

# Investigating spatial heterogeneity of von Bertalanffy growth parameters to inform the stock structuration of common sole, *Solea solea*, in the Eastern English Channel

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## Abstract :

In fisheries science, a mismatch between the delineation of a fish stock and the underlying biological population can lead to inaccurate assessment and management. Previous results suggested a potential spatial structuration of the Eastern English Channel (EEC) stock of common sole, *Solea solea*, in three sub-populations. In this article, we propose to investigate the spatial population structure of common sole in the EEC using the von Bertalanffy Growth Function parameters as indicators of population segregation. In order to test the sub-population hypothesis and evaluate its robustness to data sources, we developed three models, all including an area effect on growth parameters. The first model was aimed at testing a potential data source effect (in addition to the area effect) using commercial and scientific survey data jointly. The two other models used either scientific survey or commercial fishery data and focused on spatial differences in growth parameters. Our results showed that the growth parameter estimates indeed differed depending on the type of data used, with higher estimated asymptotic length and length at age two (L2) using commercial data. They also highlighted spatial differences in asymptotic length, consistent between models, which tend to confirm a spatial structuration of sole in the EEC. While these results need to be strengthened by marking and genetic studies, they constitute a first step towards a better understanding of the population spatial structuration of common sole in the EEC.

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## Highlights

► Von Bertalanffy growth parameters are used to inform the spatial structuration of an exploited species. ► Spatial differences in asymptotic length reinforce the metapopulation hypothesis. ► Growth parameters estimates differ depending on the type of data used - scientific survey or commercial fisheries.

**Keywords :** Key-words, von Bertalanffy growth function, Stock structuration, Solea solea, Flatfish, Life-history traits, Metapopulation

## Abbreviations

- VBGF, von Bertalanffy growth function;
- EEC, eastern english channel;
- SW, southwest;
- NE, northeast;
- ICES, International Council for the Exploration of the Sea;
- UK-BTS, UK beam trawl survey;
- NLR, non-linear regression;
- GNLS, generalized nonlinear least squares

## 1. Introduction

Harvested species are usually assessed and managed at the stock-unit scale, a stock being defined as an intraspecific group of individuals randomly mating and maintaining its integrity in time and space (Ihssen et al., 1981). Boundaries of these stock units are supposed to reflect the underlying population structures in terms of biological rates such as mortality and growth (Cadrin et al., 2014; Kerr et al., 2016). Recent research suggests that a strong population structuration in marine fish is a relatively common situation (Ames and Lichter, 2013; Ciannelli et al., 2013; Reiss et al., 2009; Waples and Gaggiotti, 2006), and is mainly driven by oceanographic and environmental factors and larval diffusion (Cowen, 2006; Jorgensen et al., 2005), but also by species' specific migratory behaviour (Secor, 2015) and sequential occupancy of various habitats throughout the lifespan (Petitgas et al., 2013, 2010). An assumed single homogeneous population can sometimes turn out to be a set of sub-populations linked by dispersal, i.e., a metapopulation (Alex Smith and Green, 2005; Hanski, 1998; Kritzer and Sale, 2004). Mismatch between the stock-unit delineation and the true metapopulation structure may impede our capacity to provide adequate management recommendations (e.g., Total Allowable Catch) and may lead to overfishing of the less productive sub-populations while the more productive sub-populations are underexploited (Cadrin and Secor, 2009; Frank and Brickman, 2000; Fu and Fanning, 2004; Ricker, 1981). In the past decade, stock identification has been explored for numerous fish stocks, such as blue whiting, Atlantic cod, and horse mackerel (Abaunza et al., 2008; Mahe et al., 2007; Zemeckis et al., 2014) and led to revise stock boundaries.

The Eastern English Channel (EEC) common sole, *Solea solea*, is a nursery-dependent flatfish species harvested across its entire range, from the Mediterranean to Baltic Sea

(Wheeler, 1978). Reproduction occurs from winter to spring throughout the distribution area, resulting in several weeks of pelagic larval drift before settlement and metamorphosis in coastal and estuarine nursery grounds (Rochette et al., 2012) . After two years, mature common soles are recruited to the stock and can in turn reproduce (Dorel et al., 1991; Riou, 2001). The common sole is a high value targeted fish in the EEC with some fleets highly dependent on it. Fishing mortality on EEC common sole has decreased over the last decade and was estimated below  $F_{msy}$  - the fishing mortality that produces the maximum sustainable yield (ICES, 2017) - for the first time in 2017 (ICES, 2017) due to a series of low recruitments. However, the biomass is still below the targeted value ( $MSY_{Btrigger}$ ; ICES, 2017).

Contrasts in the length structure of French landed common sole between the North and South of the EEC raise concerns about a possible misunderstanding of the stock structure (Du Pontavice et al., personal communication). The fleets fishing on the EEC sole are segregated in space, across areas corresponding to potentially different components of the population. It is therefore crucial to improve our knowledge of spatial structuration and population connectivity within the EEC stock and to check whether the hypothesis of a unique stock matches the underlying population structure. A body of research already investigated the level of connectivity of common sole population in the EEC at different stages of the life cycle. First, larval advection to coastal nursery grounds has been shown to limit the connectivity between the different spawning and nursery grounds (Rochette et al., 2012). Second, previous analyses evidenced juveniles common sole as sedentary in their nursery grounds during the two first years of life (Coggan and Dando, 1988; Le Pape and Cognez, 2016). Finally, former mark-recapture surveys suggested low mobility of adult common sole (Burt and Millner, 2008; Kotthaus, 1963). On the basis of these

results, recent modelling studies hypothesized the existence of three sub-populations spatially structured within the EEC (Figure 1; (Archambault et al., 2016; Rochette et al., 2012). Archambault et al., (2016) assessed the effect of adult-mediated connectivity on population dynamics and stock assessment and concluded that ignoring possible metapopulation could lead to overexploitation of local populations in the EEC. The authors also suggested that research should focus on the adult-mediated connectivity, which remained largely unknown and which magnitude could be a strong driver of spatial structuration within the EEC (Frisk et al., 2014). Recently, the improvement and the multiplication of stock identification tools has made stock delineation increasingly precise (Cadrin et al., 2014; Kerr et al., 2016; Pita et al., 2016). In particular, the use of life-history parameters (e.g., age, growth and mortality) is particularly relevant and cost-efficient (Cadrin et al., 2014). For instance, Barrios et al. (2017) coupled individual growth trajectories and length-at-age datasets in mixed-effects models to investigate stock identification of whiting in the North East Atlantic. Erlandsson et al. (2017) suggested a reconsideration of assessment models of European Flounder based on the spatiotemporal structure of body size in the Baltic Sea. Given the before-mentioned differences in EEC common sole length structure, we propose to study the spatial heterogeneity in length at age as a way to identify spatial structuration within the stock and to test the three common sole sub-populations hypothesis mentioned earlier. Growth is usually modelled using the von Bertalanffy Growth Function (VBGF; Von Bertalanffy, 1938) which provides a non-linear relationship between length and age of organisms. In the present work, we do not aim at describing the growth processes but rather at summarising the characteristics of the length-at-age relationship in delineated subareas in the EEC stock using the three parameters of the VBGF. To avoid bias in the

analysis, length-selection in data collection must be avoided and the spatial and temporal coverage has to be representative of the spatial entity considered. In the EEC, two types of data were available to us: data from a scientific survey (the UK Beam Trawl Survey) and sampling data from French commercial landings. Differences in length-at-age between survey and commercial data can be expected: scientific survey are designed to reflect the length structure of the population, while the length structure of commercial landings is influenced by the minimum landing size imposed by EU on common sole, through fishing strategy (e.g., commercial fisheries tend to fish in areas with the biggest common soles), size-selectivity, and discarding practices.

In this study, we investigated the spatial variability in VBGF parameters within the EEC stock of common sole in order to inform current interrogations about population spatial structuration. Based on the three subpopulations hypothesis (Archambault et al., 2016; Rochette et al., 2012), we first evaluated the spatial differences in VBGF parameters accounting for potential bias due to the type of data used (i.e., commercial or survey data). Then, we used the two types of data separately to inform spatial growth differences between the three subareas of the EEC stock of common sole.

## **2. Materials & methods**

### **2.1. Data**

Biological data for common sole in the EEC were extracted from the French commercial sampling program and onboard sampling during the UK Beam Trawl scientific Survey (UK-BTS).

#### **2.1.1. Data from French commercial fisheries**

Samples from commercial fisheries were collected in fish markets and provided individual information on age and total length (10mm classes) by quarter, year, ICES division and fishing gear. In order to determine the subarea of origin, the fishing location of each sample had to be identified (Figure 1): Each sampled fish was linked to a statistical rectangle by using logbook information for the corresponding fishing trip. Two main assumptions had to be made for this association: (i) sampled common soles were allocated to the statistical rectangle where the fishing vessel caught the largest volume of common sole during the trip and (ii) in the NE subarea, common soles caught by netters in a statistical rectangle shared by two subareas were assigned to the subarea closest to the shore (for instance in ICES statistical rectangle 30F1 (Figure 1), common soles caught by netters were assigned to the NE subarea). Indeed French netters usually operate in French coastal zones within subareas NE and SW (Figure 1). Biological data from commercial sampling comes from trammel netters in the NE of the EEC and from trammel netters (31%), bottom trawlers (63%), and unidentified gears (5%) in the SW. The French sampling program operates quarterly and individuals are randomly selected in the fish markets using a stratified sampling by sex and length-class. The data used cover the period 2010 to 2015.

