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Could we consider a single stock when spatial sub-units present lasting patterns in growth and asynchrony in cohort densities? A flatfish case study

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ABSTRACT

An accurate representation of the spatial structure of marine fish populations is a prerequisite for unbiased stock assessment, to build appropriate management measures. The common sole (*Solea solea*, L.) of the Eastern English Channel (EEC) is a commercial flatfish species, whose stock is currently assessed as a single homogeneous population and has been overexploited over the last decade. Previous studies have highlighted the stock's low connectivity and the lack of understanding in sub-adults and adults mixing between putative subunits, raising the issue of a potential spatial structure of this stock. Here, we examined evidence of spatial structure by analyzing spatiotemporal patterns of length and density-at-age using time series (1989–2015) obtained from a scientific survey (UK-BTS). We tested for various hypotheses of spatial structure, based on both scientific and expert knowledge, including three isolated subunits, their combination, and no spatial structure. We combined two sets of analyses: (1) a selection of the von Bertalanffy growth model with spatial effects capturing the most accurate spatial structure of the stock and the analysis of long-term spatial patterns (gradients, trends, synchrony) in growth parameters; and (2) an analysis of the synchrony among density-at-age time series between spatial subunits. Growth analysis revealed a spatial structure in three subunits (i.e. the southwestern, north-eastern and English parts of the EEC) and an overall decline of length-at-age, suggesting Fishery-Induced Evolution. The synchrony analysis revealed high spatiotemporal integrity at the level of the southwestern subunit of the EEC. Our two analyses thus detected a lasting signal of spatial stock structure with a probable isolation of the southwestern subunit from the rest of the EEC. Future research should build on our study by investigating the connectivity of sole throughout its entire life cycle, to improve stock assessment and fishery management.

1. Introduction

According to Ihssen et al. (1981), a stock is a monospecific group of individuals that randomly mate and displays spatiotemporal group integrity. Accurate delineation of stocks is a prerequisite for setting appropriate fisheries management measures (Kutkuhn, 1981; Smith et al., 1990; Begg et al., 1999a). However, the existence of population structure at different geographic scales and life stages is common (Waples and Gaggiotti, 2006; Reiss et al., 2009; Ames and Lichter, 2013; Ciannelli et al., 2013), and should be considered in stock assessments (Carson et al., 2011; Petitgas et al., 2013; Frisk et al., 2014). Inaccurate representation of the spatial structure of (meta-)population, e.g. by ignoring the existence of independent subunits, or of connectivity and exchanges with other stocks, biases estimates of population vital rates (i.e., growth, maturity and mortality) (Cadrin et al., 2013; Kerr et al.,

2017). When the understanding of stock structure and delineation is limited (Cadrin et al., 2010; Zemeckis et al., 2014; Mahe et al., 2016), current practice assumes homogeneous vital rates without contrasts between putative subunits (Cadrin et al., 2013). This can induce a mismatch between the management unit and ecological connectivity (Hawkins et al., 2016; Kerr et al., 2017), resulting in the over-exploitation of less productive subunits and underexploitation of more productive ones (Fu and Fanning, 2004; Cadrin and Secor, 2009; Ying et al., 2011; Goethel and Berger, 2017).

Different methods exist to identify and delineate stocks (Östman et al., 2017). Genetic markers (microsatellites (e.g., Cuveliers et al., 2012; Jasonowicz et al., 2016), or Single Nucleotide Polymorphism (e.g., Milano et al., 2014; Laconcha et al., 2015)); morphometry and meristics (Allaya et al., 2016; Sley et al., 2016); parasites (Catalano et al., 2014; MacKenzie and Abaunza, 2014); otolith (shape (Hüssy

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et al., 2016; Mahe et al., 2016) or microchemistry (Tanner et al., 2016; Moreira et al., 2018)); and tagging (Rogers et al., 2017; Le Bris et al., 2018) are widely used. Although easily available from survey data, life history traits such as abundance, growth, and maturity are rarely used to analyze the spatial structure of populations (Begg and Waldman, 1999; Begg et al., 1999b; Cadrin et al., 2013; Erlandsson et al., 2017). Yet, long-term time series derived from field surveys are frequently available at no cost, allowing the assessment of spatial structure while accounting for temporal integrity (Begg et al., 1999a; Cope and Punt, 2009).

