
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.

Keywords : Bottom-up processes, von Bertalanffy growth function, Logistic growth, Norway pout, Prey availability effects, Density-dependence, Predator-prey interactions, Resource limitation, Competition

1 **1. Introduction**

2 Understanding factors regulating population dynamics is a cornerstone in ecol-
3 ogy, particularly in exploited ecosystems (Frederiksen et al., 2006, Laundré et al.,
4 2014). The size of a population is strongly influenced by its position within the
5 trophic network to which it belongs (Cury et al., 2003) and by the productivity of
6 the ecosystem, its carrying capacity. In heavily exploited marine ecosystems, assess-
7 ing the size (biomass and/or abundance) of commercial fish stocks with a sufficient
8 accuracy is of primary importance to support fisheries management.

9 In an ecosystem approach to fisheries management (FAO, 2003), multi-species
10 stock assessment tools have been developed to better integrate trophic interactions
11 in fisheries diagnostics (ICES, 2012). These tools generally allow the estimation of
12 top-down effects, *i.e.* control exerted by predators on prey populations, through an
13 estimation of predation mortalities, see Plaganyi (2007), section 2.2, for a review.
14 However, the reverse effects (bottom-up), *i.e.* the potential regulation of predator
15 populations through prey availability, are often not estimated despite their recognized
16 importance (Frederiksen et al., 2006). Understanding these bottom-up processes is
17 necessary to gain insights into interspecific competition which involves relationships
18 through shared preys in both directions (top-down and bottom-up).

19 Saithe (*Pollachius virens*) is a major top-predator fish species in the North Sea,
20 and it is commercially important for several European countries, *i.e.* Germany,
21 France, United-Kingdom and Norway. Recent stock assessments suggest that North
22 Sea saithe Spawning Stock Biomass (SSB), mean weight-at-age (Figure 1) and growth
23 have decreased in recent years (ICES, 2014a). This decrease might affect stock pro-
24 ductivity and the sustainability of dependent fisheries (Brander, 2007). Many factors,
25 related to genetic and/or phenotypic plasticity may affect fish growth (Sinclair et al.,
26 2002). Genetic effects may be induced by fisheries (Stokes & Law, 2000). The result-
27 ing changes on growth rate are supposedly slow: 0.1% per year according to Andersen
28 & Brander (2009), and therefore might be highlighted only in long-term studies. In
29 contrast, substantial changes related to phenotypic plasticity can be observed on
30 shorter time scales.

31 Three environmental factors are commonly assumed to affect fish growth: density-
32 dependence (Lorenzen & Enberg, 2002, Sinclair et al., 2002), temperature (Brunel
33 & Dickey-Collas, 2010, Baudron et al., 2011), and food availability (Krohn et al.,
34 1997, Gjøsaeter et al., 2009). Density-dependent regulation generally results from
35 an increased intraspecific competition for food at large stock size (Sinclair et al.,
36 2002, Brunel & Dickey-Collas, 2010). Density-dependent growth was recognized as a
37 common process for marine species (Lorenzen & Enberg, 2002, Sinclair et al., 2002).
38 Density-dependent effects need to be taken into account while managing species as

39 their removal and/or conservation might decrease or increase these effects (Lorenzen
40 & Enberg, 2002).

41 Changes in temperature might also affect food availability (Möllmann et al., 2005,
42 Baudron et al., 2011) or have more direct effects on fish physiology. Indeed, there
43 is an optimum temperature for growth (Jennings et al., 2001), which declines with
44 decrease of food rations (Sinclair et al., 2002). In the theoretical case of unlimited
45 food availability, growth would be determined by temperature only (Brett & Groves,
46 1979). There is currently insufficient available information to relate saithe growth to
47 environmental changes and density-dependent effects are currently neglected (ICES,
48 2014a). Hence, regulation through food availability, which is entangled with density-
49 dependence and temperature, needs to be investigated.

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

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

70 In order to understand the potential impacts of hake on saithe population in
71 the North Sea, it appears necessary to first understand the potential relationships
72 between Norway pout biomass and saithe growth characteristics that were never
73 investigated in this area. Norway pout is a short-lived species, and its dynamics are
74 driven by changes in recruitment and/or predation mortality rather than by fishing
75 mortality that is relatively low for this species (ICES, 2014a). The environmental
76 factors driving Norway pout recruitment are highly variable. Predation mortalities

77 are exerted on all ages by both saithe and hake (Lambert et al., 2009, ICES, 2014a,b).

78 Both Norway pout and saithe are northern species with overlapping areas of
79 distribution in the North Sea and Skagerrak (Lambert et al., 2009, ICES, 2014a).
80 However, only adult saithe show spatial overlap with Norway pout. Saithe juveniles
81 are distributed inshore where Norway pout (and adult saithe) are rarely present
82 (ICES, 2014a). Hence, high Norway pout biomass (or saithe abundance) is expected
83 to have only little negative impacts on saithe through predation (or cannibalism) on
84 juveniles, which allows to disentangle top-down and bottom-up effects. In addition,
85 Cormon et al. (2014) showed a positive relationship between Norway pout and saithe
86 probability of presence in the North Sea while Lynam et al. (2015) showed a positive
87 correlation between Norway pout and saithe biomass. For these reasons, it may be
88 reasonable to assume that Norway pout biomass is a suitable descriptor of food avail-
89 able to saithe, particularly when investigating limitation of resources due to potential
90 competition between saithe and hake. Evidencing resource limitation is a require-
91 ment to assume competitive interactions between two species (Link & Auster, 2013).
92 While difficult to highlight at large scale, this process may be evaluated through indi-
93 rect methods such as the study of relationship between prey availability and predator
94 growth.