#### **2.1.2. Data from scientific survey**

The UK-BTS survey has been carried out annually in July/August since 1989 by the Centre for Environment Fisheries and Aquaculture Science (CEFAS) , using a commercially rigged 4m steel beam trawl (ICES, 2009). Samples from UK-BTS provided individual information on age and total length with the exact haul position (Figure 1). At each haul, individuals are randomly selected using a stratified sampling by sex and length-class. UK-BTS data are publically available and were extracted from the International Council for the Exploration of the Sea (ICES) database ([www.ices.dk/marine-data/](http://www.ices.dk/marine-data/)) for the period 2010 to 2015.

#### 2.1.3. Differences between the two data sources

The two data sources differ by their spatial and temporal coverage, and observed age composition. In both biological data sources, age estimation was conducted by otoliths sagitta reading by IFREMER in France for commercial data and by CEFAS for survey data. Reader effects on otolith reading have been tested in workshops (involving both IFREMER and CEFAS) and agreement between institutes was 91% for all ages (ICES, 2009). Both data series are available over the period between 2010 and 2015. Survey data are substantial from age 1 (common soles at age 1 represent 21% of total number of fish) while commercial data become substantial only from age 2 (<1% of age 1 in the third quarter). This is likely due to the minimum landing size of 24 cm in place for sole (Supplementary material S1).

#### 2.2. Model formulation

Differences in length at age were investigated through analyses of the VBGF parameters. As in Rindorf et al. (2016), cohort effects were ignored considering the short period of observations in comparison with common sole life span. Year effects, usually included as proxies for annual environmental conditions, were also neglected because the purpose

was not to assess precisely growth parameters but rather to focus on differences between subareas and data sources. The growth equation was parameterized from age 2,

$$L_{t,i} = L_{\infty} - (L_{\infty} - L_2) \times \exp(-K \times (t_i - 2)) + \varepsilon_i \quad \text{Eq. 1}$$

where  $\varepsilon_i$  is a normally distributed error term.

$L_{t,i}$  is the length of the individual  $i$  at age  $t$ ,  $L_2$  the length at age 2,  $L_{\infty}$  the asymptotic maximum length, and  $K$  ( $\text{year}^{-1}$ ) is the intrinsic somatic length growth rate (i.e., the speed at which the asymptotic length is reached).

To identify the influence of subareas and data sources on the estimates of the growth parameters, a generalized nonlinear least squares (GNLS) model was used. This model was formulated using a two-stage framework (Pinheiro and Bates, 2000).

First, the length of the  $i$ -th common sole is modelled by Eq. 1.

Second, covariates were introduced in the model. The covariates tested included (i) the three subareas (denoted “subarea”), (ii) the two data sources (denoted “data”), (iii) the sexual dimorphism (denoted “sex”), and (iv) the annual growth continuity (denoted “quarter”). The three growth parameters can be expressed as a vector:  $\phi_j = [K, L_{\infty}, L_2]$  with  $\phi = A \cdot \beta$ .  $A$  is the designed matrix whose size depends on the number of covariates and the number of groups in each covariate, and  $\beta$  is the vector of parameters for the covariates.

For example, in a model considering the three subareas in the EEC (NE, SW, and UK) and the sexual dimorphism (Male or Female) (i.e., Model 2),  $K$ ,  $L_{\infty}$ , and  $L_2$  can be expressed as:

$\{K = \beta_1 + \beta_2 \cdot \text{SubareaSW} + \beta_3 \cdot \text{SubareaUK} + \beta_4 \cdot \text{SexMale}\}$ ,  $\{L_{\infty} = \beta_5 + \beta_6 \cdot \text{SubareaSW} + \beta_7 \cdot \text{SubareaUK} + \beta_8 \cdot \text{SexMale}\}$ ,  $\{L_2 = \beta_9 + \beta_{10} \cdot \text{SubareaSW} + \beta_{11} \cdot \text{SubareaUK} + \beta_{12} \cdot \text{SexMale}\}$ .

Subarea and data were the covariates of interest: subarea captures potential variations in length-at-age between subareas in the EEC and data documents the potential differences in the perception of length-at-age relationships between commercial and survey data.

Both sex and quarter effects were used to avoid bias in estimation. Indeed, sexual dimorphism was described for common sole by several authors (De Veen, 1976; Rijnsdorp and Van Beek, 1991). Moreover, the fishing strategy (fishing area and period) of commercial fisheries leads to a high share of female in the capture (81%) compared to the scientific survey (45%). The quarter effect aimed at capturing the variability caused by the annual growth continuity and reducing the incidence of unbalanced sampling in the commercial fisheries. Indeed, in the NE of the EEC common sole are sampled homogeneously throughout the year, while, in the SW, 83% of common sole are sampled in the 2<sup>nd</sup> and the 3<sup>rd</sup> quarter.

This general form was then applied in three alternative models which differed by the datasets and the covariates considered (Summarised in Table 1).

*Table 1: Summary of the three models implemented to analyse the effects of sex, subarea, quarter, and data source on growth parameters  $K$ ,  $L_{\infty}$  and  $L_2$ , across the three subareas NE, SW and UK. For each model, the ticks represent the inclusion (or not) of effects tested on each growth. The green boxes are the effects selected by the models. Q stands for Quarter.*

## **2.3. Model description**

### **2.3.1. Model 1: commercial and survey data**

The first model (Model 1) was aimed at verifying if commercial and scientific data may be jointly used in estimation or if a data-source bias exists. To allow comparison between the two data sources, we only considered commercial data collected during quarter 3 (because the scientific survey is carried out in July and August), and survey data from NE and SW subareas due to the absence of catch by French commercial fisheries in the UK

subarea. The model was fitted on a resulting dataset of 3,113 length-age couples from survey (45%), and commercial fishery (55%).

The effect of sex ( $\beta_1$ ), subarea ( $\beta_2$ ), data source ( $\beta_3$ ) and the interaction between subareas and data source ( $\beta_4$ ) were included in the model. Consequently, the model produces independent estimations for each combination of data source and subarea.

2.3.2. Model 2 and 3: independent analysis of commercial and survey data: subarea effect on the estimates of growth parameters

Model 2: Survey data

The second model was fitted to survey data only and aimed at detecting potential differences in length at age between the three subareas, independent from bias due to different fishing practices across regions (e.g., differences in mesh size, targeting of sizes and discards). The non-linear model tested the effects of subarea ( $\beta_1$ ) and sex ( $\beta_2$ ).

We considered 2,863 individuals of age 1 to age 23 from UK-BTS for the 3 subareas: NE (33%), SW (16%) and UK (50%) (the age structure in the dataset is described in Supplementary material S2). We noted that the quantity of data in the SW subarea is relatively low in comparison with the NE and UK subareas.

Model 3: Commercial data

Model 3 was fitted to data from commercial fisheries and tested the effects of subarea ( $\beta_2$ ), season ( $\beta_3$ ) and sex ( $\beta_1$ ). As for model 1, data were available only in the two subareas fished by the French commercial fleets (i.e., NE and SW subareas). Commercial data are sampled throughout the year, thus a quarter effect was added in order to consider the annual growth continuity.

The interest of this model lies in the quantity of available data (5,391 individuals of age 1 to age 24) particularly in the SW subarea wherein the quantity of data was low in the

scientific survey in comparison with the NE and the UK subareas (Supplementary material S3 and S4). We considered a quarter effect on K, because the speed of growth may depend on environmental seasonal conditions. Inversely we did not consider a quarter effect on the asymptotic length, which is viewed as the maximum length reached by the population and reflects the cumulative growth history of fish thus constant throughout the year at population scale.

#### **2.4. Model selection**

The three models were implemented in the statistical software R (R Core Team, 2016) using the 'gnls' function (package 'nlme'; (Pinheiro and Bates, 2000). Backward stepwise procedure was performed and the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) were used to select the best model. The initial model was the full model (all covariate effects on all three parameters) and the impact on the criteria of the sequential deletion of each covariate on each parameter was assessed. The covariates whose deletion either improved the model (by reducing AIC and BIC) or did not deteriorate its quality (not significant difference in AIC and BIC) were eliminated. The process was repeated until no further improvement was possible. The significance of the parameters was assessed using a Wald chi-square test. Graphical methods (e.g., residual diagnostic plots) were used to check that the final models verified the normality assumption (Supplementary material S12).

Finally, in order to evaluate the robustness of the conclusions to the shape of the growth curve, we estimated a logistic growth model as an alternative to the VBG model using the UK-BTS data in the SW of the English EEC and the effects selected in Model 2 (Described in the following section; Supplementary material S13). Models were compared using AIC and BIC.