The analysis of correlations in temporal fluctuations of life history traits and demographic attributes among populations (e.g., spatial synchrony; Walter et al., 2017) is an underused but valuable method to investigate the spatiotemporal structure of natural populations (Botsford and Paulsen, 2000; Rushing et al., 2016; Rogers et al., 2017). Dispersal and Moran effects (i.e., effects of correlated fluctuations in environmental drivers on synchrony among populations); have repeatedly been highlighted as structuring observed patterns (Ranta et al., 1995; Liebholt et al., 2004). In the context of stock structure identification, if there were synchronous environmental drivers over stock subunits and spatially asynchronous life history traits, it would indicate that the stock is spatially structured. The stock is “spatially structured” in case of persistent spatial asynchrony in life history traits among subunits.

For decades, stock assessments of the common sole (*Solea solea*, L.), a commercial species of main interest (ICES, 2017b), have considered three independent stocks in the English Channel-North Sea Region: the North Sea (ICES division IVc), the Eastern English Channel (EEC; ICES division VIIId) and the Western English Channel (ICES division VIIe) stocks (Fig. 1). This separation is in accordance with patterns of isolation by distance (Diopere et al., 2017). In the EEC, reproduction occurs in early spring on relatively coastal spawning grounds (Rochette et al., 2012). Once hatched, pelagic larvae drift for almost 2 months towards shallow estuarine and coastal nursery grounds (Grioche, 1998; Savina et al., 2010; Rochette et al., 2012). After metamorphosis, juveniles grow

on these shallow nursery grounds for about two years before moving to deeper offshore adult foraging grounds (Riou et al., 2001; Rochette et al., 2010). Uncertainty remains regarding the spatial unity of the stock (Rochette et al., 2013; Archambault et al., 2016; ICES, 2017a). Larval connectivity is low since spawning areas directly feed adjacent coastal and estuarine nursery grounds (Rochette et al., 2012). Besides, very moderate movements of juvenile fish at small scales (< 10 km; Le Pape and Cognez, 2016) and their strong dependence upon local nursery habitats (Riou et al., 2001) result in low juvenile connectivity (Coggan and Dando, 1988). However, connectivity among subunits as a result of adult movement, a potentially important driver of population segregation (Mullon et al., 2002; Frisk et al., 2014) still remains partially unknown (Burt and Millner, 2008; Archambault et al., 2016). Based on several lines of evidence, three subunits of the stock appeared a realistic hypothesis in the EEC (Rochette et al., 2012; Archambault et al., 2016): the Bay of Seine (southwest subunit, SW), the Northern French coast (northeast subunit, NE) and the English coast (English subunit, UK) (Fig. 1). Natural barriers with unsuitable habitats for adult sole (i.e., large and deep gravel grounds in the middle of Eastern Channel, wide rocky reefs from shallow to deep areas; Rochette et al., 2012; Archambault et al., 2016) separate these subunits. Considering metapopulation dynamics among these potential subunits in the EEC would drastically change inferences on population dynamics and stock assessment (Archambault et al., 2016).

Based on a von Bertalanffy growth model (VB) to analyze length-at-age data from commercial landings and scientific survey over a short time period (2010–2015), Du Pontavice et al., (2018) found spatial differences in asymptotic length and length-at-age 2 between the three subunits described above. However, limitations prevented to conclude on spatial structure from this study. First, the use of a single stock identification method is not sufficient to provide robust conclusion about the stock structure. Indeed, different stock identification methods may provide inconsistent results about the stock structure, and the use of a multiple approach is recommended (Begg and Waldman, 1999; Waldman, 1999; Cadrin et al., 2013). Second, authors investigated