95 Growth characterisation generally involves the determination of the size of an
96 organism (length or weight) in relation to time. Numerous models have been used
97 to describe fish growth, of which the von Bertalanffy Growth Function (VBGF)
98 model is probably the most common (Jennings et al., 2001, Katsanevakis, 2006,
99 Haddon, 2011). VBGF describes an organism's length in relation to its age. It
100 is based on three parameters: (i) an asymptotic length representing the maximum
101 size the organism can reach; (ii) a growth constant representing how swiftly the
102 organism's size converges towards its asymptotic value; and (iii) the theoretical age
103 of an organism of size 0. The *a priori* use of the VBGF, even when providing a good
104 description of most fish species growth (Jennings et al., 2001), may be problematic
105 (Katsanevakis, 2006). Particularly, asymptotic length and age-at-size 0 estimations
106 must be extrapolated and might lack biological meaning (Haddon, 2011). Kienzle
107 (2005) recognised the issue of using VBGF for the description of saithe growth, which
108 does not show an asymptotic length. In this context, different characterisations of
109 saithe growth need to be investigated. Finally, to study potential effects of the
110 environment on saithe growth, biologically meaningful growth parameters must be
111 used.

112 In this study, we investigated the interannual variability of North Sea saithe
113 growth in relation to different biotic and abiotic environmental factors. Saithe growth
114 was first described using annual mean weight-at-age increments. Secondly, the re-

115 lationship between saithe length and age was investigated. To this purpose, three
116 models, describing saithe growth through either linear or asymptotic age-length re-
117 lationships, were considered. Environmental factors considered were (i) main prey
118 availability, represented by the total total biomass of Norway pout, a prey that also
119 represents a major component of hake diet; (ii) density-dependence, represented by
120 saithe abundance; and (iii) temperature.

121 **2. Material and methods**

122 *2.1. Data*

123 *2.1.1. Saithe size-at-age characteristics*

124 Saithe (*Pollachius virens*) mean weight-at-age (kg), from age 3 to age 10 (yrs),
125 were extracted from ICES (2014a), over the period 1987-2012. Age-Length Keys
126 (ALK) were compiled on the basis of length measurements and age-reading on
127 otoliths, using both survey and commercial data sources. ALK survey data were
128 collected during the North Sea International Bottom Trawl Survey (IBTS) and sub-
129 sequently extracted from the International Council for the Exploration of the Sea
130 (ICES) online DATabase of TRAwling Survey (DATRAS) for the period 1991-2012
131 (except for 2006 for which data were missing). Data were explored by age for length
132 values and outliers (extreme values considered biologically meaningless) were ignored
133 in subsequent analyses. The final survey database included ALK from ages 2 to 10
134 years (Table 1).

135 *2.1.2. Environmental factors*

136 Annual Norway pout (*Trisopterus esmarkii*) Total Stock Biomass (TSB) (t),
137 and saithe abundance, in total number of individuals, were extracted from assess-
138 ment report (ICES, 2014a) for the period 1987-2012. Sea bottom temperatures
139 ($^{\circ}\text{C}$), measured using Sonde (CTD) devices, were extracted from the ICES Oceano-
140 graphic online database (OCEAN) at quarter and statistical rectangle (1° longitude
141 \times 0.5° latitude) resolution. Bottom temperatures were averaged annually from 1987
142 to 2012 over the study area (Figure 2).

143 *2.2. Saithe growth characteristics*

144 *2.2.1. Annual mean weight increments*

145 First, saithe annual mean weight increments were calculated (Equation (1)) for
146 each age using mean weight-at-age data described previously. Because age 2 saithe
147 individuals are not in the North Sea (ICES, 2014a), we did not calculate the annual
148 weight increment between ages 2 and 3. Age 10 is considered as a *plus* group (age 10

149 and older) by ICES (2014a). Therefore, the calculation of an annual weight increment
 150 between age 9 and age 10 was not possible (Table 1).

$$151 \quad \delta w_{at} = w_{at} - w_{a-1t-1} \quad (1)$$

152 where δw is the annual average weight (w) increment in kilos; a the age in years;
 153 and t the time in years.

154 2.2.2. Age-length relationship

155 Three candidate growth models were fitted to saithe age-length data. First,
 156 the traditional von Bertalanffy Growth Function (VBGF) was fitted (Equation (2)).
 157 Second, a Verhulst logistic growth model (Equation (3)) was fitted and, third, a more
 158 pragmatic linear model was fitted (Equation (4)).

159 The VBGF model (VB) assumes an asymptotic relationship between length, l ,
 160 and age, a , depending upon three parameters: an asymptotic length, l_∞ , a growth co-
 161 efficient, K_{VB} , which determines how swiftly length, l , converges towards its asymp-
 162 totic value, and a_0 which represents the theoretical age at which individuals are of
 163 size null.

$$164 \quad l_a = l_\infty \times (1 - e^{-K_{VB} \times (a - a_0)}) \quad (2)$$

165 where l_∞ is in centimetres; K_{VB} in year⁻¹; and a_0 in years.

166 The logistic model (LG) assumes a sigmoidal relationship between length, l , and
 167 age, a , depending upon three parameters: an asymptotic length, l_∞ ; a relative growth
 168 coefficient, K_{LG} ; and a_i , a sigmoidal curve inflection point, which represents the
 169 theoretical age at which individuals growth trajectory changes.

$$170 \quad l_a = l_\infty \times \frac{1}{(1 + e^{-K_{LG} \times (a - a_i)})} \quad (3)$$

171 where l_∞ is in centimetres; K_{LG} in year⁻¹; and a_i in years.

172 The linear model (LM) assumes that within the range of data available, length,
 173 l , is linearly related to age, a , depending upon an intercept, l_0 which represents the
 174 length at age 0 and a regression coefficient, K_{LM} , here representing growth.

$$175 \quad l_a = l_0 + K_{LM} \times a \quad (4)$$

176 where l is in centimetres; a in years; and K_{LM} in centimetres per year.