### 3. Results

#### 3.1. Data source effect on growth parameters

Model 1 was based on commercial fisheries and survey data in the two subareas NE and SW of the EEC and considered the effects of sex, subarea, data and interaction subarea x data on growth parameters. It revealed a data source effect on  $K$  and  $L_2$  with different magnitude depending on the subarea globally higher in the NE than in the SW.. It also suggested differences in growth between subareas.

The model considering the four effects on the three growth parameters ( $K$ ,  $L_\infty$  and  $L_2$ ) was always selected based on the AIC selection criteria (Supplementary material S6 and S7). In the case of the more conservative BIC criteria, the gain obtained by considering the effect on the growth parameter was  $K$  quite low ( $\Delta BIC_{S1-S0} = 1.07$  and  $\Delta BIC_{S4-S0} = 0.4$ ). Consequently, we kept the full model keeping in mind that the four effects on  $K$  might be unclear.

Wald chi-square test indicated that all the parameters were significant with a  $p$ -value  $< 0.001$ , except for the parameter  $L_\infty$  associated to the commercial data in the SW subarea ( $p$ -value=0.055).

The sex effect on the three growth parameters was significant and of similar amplitude as the three other effects (Supplementary material S6 and Table 2).

Interaction effect in Model 1 allowed to provide independent estimates for each data source in each subarea. The results showed that differences depending on the data sources in  $L_\infty$ ,  $L_2$  and  $K$ .  $L_\infty$  was 14.5% (46.5mm) higher using commercial data than using UK-BTS in NE, and 5.5% (19mm) in the SW.  $L_2$  was 14.5% (32.5mm) higher using commercial data than using UK-BTS in NE and 9% (20mm) in SW.  $K$  was 33% lower using

commercial data than using UK-BTS in NE whereas, in the SW, K was 4% higher using commercial data.

The asymptotic length and the length at age 2 were significantly higher using the commercial data compared to the UK-BTS data in the SW and the NE of the EEC, while K were significantly lower using commercial data in the NE and higher in the SW.

*Table 2 : Growth parameters of the von Bertalanffy equation computed from the model fitted to data from the scientific survey UK-BTS and commercial sampling, considering data source effect and sex effect. The columns '% variation' specifies the percentage of variation in each subarea between the data from commercial fisheries and the data from UK-BTS.*

The results also showed differences in growth parameters between the two subareas with the two data sources (Figure 2), which were consistent across data source for  $L_{\infty}$ , i.e., higher  $L_{\infty}$  in the SW of the EEC.

In the following part, the subarea effect was analysed in details separating data from scientific survey and from commercial fisheries.

### **3.2. Variations in growth parameters across subareas in the EEC**

#### **3.2.1. Scientific survey UK-BTS data within the three subareas in the EEC**

In Model 2, which considered the subarea and sex effects using scientific survey data, the complete model considering all effects on all parameters was selected based on the AIC selection criteria (Supplementary material S8 and S9). On the basis of the BIC criterion, the sub-model S4 would be selected (which releases the subarea effect on K). Even if AIC and BIC criteria did not provide the same message on the model selection, we chose to keep the subarea effect on K to be able to look at the potential subarea effect. Wald chi-square test indicated that all the parameters were significant with a p-value < 0.001.

In this model, sexual dimorphism had a larger effect on the three growth parameters than subareas.  $L_{\infty}$  and  $L_2$  were lower in males than females, and  $K$  was higher in males (Figure 3 and Table 3).

The asymptotic length,  $L_{\infty}$ , showed the largest variation across the three subareas.  $L_{\infty}$  was much higher in the SW than in the NE of the EEC (+10% for males and +9% for females) and in the UK (+7% for males and +6% females) (Table 3). The same result was observed, to a lesser extent, for  $L_2$  (+4% and +5% between the NE and SW subareas and +2% between the UK and SW subareas). The subarea effect on  $K$  followed a different pattern with  $K$  around 0.40 for males (and 0.31 for females) in the SW and NE subareas whereas it reached 0.46 for males (and 0.37 for females) in the UK subarea.

Both  $L_{\infty}$  and  $L_2$  were higher in the SW of the EEC than in the UK and the same parameters were higher in the UK than in the NE. This means that the differences in terms of length-at-age exist from youngest age and spread throughout the life cycle of the common sole.

*Table 3 : Growth parameters of von Bertalanffy equation computed from the model fitted on data from French commercial fisheries considering subarea effect and sex effect. The columns '% variation' indicates the percentage of variation between the subareas with the SW subarea as the reference.*

### 3.2.2. Commercial fisheries data within the two subareas in the EEC

Model 3 is based on commercial fisheries data with three effects (subarea, quarter and sex) on the three growth parameters. Unlike the two previous models, the fit of this model required four steps and led to the removal of the subarea effect on  $K$  and  $L_2$  and the sex effect on  $K$ , based on both AIC and BIC (Supplementary material S10 and S11). The Wald chi-square test indicated that all the parameters were significant with a  $p$ -value < 0.001.

The subarea effect and the sex effect were retained for  $L_{\infty}$ . This parameter was significantly higher in the SW than in the NE subarea (+14% for male and +11% for female) (Table 4). This was consistent with the results obtained with the survey data. K showed quarterly variation with higher values for the quarters 2 and 3 that were not consistent with intra-annual growth. Finally, sexual dimorphism induced variations in  $L_{\infty}$  and  $L_2$  but not in K.

*Table 4: Growth parameters of von Bertalanffy equation computed from the model fitted on data from French commercial fisheries considering subarea effect, sex effect and quarter effect.*

The results showed significant differences across subareas in asymptotic length,  $L_{\infty}$ , in all models, and differences in length at age 2 ( $L_2$ ) with the scientific survey data (Model 1 and Model 2) (Table 1 in green). Asymptotic length was systematically higher in the SW of the EEC than in the NE. Same results were found to a lesser extent for length at Age 2 ( $L_2$ ) which was higher in the SW of the EEC than in the NE. The growth rate (K) showed small variations between the SW and the NE. The UK subarea was explored only with the data from scientific survey in the Model 2. Nevertheless, the results indicated that K was much higher in the UK subareas than in the two other subareas, whereas the value of  $L_{\infty}$  was intermediate between those in the SW and in the NE subareas.

## 4. Discussion

The use of life-history traits, especially growth parameters, is a well-known method to inform stock identity (Abaunza et al., 2008; Barrios et al., 2017; Cadrin et al., 2014; Sequeira et al., 2012). Herein, we investigated the stock spatial structuration of common sole in the EEC using VBGF to estimate growth parameters, according to an existing three sub-populations hypothesis (Archambault et al., 2016; Rochette et al., 2012). From a methodological perspective, we compared growth parameter estimates using length-at-age data from a scientific survey and a commercial fisheries sampling program. While the estimation of VBGF parameters,  $K$  and  $L_{\infty}$ , for common sole was not the primary aim of the study, the parameters obtained are in the range (or slightly lower for  $L_{\infty}$ ; Deniel, 1990; Lorenzen and Enberg, 2002) of those estimated for the same species in surrounding regions (Carpentier et al., 2009; De Veen, 1976; Deniel, 1990; Lorenzen and Enberg, 2002).

### 4.1. Effects of the data source on the growth parameter estimates

*Different fishing practices provided different perceptions of length-at-age population structure*

Model 1 was developed to test a potential data source effect on the growth parameter estimates. We found that the three growth parameters estimates were indeed strongly influenced by the data source used in the VBGF model. More precisely, in the two subareas considered in Model 1 (i.e., the SW and NE subareas),  $L_{\infty}$  and  $L_2$  estimates were higher using commercial data compared to survey, particularly in the NE subarea.

This data source effect can be attributed to size-selectivity differences between the commercial and scientific fishing practices. The smallest common soles at age 2 (and notably the males, which are smaller) are not captured or not landed by commercial

fisheries, while the scientific survey catches common soles from age 1. Commercial fleets are much more size-selective than scientific survey due to a minimum landing size (24 cm) imposed by the European Union regulation, and the low commercial value of the smallest commercial category of common sole. This selectivity is induced by gear characteristics (such as mesh size) and by the targeting behaviour. Commercial fisheries tend to fish in areas with the biggest common soles, while scientific survey aims at sampling the entire population using a stratified random design. The perception of the population structure is consequently dependent of the type of data used. Differences in the magnitude of the data source effect between the NE and the SW of the EEC were presented and they may be due to differences in the fishing gears used by the commercial fishery in these two subareas. In the NE, the fishery is mainly composed of trammel nets with smaller mesh size whereas, in the SW, it is composed of trammel nets with bigger mesh size, and bottom trawls.

Ones should be careful when combining length-at-age data from various data sources and especially commercial and survey data to build models. Ignoring data source can lead to skew the perception of length-at-age population structure.

#### *Methodological limitations: significance of the estimates and correlation between von Bertalanffy Growth parameters*

In the paper, we used the well-known VBGF as a way to summarise the length-at-age in the population. A logistic growth model was also tested and suggested significant differences between subareas as well. However, the best fits were obtained using VBG model (Supplementary materials S13).

We included a season effect in the model applied to commercial data as a covariate instead of using decimal ages to account for continuous growth. Indeed, as evidenced by

the estimates of the quarter effect, intra-annual continuous growth was not supported by the data (Supplementary materials S14). This surprising result will lead to further analysis in the future. Meanwhile, accounting for the quarter effect avoids propagating the bias in VBGF estimates.

