euphausiid abundance and saithe body condition on the Scotian Shelf. It is the first time that such processes are highlighted for North Sea saithe and Norway pout. This is particularly relevant for anticipating the ecological effect of the emergence of a potential competitor, such as hake (Baudron & Fernandes 2014, Cormon et al. 2014), on well-established species such as North Sea saithe.

In this context, the emergence of hake in the North Sea may partially explain the recent decrease in saithe growth as reported in the present study, as Norway pout is also an important ingredient of hake diet (ICES 2014b). In addition, the significant relationship between Norway pout and saithe growth may add support to the saithe and hake competitive interaction hypothesis recently suggested by Cormon et al. (2014) by highlighting the potential limitation in their common resources. Therefore, these results provide, in addition to their relevance for saithe population and fisheries management, a further step towards a global understanding of the trophic-related processes involved at the population level in a large exploited marine ecosystem such as the North Sea.

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