177 Age proportions within each year were checked to ensure sufficient and similar
 178 representation of the different ages. As different ages represented within a year be-
 179 long to different cohorts and in order to reduce the cohort-related correlation, the

180 three models were fitted for each year separately (ICES, 1991). Therefore, each year
 181 was considered as an independent sub-population allowing us to identify potential
 182 short-term variations by representing saithe annual average growth (Haddon, 2011)
 183 rather than focus on cohort average growth, which may involve longer-term effects.
 184 Linear models (Equation (4)) were fitted using linear regression, while asymptotic
 185 models (Equations (2) and (3)) were fitted using Non-linear Least Squares (NLS)
 186 regression. NLS iterations were optimized using Marquadt’s algorithm and starting
 187 values set as follows: $K = 0.07$ (Jennings et al., 1998); $l_\infty = 177.1$ cm (Jennings
 188 et al., 1998); $a_0 = -0.8$ years (Froese & Pauly, 2014); and, $a_i = 5$ years based
 189 on saithe age at first maturity (Froese & Pauly, 2014, ICES, 2014a). NLS regres-
 190 sions were optimized using R 2.15.3 and `nlxb` function of `{nlmrt}` (Nash, 2013). The
 191 three candidate model were evaluated based on the comparison of their corrected
 192 Akaike Information Criterion (AICc), which is used to compare non-nested mod-
 193 els Goodness-of-Fit (GoF) (Burnham & Anderson, 2002). Differences between all
 194 models (ΔAIC_c) were calculated and the model with smallest AICc was selected.

195 2.3. Effect of the environment

196 2.3.1. Annual mean weight increment analysis

197 Generalized Least Squares (GLS) were used to fit the relationships between saithe
 198 annual mean weight increment, δw_{at} , and environmental factors prevailing during the
 199 year of the increment ($t - 1$) as described by Equation (5),

$$200 \quad \delta w_{at} \sim \mu + \beta_1 \cdot n_{TSB_{t-1}} + \beta_2 \cdot s_{NB_{t-1}} + \beta_3 \cdot \Theta_{t-1} + \epsilon_t \quad (5)$$

201 where a is the age; t the time in years; μ the intercept; β_1 , β_2 and β_3 are the coeffi-
 202 cients associated to Norway pout TSB (n_{TSB}) representing food availability, saithe
 203 abundance (s_{NB}) representing density dependence and mean bottom temperature
 204 (Θ), respectively; and ϵ the residual error. Residuals were checked for time autocor-
 205 relation using correlograms.

206 When significantly autocorrelated, the residuals’ error structure could be de-
 207 scribed by, either an AutoRegressive model (AR) where residuals (ϵ_t), depend upon
 208 lagged (s) residuals (ϵ_{t-s}); a Moving Average model (MA) where (ϵ_t) depends upon
 209 both random noise indexed at time t (v_t), and its lagged value (v_{t-s}); or an Au-
 210 toRegressive Moving Average model (ARMA), combining both (Zuur et al., 2009).
 211 The error structure was determined by examining the autocorrelation and partial
 212 autocorrelation functions (Zuur et al., 2009, Groeger et al., 2014). The regression
 213 described by Equation (5) was modified to include in the residuals, ϵ_t , the suitable
 214 time correlation structure chosen among the previously mentioned ones. The GoF of

215 the error-structured model was compared to original models based on Akaike Infor-
216 mation Criterion (AIC). Equation (6) describes a first order (1,1) ARMA process.

$$217 \quad \epsilon_t = \phi \cdot \epsilon_{t-1} + v_t + \theta \cdot v_{t-1} \quad (6)$$

218 where t is the time in years, ϕ the AR parameter, v the random noise and θ the MA
219 parameter. When residuals were not autocorrelated, the regression was equivalent to
220 an Ordinary Least Squares (OLS) regression. Least-squares optimisation was made
221 using Nelder & Mead (1965) algorithm.

222 Contribution of the different descriptors was tested using either *F-test*, when
223 residual errors were not significantly autocorrelated, or *Wald-test*, when residuals
224 autocorrelation was taken into account. Variables with the highest p-values were
225 dropped one by one to select significant variables by backward elimination ($\alpha < 0.05$).
226 As multiple tests were carried out (one test per mean weight-at-age increment), p-
227 values were adjusted using Holm correction (Wright, 1992) to keep the family-wise
228 type I error rate at level $\alpha = 0.05$. In total six regression models, from age incre-
229 ment 3-4 (δw_4) to age increment 8-9 (δw_9), with different descriptor coefficients and
230 descriptor significance per model, were fitted. Regression residuals, after autocor-
231 relation was taken into account if necessary, were tested for trends, normality and
232 homoscedasticity.

233 2.3.2. Growth coefficient analysis

234 The study of environmental effects focused on temporal variations of saithe
235 growth coefficient, K , as other growth parameter might result from extrapolation
236 or are biologically meaningless (Kienzle, 2005, Haddon, 2011). First, the trends of
237 the three environmental variables (n_{TSB} , s_{NB} and Θ) were compared to annual K
238 trends estimated with selected growth models. Pearson correlation coefficients (r)
239 between K and environment time-series were calculated. To study the short-term
240 variations of growth, we used a 1 year time-lag for the exploration of environmental
241 effects. Thus, we focused on short-term environmental effects (conditions prevailing
242 the year before) on saithe annual average growth. Secondly, the relationships be-
243 tween K and the environment were investigated with regression techniques similarly
244 to annual mean weight-at-age increments (see section 2.3.1). Regression residuals
245 were checked for autocorrelation, resulting in the error term potentially including
246 adequate ARMA model (Equation (6)). Contribution of the different descriptors
247 was tested using either *F-test*, when no significant time autocorrelation was found,
248 or *Wald-test*, otherwise. Significant variables were selected by backward elimination
249 ($\alpha < 0.05$). Regression residuals, after autocorrelation was taken into account if
250 necessary, were tested for trends, normality and homoscedasticity.