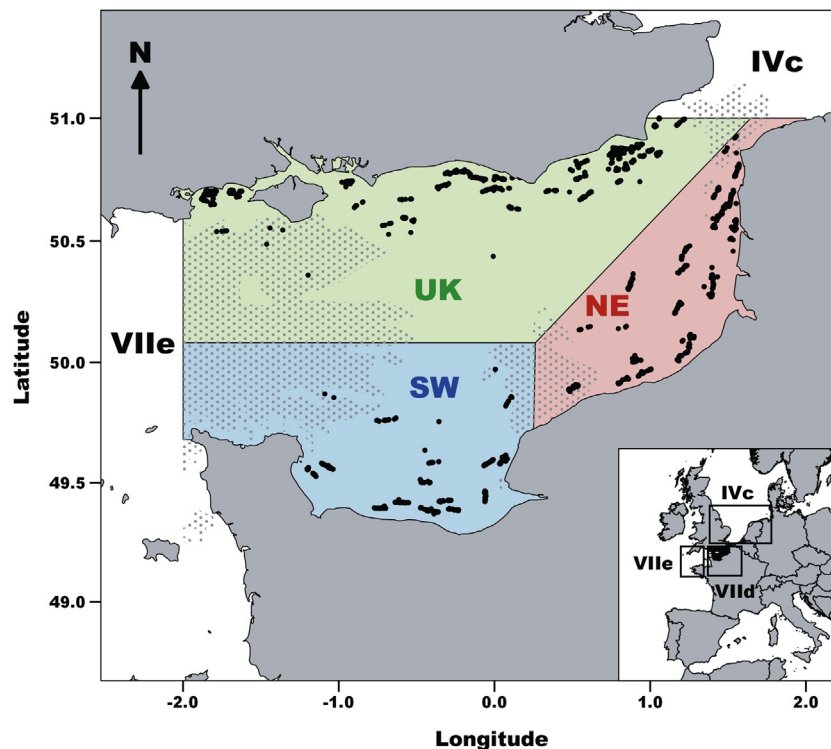


Fig. 1. Map of the Eastern English Channel common sole stock (ICES division VIIId) including the three putative subunits tested for in this study (UK, NE and SW). Light grey dots indicate rocky reefs. Black dots correspond to the location of the UK-BTS sampling stations from 1989 to 2015.

spatial patterns of growth parameters over a short period, but the temporal evolution was not examined, despite its importance to understanding spatial stock structure (Begg et al., 1999b). Thirdly, Du Pontavice et al. (2018) only tested the three-subunits hypothesis whereas alternative hypotheses deserve to be tested to investigate the stock structure. Here, we investigate the spatiotemporal consistency of a stock sub-structure in the EEC by analyzing spatiotemporal patterns of key life history traits over 26 years. We expanded from Du Pontavice et al. (2018) by analyzing, over a longer series (1989–2015), density-at-age in addition to length-at-age data, both estimated from a scientific survey dataset. We tested for different configurations of spatial structure, including three isolated subunits (Rochette et al., 2012; Archambault et al., 2016; ICES, 2017a; Fig. 1); two isolated subunits (combination of the 3) or a single stock (no spatial structure, i.e. the present management unit). Specifically, we combined two sets of analysis: (1) we used model selection to select the VB growth model that reflected the more probable spatial structure, then we investigated long-term spatial differences and synchrony in growth parameters; (2) we used multivariate time series analyses to assess intra-subunit synchrony among density-at-age time series. The growth analysis focused on patterns, trends and spatial synchrony among subunits, whereas the density-at-age analysis examined the strength of the intra-subunit synchrony to assess the spatial structure of the EEC stock of common sole. We assume that long-term differences and spatial asynchrony in growth parameters among stock units, combined with strong intra-subunit synchrony in density-at-age time series are convergent indices of a spatial structure.

2. Material and methods

2.1. Challenging various hypotheses of spatial structure

Growth and density-at-age data were analyzed using 5 different hypotheses of spatial structure in the EEC (Fig. 1, Table 1). The null hypothesis (H0) considered that the EEC is a single stock (i.e., no spatial structure), while the remaining four alternative hypotheses assumed for the stock to be partitioned into two or three subunits.

2.2. Length-at-age and density-at-age datasets

The UK- Beam Trawl Survey (BTS) is an annual scientific survey conducted by the Center for Environment Fisheries and Aquaculture Science (CEFAS) since 1989. It covers the EEC and the southern part of the North Sea. Sampling takes place in July and August, following the same survey design each year (Fig. 1), using a commercial 4 m beam trawl (ICES, 2009). Each sole caught is measured (total length), sexed and aged by reading otolith increments. Data from this survey provide consistent time series of lengths and abundances-at-age by sex throughout the EEC over the period 1989–2015.

However, to ensure sufficient numbers of common sole per age, sex and subunit categories, we removed three cohorts (1992, 2006 and

Table 1

Hypotheses of spatial structure inside the common sole stock of the Eastern English Channel. The 3 subunits (H1) considered are the UK (along the UK coast), NE (North East French coasts) and SW (South West French coasts) subunits. These primary subunits are pooled to define the null hypothesis (H0) and alternative hypotheses (H2, H3 and H4). “+” means that primary subunits are pooled.