It is important to highlight the correlation between the growth rate ( $K$ ) and the asymptotic length ( $L_{\infty}$ ). In Model 1, in the NE subarea,  $K$  estimate was lower with commercial data compared to survey data whereas the two other growth parameters  $L_{\infty}$  and  $L_2$  were higher with commercial data. In the same way, in Model 2 and 3,  $K$  was found to vary oppositely to  $L_{\infty}$ . Correlation matrix of the estimates of Model 1 and Model 2 showed a relatively high degree of correlations between in  $K$  and  $L_{\infty}$  estimates (between -0.87 and -0.81 for the same effect in both models; (Supplementary materials S15 and S16). This correlation between growth parameters may be an artefact of the models' parametrization (Schnute, 1981). However, it may also result from an interaction between two biological processes, growth and maturation especially between  $K$  and  $L_{\infty}$  (Brunel et al., 2013; Lester et al., 2004; Quince et al., 2008).

#### **4.2. A first insight into the stock structuration of common sole in the EEC**

##### *Spatial differences in the asymptotic length ( $L_{\infty}$ ), in length-at-age 2 ( $L_2$ ) and in growth rate ( $K$ )*

The second and third models integrated length-at-age data from a scientific survey (Model 2) and commercial fisheries (Model 3), respectively. Both models highlighted that asymptotic length was significantly higher in the SW than in the NE subareas, with the same magnitude between models. Model 2 showed that the length-at-age 2 were also higher in the SW than in the UK subarea. This shows that differences in terms of length-at-age exist from the youngest age and spread throughout the life cycle of the common

sole. Furthermore, model 2 highlighted that the growth rate (K) was much higher in the UK subarea compared to the NE and the SW of the EEC. However, we could not confirm these results using the French commercial data. Genetic (intrinsic) and environmental (extrinsic) components are likely to be explicative factors of such differences (Swain et al., 2007). Among extrinsic components, water temperature and density-dependent factors are particularly cited in the literature (e.g., Brett *et al.*, 1969; Brett, 1979; Weatherley, 1990; Rijnsdorp and Van Beek, 1991; Sinclair *et al.*, 2002; Castillo-Jordán *et al.*, 2010). Mollet et al. (2013) showed latitudinal variations in asymptotic length of female *Solea solea* linked to the temperature in the Northern Atlantic. In our case, further research is needed to understand if growth differences in the EEC could be explained by abiotic or biotic factors.

Spatial differences in growth parameters support the hypothesis of low mobility of common soles in the EEC. While the movements of common soles at early stages are partially understood in the EEC (Archambault et al., 2015, 2016; Rochette et al., 2012), the mobility of adults remains poorly resolved, but preliminary reprocessing of former mark-recapture surveys data (Burt and Millner, 2008; Kotthaus, 1963) suggested little exchanges between the three subareas (Véron and Rivot, pers. comm). Additional mark-recapture data are currently collected to further support this conclusion.

#### *A differential fishing impact within the EEC?*

Given the strong fishing pressure on common sole in the EEC, these differences in the estimated growth parameters between subareas may be induced, at least partly, by heterogeneous fishing pressure on common sole across areas.

One of the first and direct effect of size-selective fishing is to reduce the share of larger individuals in the population, which can lead to a genetic change toward smaller

individuals (Law, 2000; Ricker, 1981). The low asymptotic length in the NE in the EEC could therefore be due to a higher fishing pressure in this subarea compared to the SW and the UK.

More generally, fish growth can be subject to a high degree of genetically-based variations and therefore has the potential to evolve rapidly in response to harvesting (Law, 2000; Lorenzen, 2016). Evolutionary effects of fishing on growth may arise from multiple mechanisms including size selective fishing (Enberg et al., 2012). Fishing induced evolution can lead to a decrease of asymptotic length, as shown by Edeline et al., (2009 and 2007) in *Esox Lucius*. The lower growth rate and asymptotic length in the NE of the EEC where the fishing effort is the highest seems to follow this pattern. This is in line with (Archambault et al., 2016) who, under the hypothesis of the existence of distinct subpopulations, estimated a higher fishing mortality in the NE than in the UK since 2000, with the lowest fishing mortality in the EEC in the SW since 1985.

The analysis presented herein was conducted on a short and recent period (2010-2015). To explore the hypothesis of differential fishing impact on the potential of common sole in the EEC, it would be necessary to study the size-at-age data throughout a longer time-series in the three subareas (using UK-BTS survey data from 1989 to 2016 for instance).

Finally, our analysis was a first step towards the investigation and the understanding of the potential spatial stock structuration of common sole in the EEC. Spatial differences in the asymptotic length appeared consistent between the models, whatever the type of data used. Moreover, the analysis of the survey showed spatial differences in growth rate and length at age 2 in Model 1 and Model 2. These results were in favour of a potential spatial stock structuration following a three subpopulations hypothesis. The confirmation of the existence of three isolated subareas could have major implications on our

493 perception of the stock and consequently for management. Currently, both stock  
494 assessment and management assume a single and homogeneous population and until  
495 2016, the EEC stock has been exploited above MSY (ICES, 2016). Accounting for  
496 metapopulation dynamics is essential in assessment models to avoid local over-  
497 exploitation (Archambault et al., 2016; Tuck and Possingham, 1994; Ying et al., 2011). To  
498 inform this potential metapopulation structure, complementary studies are required  
499 (using genetics, otoliths or other life history traits) and would deserve to be integrated in  
500 an interdisciplinary approach which is considered to be the best approach to investigate  
501 stock identity (Begg and Waldman, 1999; Cadrin et al., 2014; Pita et al., 2016).

502    **Supplementary data**

503    Supplementary materials are available at the online version of the manuscript.

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511 **Bibliography**

- 512 Abaunza, P., Murta, A.G., Campbell, N., Cimmaruta, R., Comesaña, A.S., Dahle, G., García  
513 Santamaría, M.T., Gordo, L.S., Iversen, S.A., MacKenzie, K., Magoulas, A.,  
514 Mattiucci, S., Molloy, J., Nascetti, G., Pinto, A.L., Quinta, R., Ramos, P., Sanjuan, A.,  
515 Santos, A.T., Stransky, C., Zimmermann, C., 2008. Stock identity of horse mackerel  
516 (*Trachurus trachurus*) in the Northeast Atlantic and Mediterranean Sea:  
517 Integrating the results from different stock identification approaches. *Fish. Res.*  
518 89, 196–209. <https://doi.org/10.1016/j.fishres.2007.09.022>
- 519 Alex Smith, M., Green, D.M., 2005. Dispersal and the metapopulation paradigm in  
520 amphibian ecology and conservation: are all amphibian populations  
521 metapopulations? *Ecography* 28, 110–128. [https://doi.org/10.1111/j.0906-](https://doi.org/10.1111/j.0906-7590.2005.04042.x)  
522 [7590.2005.04042.x](https://doi.org/10.1111/j.0906-7590.2005.04042.x)
- 523 Ames, E.P., Lichter, J., 2013. Gadids and Alewives: Structure within complexity in the Gulf  
524 of Maine. *Fish. Res.* 141, 70–78. <https://doi.org/10.1016/j.fishres.2012.09.011>
- 525 Archambault, B., Le Pape, O., Baulier, L., Vermard, Y., Véron, M., Rivot, E., 2016. Adult-  
526 mediated connectivity affects inferences on population dynamics and stock  
527 assessment of nursery-dependent fish populations. *Fish. Res.* 181, 198–213.  
528 <https://doi.org/10.1016/j.fishres.2016.03.023>
- 529 Archambault, B., Rivot, E., Savina, M., Le Pape, O., 2015. Using a spatially structured life  
530 cycle model to assess the influence of multiple stressors on an exploited coastal-  
531 nursery-dependent population. *Estuar. Coast. Shelf Sci.*  
532 <https://doi.org/10.1016/j.ecss.2015.12.009>