251 **3. Results**

252 *3.1. Saithe growth characteristics*

253 Trends in mean weight-at-age annual increment showed a general decrease for
254 saithe (*Pollachius virens*) of all ages between 1988 and 2000 (Figure 3). In addi-
255 tion, weights-at-age increments of the older fish were subject to large interannual
256 variations.

257 Based on corrected Akaike Information Criterion (AICc) metrics, saithe age-
258 length relationship was generally best described by a logistic growth model (Table 3).
259 The three candidate models, the linear model (LM), the logistic model (LG) and
260 the von Bertalanffy Growth Function (VBGF) model (VB), after being adjusted to
261 our range of data, were not equally meaningful in biological terms. The pragmatic
262 LM model, which assumed an infinite growth (no asymptote), estimated growth
263 parameters in a biologically meaningful range with length-at-age 0, l_0 , ranging from
264 16.41 cm to 30.41 cm and K_{LM} ranging from a length increase per year of 4.73 cm to
265 8.12 cm (Table 2). By contrast, the VB model, which builds on ecological theory, led
266 to biologically meaningless estimations of l_∞ (median $l_\infty > 80\,000$ m). In comparison,
267 l_∞ estimated using LG model were more realistic (median $l_\infty = 165$ cm) even if
268 estimates for 5 years (1998-2000, 2003, 2004) were also meaningless (maximum $l_\infty >$
269 $260\,000$ m). These extreme values of l_∞ must be caused by the age range of our data
270 which does not cover completely saithe lifespan (Cohen et al., 1990, 25 years old),
271 thus not allowing to estimate the asymptotic plateau.

272 The comparison of the three models Goodness-of-Fit (GoF) highlighted a better
273 fit of LG models that had the smallest AICc for all years except in 2010, for which
274 VB model had the best fit (Table 3). The LM and VB models had similar GoF,
275 except for years 2008, 2010 and 2011. In order to model saithe growth consistently
276 over years, and based on the models' biological meaningfulness and GoF, the logis-
277 tic model was selected as the best descriptor of saithe growth (Figure S1). Saithe
278 growth coefficient (K_{LG}) globally decreased from 1991 to 2004. At finer scale, K_{LG}
279 decreased (1991-1992; 1996-2000; 2002-2004) and increased (1992-1996; 2000-2002)
280 alternatively (Figure 4). From 2004 to 2011, there was a general increase of K_{LG}
281 except in 2009. The increase in K_{LG} observed from 2009 until 2010 was consistent
282 with that of K_{VB} , the growth coefficient of VB that had a better fit for this particular
283 year, thereby confirming that the use of the LG model in 2010 did not affect general
284 trends of annual saithe growth coefficient. Finally, K_{LG} started to decrease again
285 from 2011 to 2012. General trends were consistent between all three K estimates
286 (Figure 4) which comforted us in the trends observed (Figure 4).

287 3.2. Environmental effects

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

301 Density-dependence and prey availability explained together 46.79% of the model
302 deviance (not shown). When saithe abundance increased by 659 000 individuals,
303 saithe annual average growth, K_{LG} , dropped by 0.01 in the following year. Likewise,
304 a 503 000 t increase of Norway pout total biomass led to a K_{LG} increase of 0.001
305 in the following year. Density-dependent effects on saithe annual average growth
306 were strong and were the main driver of K_{LG} trends explaining 29.67% of deviance
307 against 17.12% deviance explained by food availability. Graphical observations of
308 different effects may suggest that food availability becomes a limiting factor only
309 when density-dependence is reduced (Figure 7). To summarise, saithe grew slower
310 when density-dependence was higher independently of the food available. However,
311 when density-dependence was reduced ($s_{NB} < 200\ 000$ t) saithe tended to grow faster
312 when more food was available.

313 Density-dependence was the only environmental factor which had a significant
314 effect on saithe annual mean weight-at-age increment (Table 4). In addition, this
315 negative effect was limited to annual weight increment between ages 5-6 (δw_6) and
316 ages 6-7 (δw_7).

317 4. Discussion

318 In this study, we found that, given the limitations of our data (older age missing),
319 saithe (*Pollachius virens*) growth is best described by a logistic relationship between
320 age and length. In addition, density-dependence and food availability had, respec-
321 tively, negative and positive significant effects on saithe growth, while temperature
322 was never found significant.

323 The generally poor performance of the von Bertalanffy Growth Function (VBGF)
324 to model saithe annual growth in terms of Goodness-of-Fit (GoF), as well as the
325 lack of biological meaning of some of the growth parameters estimated, confirms
326 the unsuitability of the VBGF to model saithe growth where the range of age-length
327 data is generally located well away from the asymptotic plateau (Kienzle, 2005). The
328 non-asymptotic behaviour of saithe growth curve, within our observation window,
329 is confirmed by the suitability of the linear model to describe saithe growth, which
330 globally performed similarly to the VBGF model. The difficulties to estimate l_∞
331 may also question the suitability of the logistic model, which is asymptotic as well.
332 However, the high GoF of the logistic model when fitted to saithe age-length data and
333 the reasonable range of the estimated parameters confirm its suitability. The yearly-
334 based estimation, instead of the cohort-based estimation often used in growth studies,
335 presents the advantage of reducing temporal correlation (ICES, 1991), thus allowing
336 to consider each year's populations as independent. This reduces the age-related
337 correlation (different ages represented within a year belong to different cohorts) and
338 enhances the focus on short-term environmental effect by averaging saithe growth
339 for each year.

340 Even if the absolute value of the estimated growth coefficients, K , cannot be
341 directly compared, as not representing growth in the same way (see Equations (2)
342 to (4)), the comparison of their time trends is possible. This comparison reveals
343 consistent trends independently of the model used to describe saithe growth. Partic-
344 ularly, a growth increase beginning in the second half of the 2000's can be observed
345 in K time-series resulting from linear, logistic and VBGF estimation as well as in the
346 mean weight increments of the younger ages (δw_4 , δw_5 , δw_6). Growth coefficient
347 K_{LG} was estimated using a logistic model, selected as the best model to describe
348 saithe annual average growth. K_{LG} shifted in 2004 from a decreasing to an increas-
349 ing trend. This trend shift coincides with the inception of three species management
350 plans within EU-Norway agreement: North Sea saithe, Northern hake (*Merluccius*
351 *merluccius*) and North Sea cod (*Gadus morhua*).

352 This coincidence might result from fishing pressure reduction (Engelhard et al.,
353 2015), although the link is not straightforward. The different management plans,
354 when successful, must result in abundance and/or biomass increase of the targeted
355 species (saithe, hake and cod). In this context, significance of the negative density-
356 dependence effects would suggest that the increase in saithe biomass (due to a de-
357 crease in fishing mortality) should, according to our result, lead to a decrease in saithe
358 growth, which is just opposite to the observed trend. There are two explanations to
359 this apparent paradox. First, the effects of management plans on fishing mortality
360 and stock abundance are unlikely to be instantaneous, particularly in a changing

361 environment context, to a more or less fast actual abundance and/or biomass in-
362 crease depending on species resilience (Miller et al., 2010). Second, management
363 plans may first have an impact on young individuals which will increase the average
364 growth rate of saithe in the first years before leading to decline. These mid-term
365 effects may be confirmed by K_{LG} decreasing trend starting in 2010. However, fishing
366 mortality alone is not always sufficient to explain growth as environmental factors
367 might influence recruitment and dynamics as well as growth in shorter terms.

368 Considering short-term effects (one year), almost half of K_{LG} temporal varia-
369 tion was significantly explained by density-dependence, represented by saithe abun-
370 dance, and food availability, represented by Norway pout (*Trisopterus esmarkii*)
371 total biomass. The opposite direction of density-dependence and food availability
372 effects are consistent with ecological theory (Jennings et al., 2001, Cury et al., 2003)
373 and confirm the entanglement of these two variables (Sinclair et al., 2002, Lorenzen
374 & Enberg, 2002). The significance of density-dependence effects on ages 5-6 incre-
375 ments (δw_6) and ages 6-7 increments (δw_7) may be related to changes in the amount
376 of energy allocated to somatic growth caused by maturation (Brett & Groves, 1979,
377 Day & Taylor, 1997), which occurs between age 4 and age 5 for saithe (ICES, 2014a).
378 In this case, we would have expected older ages increments to have significant rela-
379 tionship with density-dependence as well. The lack of observable density-dependent
380 effects could result from the high variability of the older ages annual mean weight
381 increments and suggest that annual mean weight-at-age increments, particularly for
382 the older ages, were too variable to be good descriptor of saithe growth.

383 The negative correlation between temperature and K_{LG} may suggest that annual
384 mean temperatures are over the growth optimum (Brett & Groves, 1979). The ab-
385 sence of significant effects of temperature on saithe growth might be explained by the
386 narrow range of temperature variations experienced by the North Sea saithe popula-
387 tion in the last 20 years. Because of the limited length of the times series available,
388 and the fact that we study effects at the large scale of the whole North Sea, the best
389 way to investigate temperature effects on saithe growth would be to conduct a study
390 of spatial variation in growth characteristics at a broader geographical scale *e.g.*
391 across the North Sea, the Northeast Arctic, and the Faroe Islands populations. Such
392 comparisons would be of great interest as these saithe populations all overlap with
393 Norway pout distribution (Lambert et al., 2009). Larger coverage might allow to
394 study the interactions between temperature, density-dependence and food availabil-
395 ity, which are particularly meaningful when studying growth (Brett & Groves, 1979,
396 Sinclair et al., 2002, Brunel & Dickey-Collas, 2010). Also, a study of saithe growth
397 based upon cohorts instead of years, as was done for haddock (*Melanogrammus ae-*
398 *glefinus*) in the North Sea (Baudron et al., 2011), or using asymptotic/maximum

399 body-size (Baudron et al., 2014) might highlight temperature effects.

400 The greater effect of density-dependence relative to food availability may indicate
401 that Norway pout alone is not a sufficient descriptor of food availability and that
402 other forage species may be of importance. For instance, euphausiids which are
403 high energetic value preys (Pedersen & Hislop, 2001) and which were recorded as an
404 important prey for saithe in the North Sea (Bergstad, 1991, Du Buit, 1991) may have
405 an impact on saithe growth (Carruthers et al., 2005). However, the significant effect
406 of Norway pout biomass, which increased from 2004 and decreased from 2009 (ICES,
407 2014a), on saithe growth indicates that Norway pout is a key species for saithe and
408 confirms previous studies results (Cormon et al., 2014, Lynam et al., 2015). This
409 reinforces the assumption of bottom-up processes regulating growth of North Sea
410 saithe and, combined with density-dependence effects might confirm an increasing
411 (intra- or interspecific) competition for food resource.