533 Barrios, A., Ernande, B., Mahé, K., Trenkel, V., Rochet, M.-J., 2017. Utility of mixed effects  
 534 models to inform the stock structure of whiting in the Northeast Atlantic Ocean.  
 535 Fish. Res. 190, 132–139. <https://doi.org/10.1016/j.fishres.2017.02.005>  
 536 Begg, G.A., Waldman, J.R., 1999. An holistic approach to fish stock identification. Fish.  
 537 Res. 43, 35–44. [https://doi.org/10.1016/S0165-7836\(99\)00065-X](https://doi.org/10.1016/S0165-7836(99)00065-X)  
 538 Brett, J.R., 1979. Environmental Factors and Growth, in: Fish Physiology. Elsevier, pp.  
 539 599–675. [https://doi.org/10.1016/S1546-5098\(08\)60033-3](https://doi.org/10.1016/S1546-5098(08)60033-3)  
 540 Brett, J.R., Shelbourn, J.E., Shoop, C.T., 1969. Growth Rate and Body Composition of  
 541 Fingerling Sockeye Salmon, *Oncorhynchus nerka* , in relation to Temperature and  
 542 Ration Size. J. Fish. Res. Board Can. 26, 2363–2394. [https://doi.org/10.1139/f69-](https://doi.org/10.1139/f69-230)  
 543 230  
 544 Brunel, T., Ernande, B., Mollet, F.M., Rijnsdorp, A.D., 2013. Estimating age at maturation  
 545 and energy-based life-history traits from individual growth trajectories with  
 546 nonlinear mixed-effects models. Oecologia 172, 631–643.  
 547 <https://doi.org/10.1007/s00442-012-2527-1>  
 548 Burt, G.J., Millner, R.S., 2008. Movements of sole in the southern North Sea and eastern  
 549 English Channel from tagging studies (1955-2004) (No. 144). Cefas Lowestoft.  
 550 Cadrin, S.X., Kerr, L., Mariani, S. (Eds.), 2014. Stock identification methods: applications in  
 551 fishery science, Second edition. ed. Academic Press, Amsterdam.  
 552 Cadrin, S.X., Secor, D.H., 2009. Accounting for Spatial Population Structure in Stock  
 553 Assessment: Past, Present, and Future, in: Beamish, R.J., Rothschild, B.J. (Eds.), The  
 554 Future of Fisheries Science in North America. Springer Netherlands, Dordrecht, pp.  
 555 405–426. [https://doi.org/10.1007/978-1-4020-9210-7\\_22](https://doi.org/10.1007/978-1-4020-9210-7_22)

556 Carpentier, A., Martin, C., Vaz, S., 2009. Channel Habitat Atlas for marine Resource  
 557 Management, final report (CHARM phase II). INTERREG 3a Programme, IFREMER,  
 558 Boulogne-sur-mer, France.

559 Castillo-Jordán, C., Cubillos, L.A., Navarro, E., 2010. Inter-cohort growth rate changes of  
 560 common sardine (*Strangomera bentincki*) and their relationship with  
 561 environmental conditions off central southern Chile. *Fish. Res.* 105, 228–236.  
 562 <https://doi.org/10.1016/j.fishres.2010.05.012>

563 Ciannelli, L., Fisher, J., Skern-Mauritzen, M., Hunsicker, M., Hidalgo, M., Frank, K., Bailey,  
 564 K., 2013. Theory, consequences and evidence of eroding population spatial  
 565 structure in harvested marine fishes: a review. *Mar. Ecol. Prog. Ser.* 480, 227–243.  
 566 <https://doi.org/10.3354/meps10067>

567 Coggan, R.A., Dando, P.R., 1988. Movements of juvenile Dover sole, *Solea solea* (L.), in the  
 568 Tamar Estuary, South-western England. *J. Fish Biol.* 33, 177–184.  
 569 <https://doi.org/10.1111/j.1095-8649.1988.tb05571.x>

570 Cowen, R.K., 2006. Scaling of Connectivity in Marine Populations. *Science* 311, 522–527.  
 571 <https://doi.org/10.1126/science.1122039>

572 De Veen, J.F., 1976. On changes in some biological parameters in the North Sea sole  
 573 (*Solea solea* L.). *J. Cons.* 37, 60–90. <https://doi.org/10.1093/icesjms/37.1.60>

574 Deniel, C., 1990. Comparative study of growth of flatfishes on the west coast of Brittany.  
 575 *J. Fish Biol.* 37, 149–166. <https://doi.org/10.1111/j.1095-8649.1990.tb05936.x>

576 Dorel, D., Koutsikopoulos, C., Desaunay, Y., Marchand, J., 1991. Seasonal distribution of  
 577 young sole (*Solea solea* (L.)) in the nursery ground of the Bay of Vilaine (Northern  
 578 Bay of Biscay). *Neth. J. Sea Res.* 27, 297–306. [https://doi.org/10.1016/0077-](https://doi.org/10.1016/0077-7579(91)90032-V)  
 579 [7579\(91\)90032-V](https://doi.org/10.1016/0077-7579(91)90032-V)

580 Edeline, E., Carlson, S.M., Stige, L.C., Winfield, I.J., Fletcher, J.M., James, J.B., Haugen, T.O.,  
581 Vøllestad, L.A., Stenseth, N.C., 2007. Trait changes in a harvested population are  
582 driven by a dynamic tug-of-war between natural and harvest selection. *Proc. Natl.*  
583 *Acad. Sci.* 104, 15799–15804. <https://doi.org/10.1073/pnas.0705908104>

584 Edeline, E., Le Rouzic, A., Winfield, I.J., Fletcher, J.M., James, J.B., Stenseth, N.C.,  
585 Vollestad, L.A., 2009. Harvest-induced disruptive selection increases variance in  
586 fitness-related traits. *Proc. R. Soc. B Biol. Sci.* 276, 4163–4171.  
587 <https://doi.org/10.1098/rspb.2009.1106>

588 Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S.,  
589 Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and  
590 the empirical evidence: Fishing-induced evolution of growth. *Mar. Ecol.* 33, 1–25.  
591 <https://doi.org/10.1111/j.1439-0485.2011.00460.x>

592 Erlandsson, J., Östman, Ö., Florin, A.-B., Pekcan-Hekim, Z., 2017. Spatial structure of body  
593 size of European flounder ( *Platichthys flesus* L.) in the Baltic Sea. *Fish. Res.* 189, 1–  
594 9. <https://doi.org/10.1016/j.fishres.2017.01.001>

595 Frank, K.T., Brickman, D., 2000. Allee effects and compensatory population dynamics  
596 within a stock complex. *Can. J. Fish. Aquat. Sci.* 57, 513–517.  
597 <https://doi.org/10.1139/f00-024>

598 Frisk, M.G., Jordaan, A., Miller, T.J., 2014. Moving beyond the current paradigm in marine  
599 population connectivity: are adults the missing link? *Fish Fish.* 15, 242–254.  
600 <https://doi.org/10.1111/faf.12014>

601 Fu, C., Fanning, L.P., 2004. Spatial Considerations in the Management of Atlantic Cod off  
602 Nova Scotia, Canada. *North Am. J. Fish. Manag.* 24, 775–784.  
603 <https://doi.org/10.1577/M03-134.1>

604 Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41.  
605 <https://doi.org/10.1038/23876>

606 ICES, 2017. WGNSSK. Report of the Working Group on Assessment of Demersal Stocks in  
607 the North Sea and Skagerrak (WGNSSK), 26 April - 5 May 2017, ICES Headquarters,  
608 Copenhagen. ICES CM 2017/ACOM:21: 1091pp.

609 ICES, 2016. Solea (*Solea solea*) in Division VIIId (Eastern English Channel).

610 ICES, 2009. Manual for the Offshore Beam Trawl Surveys. Revision 1.2., Working Group on  
611 Beam Trawl Surveys.

612 Ihssen, P.E., Booke, H.E., Casselman, J.M., McGlade, J.M., Payne, N.R., Utter, F.M., 1981.  
613 Stock Identification: Materials and Methods. *Can. J. Fish. Aquat. Sci.* 38, 1838–  
614 1855. <https://doi.org/10.1139/f81-230>

615 Jorgensen, H.B.H., Hansen, M.M., Bekkevold, D., Ruzzante, D.E., Loeschcke, V., 2005.  
616 Marine landscapes and population genetic structure of herring (*Clupea harengus*  
617 L.) in the Baltic Sea. *Mol. Ecol.* 14, 3219–3234. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-294X.2005.02658.x)  
618 [294X.2005.02658.x](https://doi.org/10.1111/j.1365-294X.2005.02658.x)

619 Kerr, L.A., Hintzen, N.T., Cadrin, S.X., Clausen, L.W., Dickey-Collas, M., Goethel, D.R.,  
620 Hatfield, E.M.C., Kritzer, J.P., Nash, R.D.M., 2016. Lessons learned from practical  
621 approaches to reconcile mismatches between biological population structure and  
622 stock units of marine fish. *ICES J. Mar. Sci. J. Cons.* fsw188.  
623 <https://doi.org/10.1093/icesjms/fsw188>

624 Kotthaus, A., 1963. Tagging experiments with the North Sea sole (*Solea solea*) in 1959 and  
625 1960. *Spec. Publ. Int. Commn. NW. Atlan. Fish* 123–129.

626 Kritzer, J.P., Sale, P.F., 2004. Metapopulation ecology in the sea: from Levins' model to  
627 marine ecology and fisheries science. *Fish Fish.* 5, 131–140.  
628 <https://doi.org/10.1111/j.1467-2979.2004.00131.x>

629 Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57, 659–668.  
630 <https://doi.org/10.1006/jmsc.2000.0731>

631 Le Pape, O., Cognez, N., 2016. The range of juvenile movements of estuarine and coastal  
632 nursery dependent flatfishes: estimation from a meta-analytical approach. *J. Sea*  
633 *Res.* 107, 43–55. <https://doi.org/10.1016/j.seares.2015.06.001>

634 Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of  
635 somatic growth in fishes: the cost of reproduction. *Proc. R. Soc. B Biol. Sci.* 271,  
636 1625–1631. <https://doi.org/10.1098/rspb.2004.2778>

637 Lorenzen, K., 2016. Toward a new paradigm for growth modeling in fisheries stock  
638 assessments: Embracing plasticity and its consequences. *Fish. Res.* 180, 4–22.  
639 <https://doi.org/10.1016/j.fishres.2016.01.006>

640 Lorenzen, K., Enberg, K., 2002. Density-dependent growth as a key mechanism in the  
641 regulation of fish populations: evidence from among-population comparisons.  
642 *Proc. R. Soc. Lond. B Biol. Sci.* 269, 49–54. <https://doi.org/10.1098/rspb.2001.1853>

643 Mahe, K., Delpech, J.-P., Carpentier, A., 2007. Synthèse bibliographique des principales  
644 espèces de Manche orientale et du golfe de Gascogne.

645 Mollet, F.M., Engelhard, G.H., Vainikka, A., Laugen, A.T., Rijnsdorp, A.D., Ernande, B.,  
646 2013. Spatial variation in growth, maturation schedules and reproductive  
647 investment of female sole *Solea solea* in the Northeast Atlantic. *J. Sea Res.* 84,  
648 109–121. <https://doi.org/10.1016/j.seares.2012.12.005>

649 Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K.,  
 650 Drinkwater, K., Huret, M., Nash, R.D.M., 2013. Impacts of climate change on the  
 651 complex life cycles of fish. *Fish. Oceanogr.* 22, 121–139.  
 652 <https://doi.org/10.1111/fog.12010>  
 653 Petitgas, P., Secor, D.H., McQuinn, I., Huse, G., Lo, N., 2010. Stock collapses and their  
 654 recovery: mechanisms that establish and maintain life-cycle closure in space and  
 655 time. *ICES J. Mar. Sci.* 67, 1841–1848. <https://doi.org/10.1093/icesjms/fsq082>  
 656 Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects models in S and S-PLUS. Springer, New  
 657 York.  
 658 Pita, A., Casey, J., Hawkins, S.J., Villarreal, M.R., Gutiérrez, M.-J., Cabral, H., Carocci, F.,  
 659 Abaunza, P., Pascual, S., Presa, P., 2016. Conceptual and practical advances in fish  
 660 stock delineation. *Fish. Res.* 173, 185–193.  
 661 <https://doi.org/10.1016/j.fishres.2015.10.029>  
 662 Quince, C., Abrams, P.A., Shuter, B.J., Lester, N.P., 2008. Biphase growth in fish I:  
 663 Theoretical foundations. *J. Theor. Biol.* 254, 197–206.  
 664 <https://doi.org/10.1016/j.jtbi.2008.05.029>  
 665 Reiss, H., Hoarau, G., Dickey-Collas, M., Wolff, W.J., 2009. Genetic population structure of  
 666 marine fish: mismatch between biological and fisheries management units. *Fish*  
 667 *Fish.* 10, 361–395. <https://doi.org/10.1111/j.1467-2979.2008.00324.x>  
 668 Ricker, W.E., 1981. Changes in the average size and average age of Pacific salmon. *Can. J.*  
 669 *Fish. Aquat. Sci.* 38, 1636–1656. <https://doi.org/10.1139/f81-213>  
 670 Rijnsdorp, A.D., Van Beek, F.A., 1991. Changes in growth of plaice *Pleuronectes platessa* L.  
 671 and sole *Solea solea* (L.) in the North Sea. *Neth. J. Sea Res.* 27, 441–457.  
 672 [https://doi.org/10.1016/0077-7579\(91\)90045-3](https://doi.org/10.1016/0077-7579(91)90045-3)

673 Rindorf, A., Wright, P.J., Jensen, H., Maar, M., 2016. Spatial differences in growth of lesser  
674 sandeel in the North Sea. *J. Exp. Mar. Biol. Ecol.* 479, 9–19.  
675 <https://doi.org/10.1016/j.jembe.2016.02.007>

676 Riou, P., 2001. Contribution respective de différentes nurseries côtières aux  
677 populations adultes de sole et de plie: étude par couplage de modèles linéaires  
678 généralisés avec un système d'information géographique. *Aquat. Living Resour.*  
679 14, 125–135. [https://doi.org/10.1016/S0990-7440\(01\)01110-X](https://doi.org/10.1016/S0990-7440(01)01110-X)

680 Rochette, S., Huret, M., Rivot, E., Le Pape, O., 2012. Coupling hydrodynamic and  
681 individual-based models to simulate long-term larval supply to coastal nursery  
682 areas: Modelling larval supply to coastal nurseries. *Fish. Oceanogr.* 21, 229–242.  
683 <https://doi.org/10.1111/j.1365-2419.2012.00621.x>

684 Schnute, J., 1981. A Versatile Growth Model with Statistically Stable Parameters. *Can. J.*  
685 *Fish. Aquat. Sci.* 38, 1128–1140. <https://doi.org/10.1139/f81-153>

686 Secor, D.H., 2015. Migration ecology of marine fishes. Johns Hopkins University Press,  
687 Baltimore.

688 Sequeira, V., Neves, A., Paiva, R.B., Lima, J.P. de, Vieira, A.R., Gordo, L.S., 2012. Life history  
689 parameters as possible discriminators of bluemouth *Helicolenus dactylopterus*  
690 (Delaroche, 1809) populations in Portuguese waters. *Fish. Res.* 125–126, 69–76.  
691 <https://doi.org/10.1016/j.fishres.2012.02.009>

692 Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002. Disentangling the effects of size-selective  
693 mortality, density, and temperature on length-at-age. *Can. J. Fish. Aquat. Sci.* 59,  
694 372–382. <https://doi.org/10.1139/f02-014>

695 Swain, D.P., Sinclair, A.F., Mark Hanson, J., 2007. Evolutionary response to size-selective  
 696 mortality in an exploited fish population. *Proc. R. Soc. B Biol. Sci.* 274, 1015–1022.  
 697 <https://doi.org/10.1098/rspb.2006.0275>  
 698 Tuck, G.N., Possingham, H.P., 1994. Optimal harvesting strategies for a metapopulation.  
 699 *Bull. Math. Biol.* 56, 107–127. [https://doi.org/10.1016/S0092-8240\(05\)80207-1](https://doi.org/10.1016/S0092-8240(05)80207-1)  
 700 Von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth  
 701 laws II). *Human Biol.* 10, 181–213.  
 702 Waples, R.S., Gaggiotti, O., 2006. What is a population? An empirical evaluation of some  
 703 genetic methods for identifying the number of gene pools and their degree of  
 704 connectivity: WHAT IS A POPULATION? *Mol. Ecol.* 15, 1419–1439.  
 705 <https://doi.org/10.1111/j.1365-294X.2006.02890.x>  
 706 Weatherley, A.H., 1990. Approaches to Understanding Fish Growth. *Trans. Am. Fish. Soc.*  
 707 119, 662–672. [https://doi.org/10.1577/1548-](https://doi.org/10.1577/1548-8659(1990)119<0662:ATUFG>2.3.CO;2)  
 708 [8659\(1990\)119<0662:ATUFG>2.3.CO;2](https://doi.org/10.1577/1548-8659(1990)119<0662:ATUFG>2.3.CO;2)  
 709 Wheeler, A.C., 1978. Key to the fishes of northern Europe: a guide to the identification of  
 710 more than 350 species. F. Warne, London.  
 711 Ying, Y., Chen, Y., Lin, L., Gao, T., Quinn, T., 2011. Risks of ignoring fish population spatial  
 712 structure in fisheries management. *Can. J. Fish. Aquat. Sci.* 68, 2101–2120.  
 713 <https://doi.org/10.1139/f2011-116>  
 714 Zemeckis, D.R., Martins, D., Kerr, L.A., Cadrin, S.X., 2014. Stock identification of Atlantic  
 715 cod (*Gadus morhua*) in US waters: an interdisciplinary approach. *ICES J. Mar. Sci.*  
 716 71, 1490–1506. <https://doi.org/10.1093/icesjms/fsu032>  
 717

Table 1

	Data effect		Growth comparison between subareas			
	Model 1		Model 2		Model 3	
Data Period	BTS + Commercial Q 3 - SW NE		BTS data Q 3 – All areas		Commercial All quarters - SW NE	
Effects included in full models	Sex	data x subarea	Sex	Subarea	Sex	Subarea      Quarter
K	✓	✓	✓	✓	✓	SW, NE      ✓
L <sub>∞</sub>	✓	✓	✓	✓	✓	SW, NE      Not tested
L2	✓	✓	✓	✓	✓	SW, NE      ✓

Table 2

Growth Parameters	Subarea	Sampling type	Male		Female	
			Value	% difference (ref BTS in the same area)	Value	% difference (ref BTS in the same area)
K	NE	BTS	0.40		0.33	
	NE	COM	0.28	- 30	0.21	- 36
	SW	BTS	0.39		0.32	
	SW	COM	0.41	+ 4	0.33	+ 4
L <sub>∞</sub>	NE	BTS	284		352	
	NE	COM	330	+ 16	399	+ 13
	SW	BTS	317		385	
	SW	COM	336	+ 6	404	+ 5
L <sub>2</sub>	NE	BTS	207		224	
	NE	COM	239	+ 15	255	+ 14
	SW	BTS	218		234	
	SW	COM	238	+ 9	254	+ 9