412 Finally, this study shows an effect of the forage fish availability on predator
413 growth. Similar results were obtained in past studies investigating the interactions
414 between capelin (*Mallotus villosus*) and cod (Northwest Atlantic cod, Krohn et al.
415 (1997); Barent Sea cod, Gjøsaeter et al. (2009)) or sandeel (*Ammodytes sp.*) and their
416 predators in the North Sea (Engelhard et al., 2013). Regarding, North Sea saithe,
417 no evidence on dependency of its main fish preys was reported before. However,
418 Carruthers et al. (2005) showed a relationship between euphausiids abundance and
419 saithe body condition in the Scotian Shelf. It is the first time that such processes
420 are highlighted for North Sea saithe and Norway pout. This is particularly relevant
421 to anticipate the ecological effect of the emergence of a potential competitor, such as
422 hake (Baudron & Fernandes, 2014, Cormon et al., 2014), on well-established species
423 such as North Sea saithe. Indeed, the emergence of another top-predator in the
424 North Sea might affect food availability through predation and, according to the
425 results obtained here, indirectly impact the growth of its competitors, such as saithe.

426 In this context, the emergence of hake in the North Sea might partially explain
427 the decreasing saithe growth, as Norway pout is also an important ingredient of
428 hake diet shown (ICES, 2014b). In addition, the significant relationship between
429 Norway pout and saithe growth may push forward the saithe and hake competitive
430 interaction hypothesis recently suggested by Cormon et al. (2014) by highlighting
431 a limitation of their common resource. Therefore, these results provide a further
432 step towards a global understanding of the trophic-related processes involved at the
433 population level in a large marine exploited ecosystem such as the North Sea, in
434 addition to their specific interest for saithe population and/or fisheries.

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Table 1: Overview of population size characteristics data, their units, and their age and time coverage. *2006 year is missing.

Data	Units	Age	Time
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*

Table 2: Parameters estimates distribution depending on growth model used.

Estimate parameter	Minimum	Median	Maximum
Linear model, Equation (4)			
l_0	16.41	22.40	30.41
K_{LM}	4.73	6.47	8.12
Logistic model, Equation (3)			
a_i	2.62	8.88	138.40
K_{LG}	0.10	0.18	0.39
l_∞	82	165	26.7e06
von Bertalanffy Growth Function model, Equation (2)			
a_0	-6.10	-3.14	-0.93
K_{VB}	3.7e-07	7.6e-07	0.16
l_∞	95.00	8.4e06	17.6e06

Table 3: Differences of AIC_c (ΔAIC_c) by pairs of model (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

Table 4: Significant relationships of North Sea saithe growth characteristics with environmental variables. Descriptor variables are noted n_{TSB} , for Norway pout total biomass; s_{NB} , for saithe abundance; and Θ , for temperature. ACF indicates the autocorrelation structure. *Pvalues were obtained after Holm adjustment concerning w_a .

Response	Descriptor	ACF	Coefficient	Pvalue*
Annual mean weight-at-age increment (δw_a)				
δw_6	s_{NB}	None	$-1.57e-06$	$p < 0.05$
δw_7	s_{NB}	None	$-2.21e-06$	$p < 0.05$
Growth coefficient (K_{LG})				
	s_{NB}	None	$-6.59e-07$	$p < 0.01$
	n_{TSB}	None	$5.03e-08$	$p < 0.05$

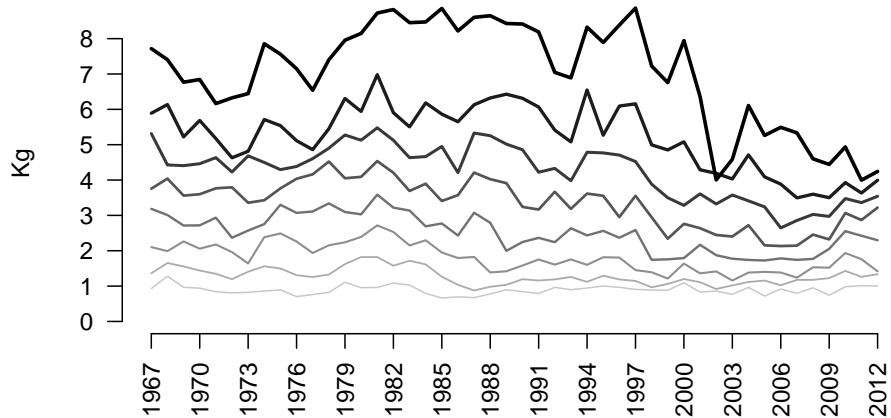


Figure 1: Saithe mean weight-at-age trends from 1967 to 2012. Saithe mean weight-at-age 3 (light grey thin line) to mean weight-at-ages 10+ (black thick line).

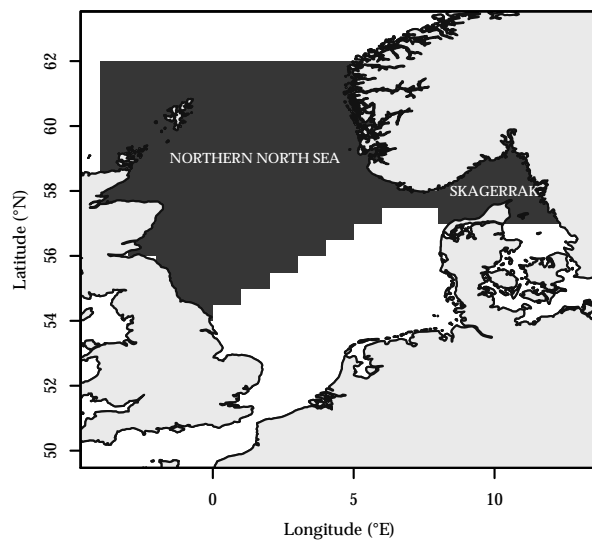


Figure 2: Map of the study area.

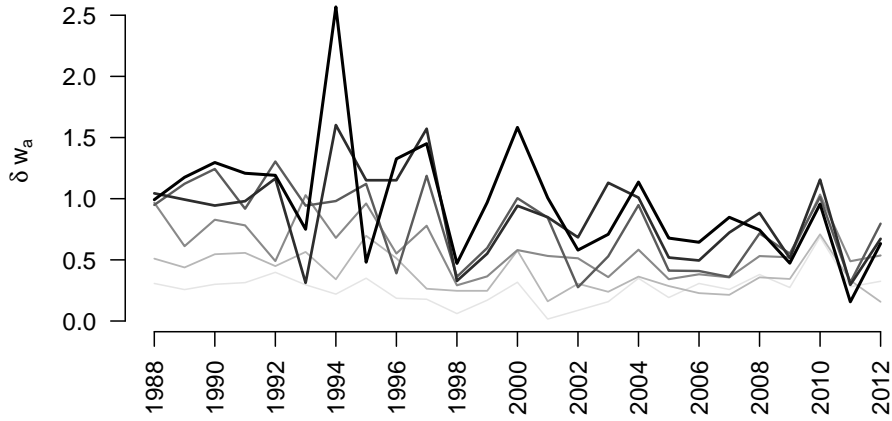
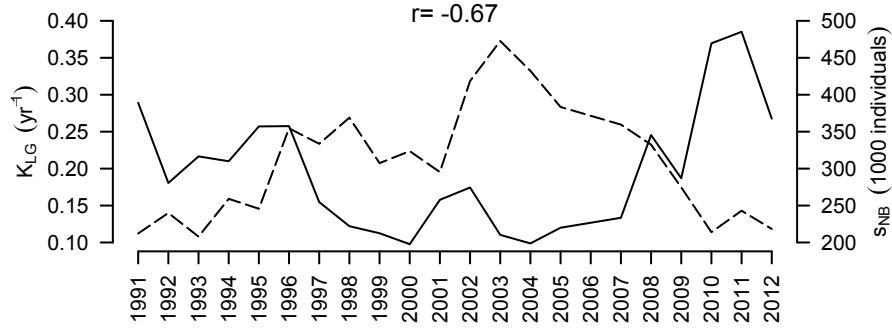


Figure 3: Temporal trends in North Sea saithe annual mean weight-at-age increment (δw_a) over the 1988-2012 period. Increments between age 3 and age 4 (δw_4 , light grey thin line) to increments between age 8 and age 9 (δw_9 , black thick line).

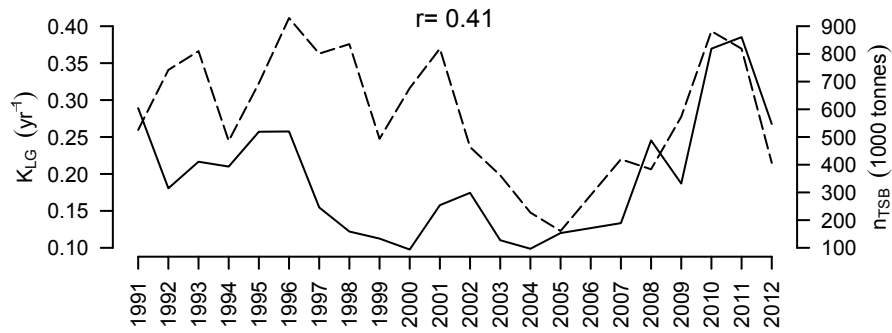


Figure 4: Growth coefficients, K , estimated for period covering 1991 to 2012 using the linear model, the Verhulst logistic growth model and the Von Bertalanffy Growth Function. The dotted line shows the linear model growth coefficient estimates, K_{LM} (Equation (4)); the solid line shows the Verhulst logistic model growth estimates, K_{LG} (Equation (3)); and the dashed line shows the VBGF model estimates, K_{VB} (Equation (2)). Y-axis are not plotted as absolute values of the different growth coefficients are not of interest.

(a) Density dependence



(b) Food availability



(c) Temperature

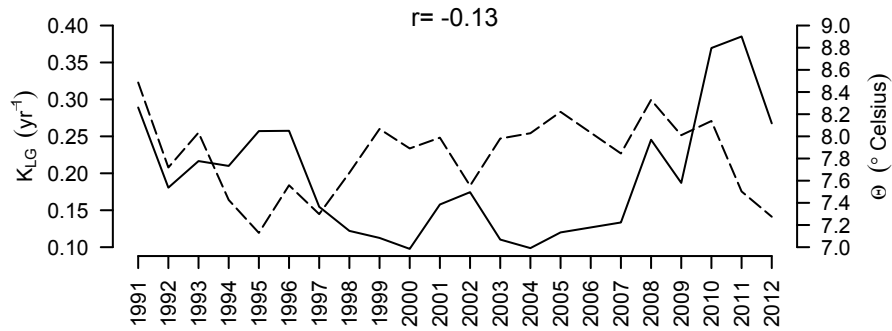


Figure 5: Environmental factors time series from 1991 to 2012 compared to saithe growth coefficient estimates and the corresponding Pearson correlation coefficient (r). Solid lines represent the growth coefficient from logistic growth model, K_{LG} ; and dashed lines represent the environmental variables of the year before (a) saithe abundance, S_{NB} ; (b) Norway pout Total Stock Biomass, n_{TSB} ; and (c) temperature, θ .

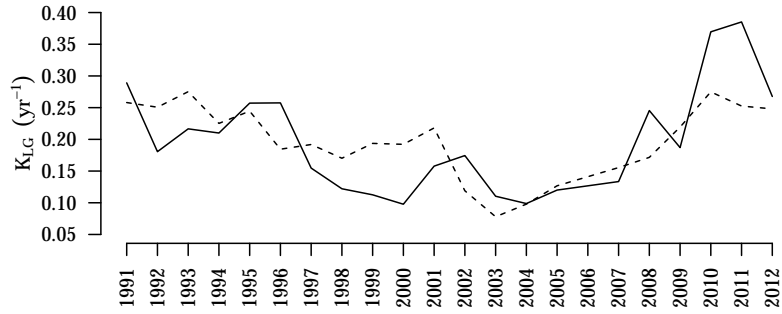


Figure 6: Observed saithe growth coefficient, K_{LG} (solid line), and K_{LG} fitted with models including significant environmental factors (dashed line).