Table 3

Growth Parameters	Subarea	Data source	Male		Female	
			Value	% difference (ref SW subarea)	Value	% difference (ref SW subarea)
K	SW	BTS	0,40		0,31	
	NE	BTS	0,41	+2%	0,32	+2%
	UK	BTS	0,46	+16%	0,37	+16%
L <sub>∞</sub>	SW	BTS	316		386	
	NE	BTS	283	-10%	353	-9%
	UK	BTS	293	-7%	363	-6%
L <sub>2</sub>	SW	BTS	217		234	
	NE	BTS	207	-5%	224	-4%
	UK	BTS	212	-2%	229	-2%

Table 4

			Male		Female	
Growth Parameters	Subarea	Quarter	Value	% difference (ref NE subarea)	Value	% difference (ref NE subarea)
K	NE/SW	1	0.20		0.20	
	NE/SW	2	0.26		0.26	
	NE/SW	3	0.26		0.26	
	NE/SW	4	0.20		0.20	
L <sub>∞</sub>	NE	1/2/3/4	310		386	
	SW	1/2/3/4	352	+ 14	428	+ 11
L <sub>2</sub>	NE/SW	1	243		253	
	NE/SW	2	220		230	
	NE/SW	3	244		254	
	NE/SW	4	258		267	

Figure1

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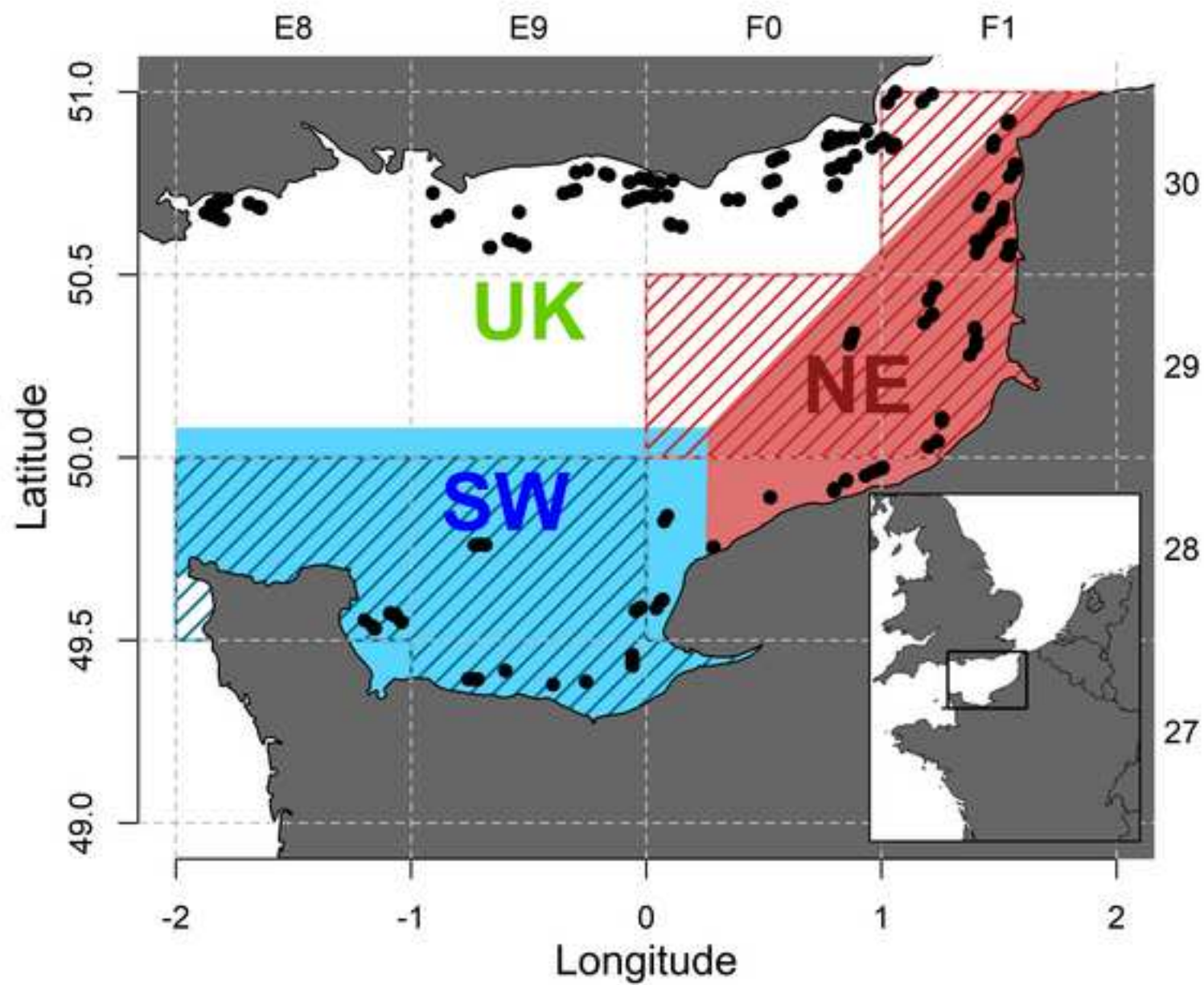


Figure2

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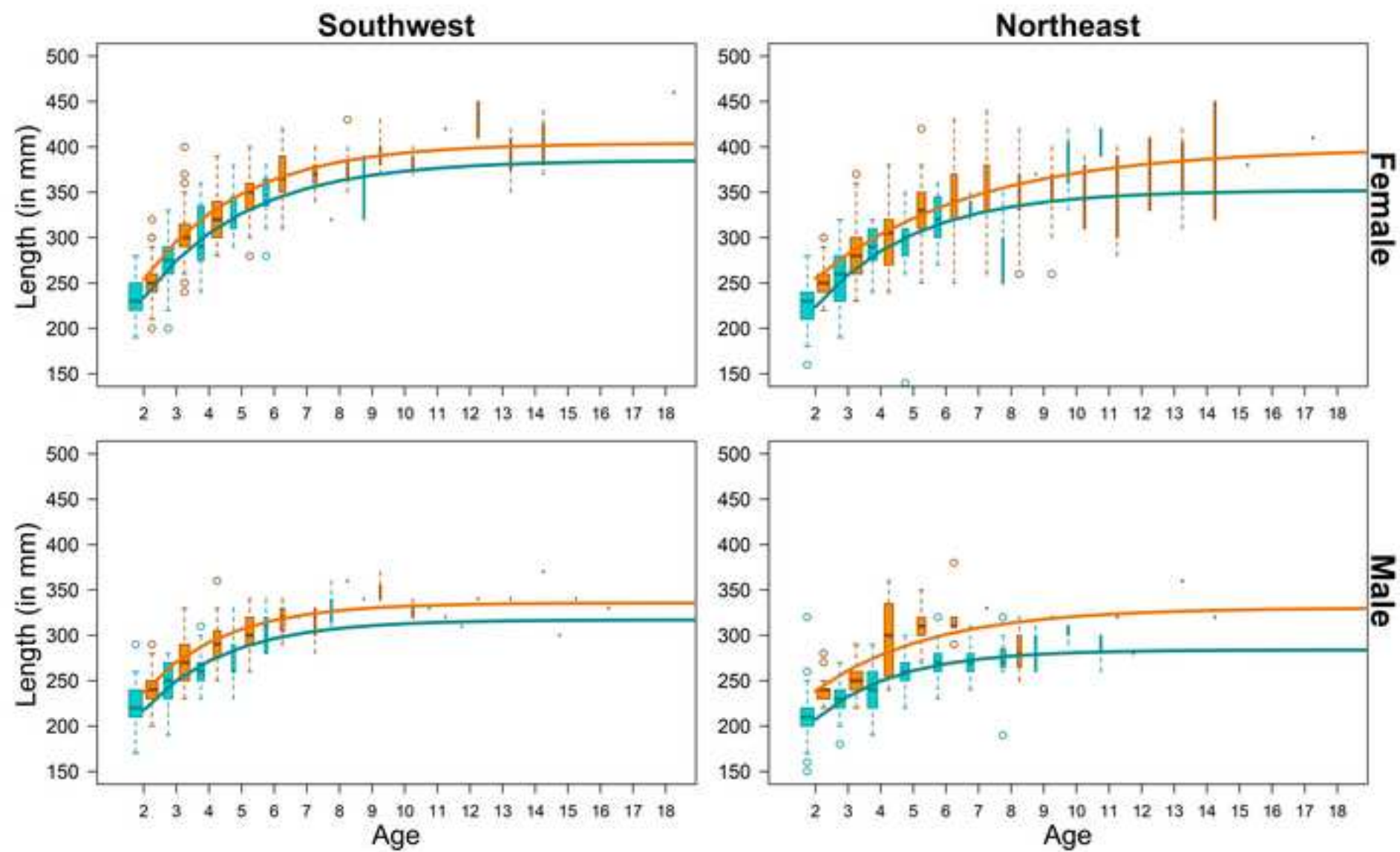