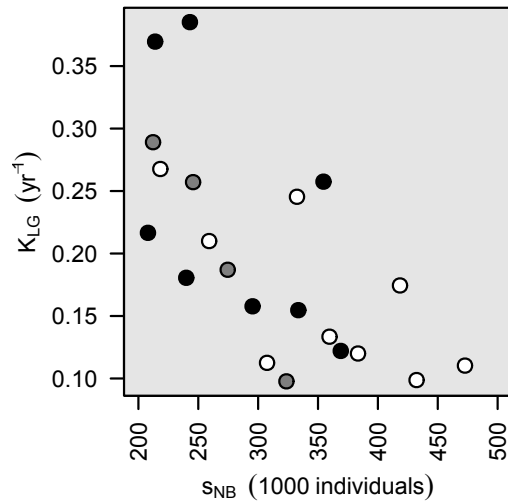


Figure 7: Saithe average growth (K_{LG}) as function of saithe total abundance (s_{NB}). Color filling represents Norway pout availability (n_{TSB}). White: low availability ($n_{TSB} < 500\,000$ t). Grey: medium availability ($500\,000$ t $< n_{TSB} < 700\,000$ t). Black: high availability ($n_{TSB} > 700\,000$ t).

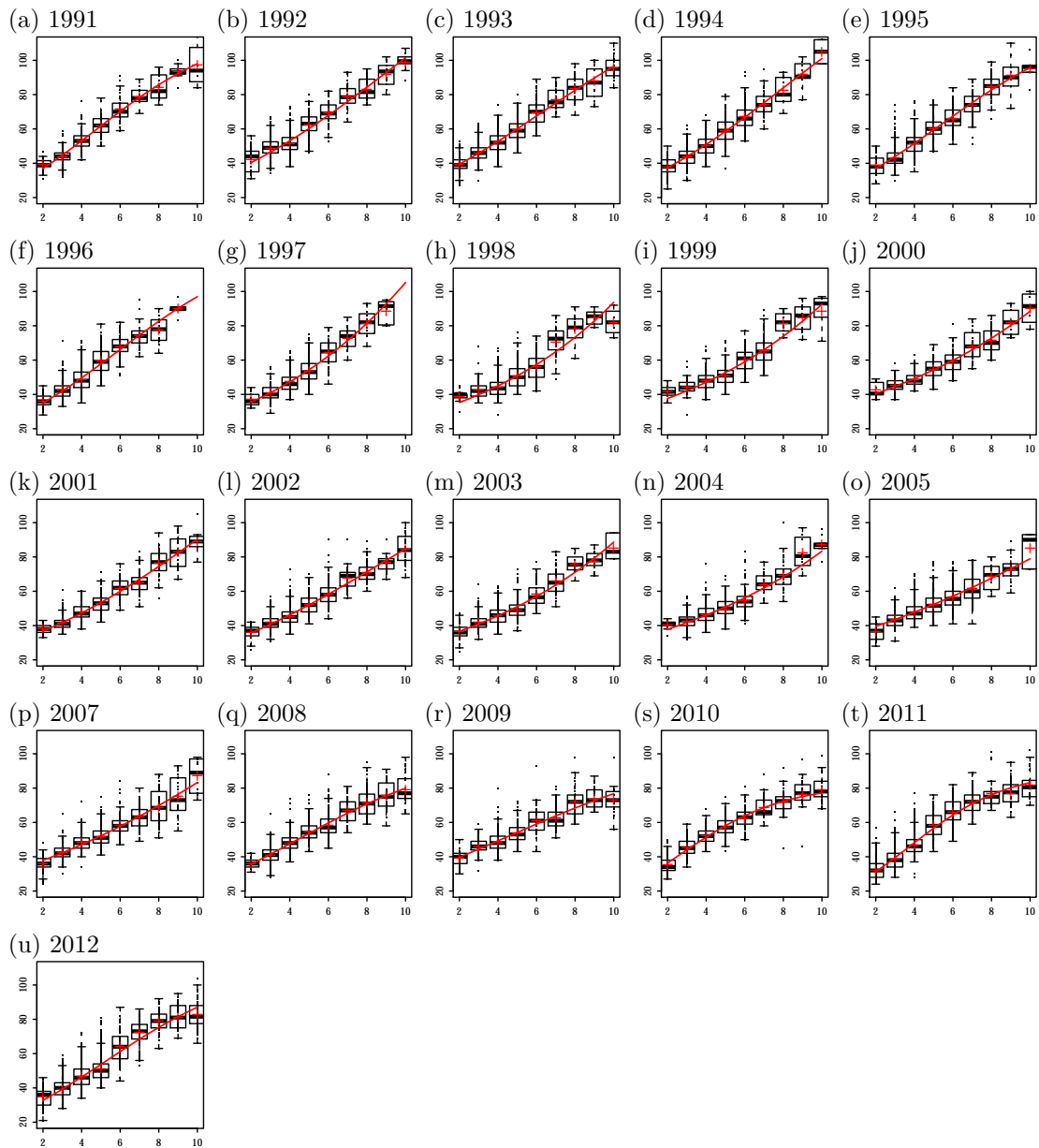


Figure S1: North Sea saithe length measured during the different survey years as function of the age. Red crosses represent mean length-at-age, red lines represent fitted logistic growth curves.

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