Figure3

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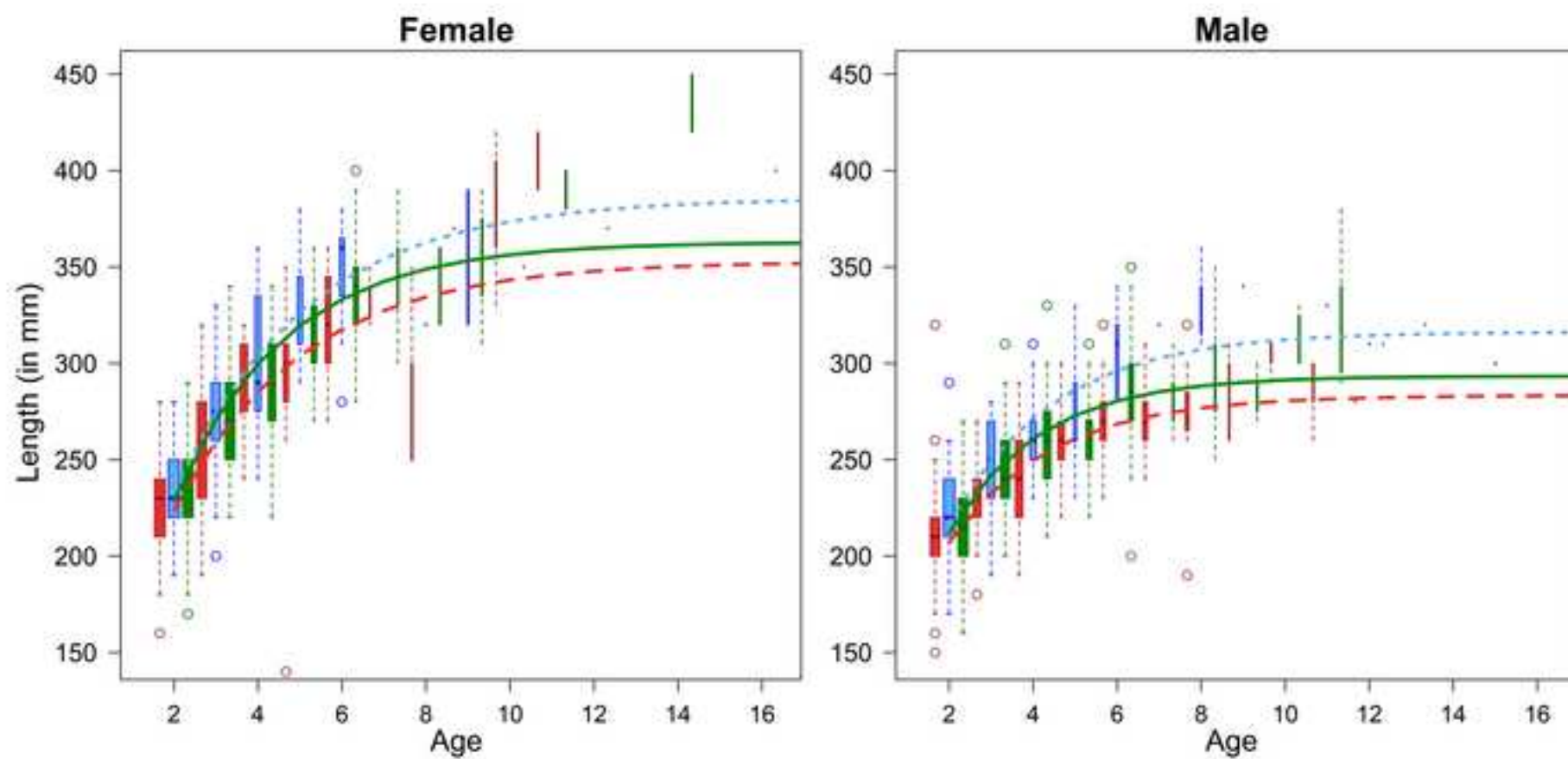
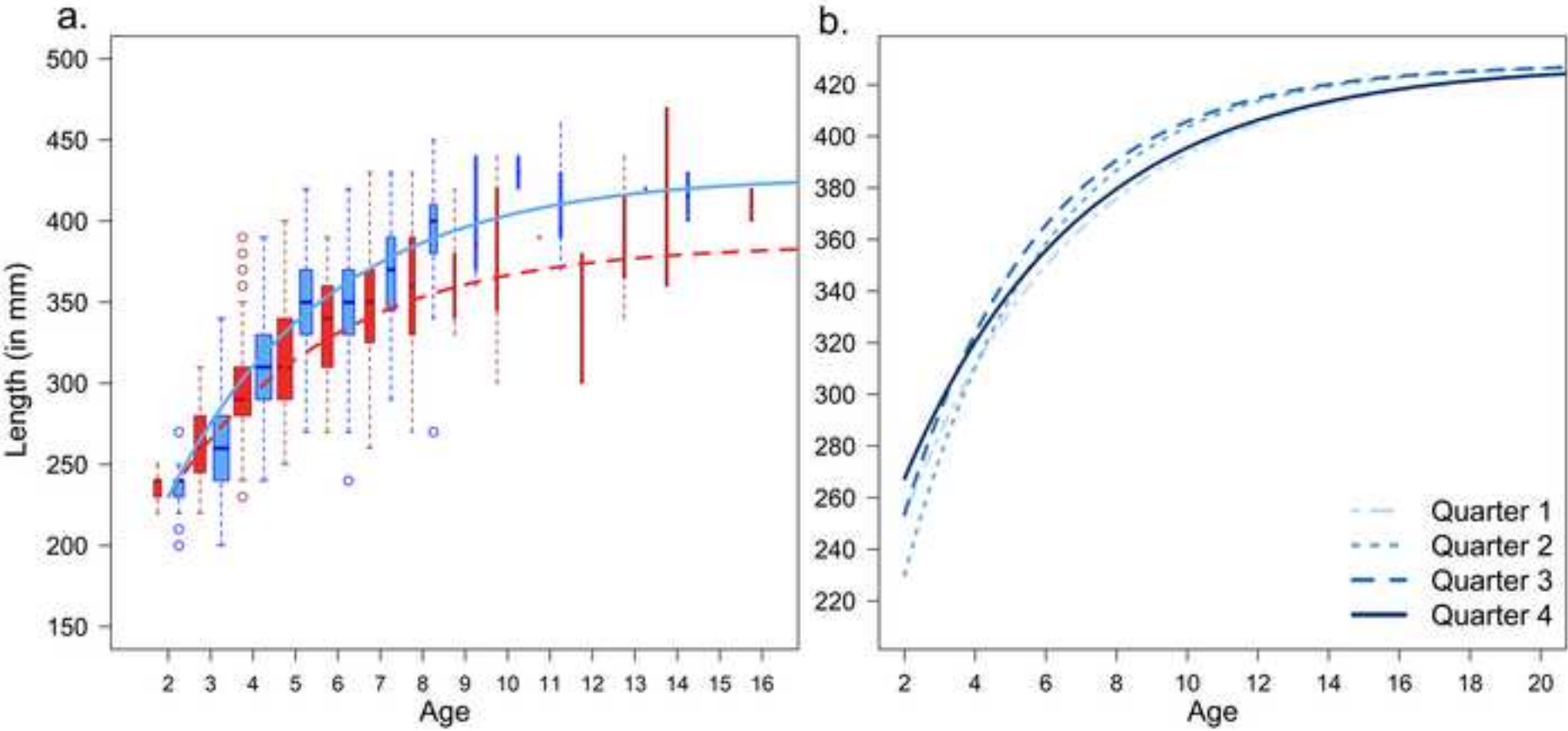


Figure4

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**Figure captions :**

Figure 1: The three subareas of the Eastern English Channel as proposed in (Archambault et al., 2015; Rochette et al., 2012) (UK: United Kingdom, NE: Northeast, SW: Southwest). The points represent haul positions of the UK-BTS (UK Beam Trawl Survey). The two coloured areas SW and NE in represent the subareas with French commercial sampling and the cross-hatching ICES (International Council for the Exploration of the Sea) statistical rectangles were assigned to the Northeast and Southwest subareas respectively. Top and right axes correspond to the ICES statistical rectangle coordinates.

Figure 2: Von Bertalanffy growth curves for the Northeast and Southwest subareas of the Eastern English Channel for each data source, UK-BTS (UK Beam Trawl Survey) (dashed line in blue) and French commercial fisheries (solid line in orange). The curves separate female and male and were plotted from growth parameters computed from the model fitted with the two data sources. The boxplots represent the data distribution at each age, their widths are proportional to the number of data at each age and for each data source and the dots are the outliers at each age.

Figure 3: Von Bertalanffy growth curves for Northeast (dashed line in red), Southwest (dotted line in blue) and UK (solid line in green) subareas of the Eastern English Channel separating female and male, plotted from growth parameters computed from model fitted with scientific survey. The boxplots represent the data distribution at each age, their widths are proportional to the number of data at each age and in each subarea and the dots are the outliers at each age.

Figure 4 : Von Bertalanffy growth curves plotted from growth parameters computed from model fitted with commercial fisheries: a. for Northeast (dashed line in red) and Southwest (solid line in blue) subareas for females during the quarter 2. b. for each quarter for females in the SW subareas. The boxplots represent the data distribution at each age, their widths are proportional to the number of data at each age and in each subarea and the dots are the outliers at each age.

**Supplementary material for on-line publication only**

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