Hypotheses	Subunits	Number of subunits
H0	UK + NE + SW	1 single stock
H1	UK, NE and SW	3
H2	(NE + SW) and UK	2
H3	(UK + SW) and NE	2
H4	(UK + NE) and SW	2

Table 2

Number of common soles sampled by the UK-Beam Trawl Survey (BTS) in the Eastern English Channel and used in growth and density-at-age analyses.

	Selected ages	Selected cohorts	Number of fish			
			Subunit	Sex		Total
				Females	Males	
Growth	1–19	1989–1991 + 1993–2005 + 2008	UK	2903	2740	5643
			NE	1339	1704	3043
			SW	1348	1262	2610
Density	1–5	1989–1991 + 1993–2005 + 2008–2010	UK	3187	2954	6141
			NE	1511	1861	3372
			SW	1397	1307	2704

2007) from the dataset, due to the low occurrence and abundance of sole.

Regarding the growth analysis, to avoid bias in estimates of growth parameters, we removed post-2008 cohorts, as old individuals (i.e. age > 8) have not been caught yet, preventing from accurately estimate L_{∞} (i.e. the asymptotic length) in VB growth models. 17 cohorts from 1989 to 2008, corresponding to a sufficient number of females and males (age 1 to 19), caught in the three putative subunits were finally selected (Table 2).

Regarding the density-at-age analysis, to ensure sufficient numbers of fish per age, cohort, sex and subunit categories, we only included soles between ages 1 and 5 (19 cohorts, from 1989 to 2005; Table 2).

The full data set consists of 11,296 and 12,217 common soles available for growth and density-at-age analyses, respectively (Table 2).

All growth and density-at-age analyses detailed below were performed using the R software (R Development Core Team, R.3.1.1, 2016).

2.3. Growth modelling

Length-at-age data were analyzed using the von Bertalanffy Growth Function (von Bertalanffy, 1957). We applied the same method as Du Pontavice et al., (2018) to assess estimates of growth parameters with a von Bertalanffy growth function, from age 1 (Eq. 1):

$$L_{t,i} = L_{\infty} - (L_{\infty} - L_1) \times \exp(-K \times (t - 1)) + \varepsilon_i \quad (1)$$

with $L_{t,i}$, representing total length of the sole i at age t (in mm); ε_i , a normally distributed error term considered independent among all individuals and with a homogeneous variance; L_1 , total length at age 1; L_{∞} , asymptotic length and K , growth rate (in year⁻¹). The three parameters were estimated using a maximum likelihood framework using the nonlinear least squares procedure (*nls()* function) of the R package *stats()*.

2.3.1. Model selection

Since sexual dimorphism in growth has been documented for the common sole (Rijnsdorp and Van Beek, 1991), we introduced a “sex” effect on growth parameters. Thus, for each sex, we investigated variations in growth parameters across time (cohorts) and space (subunits) to test for a signal of spatial stock structure.

We selected the most appropriate combination of “cohort”, “sub-unit” and “sex” effects on the three estimated parameters of the VB based on the resulting Akaike Information Criterion (AIC). As preconized by Burnham and Anderson (2003), we also included AIC weights to compare the probability of each model. AIC weights were assessed using the *Akaike.weights()* function of the *qpcR* package.

We first tested models which considered the sequential introduction of effects on each parameters separately (L_1 , L_{∞} or K), on two parameters (L_1 and L_{∞} , L_1 and K , L_{∞} and K) and on each parameters simultaneously (L_1 , L_{∞} and K). The sequential introduction of effects on parameter(s) consisted in introducing the “sex” effect then the “cohort”

effect and finally the “subunit”, by contrasting the 5 hypotheses of spatial structure (H0–H4; Table 1).

2.3.2. Assessing spatiotemporal patterns of growth parameters

As estimates of K and L_∞ are negatively correlated in the VB (Schnute, 1981), the inter-cohort variability for both parameters can represent statistical flukes rather than an ecological signal in the data. Therefore, we used L_{10} (the estimated length at age 10) as an indicator of growth, as it is more robust to statistical correlation than parameters taken individually. We arrived at L_{10} by preliminarily testing the correlation between parameters K and L_∞ and L_{age} and found that L_{10} was the appropriate parameter to investigate growth in this study focused on adult stages. L_{10} was chosen to explore spatial structure since it is more influenced by L_∞ than by K and L_1 , more relative to growth of juveniles.

Variance estimates were calculated using the delta method, which is a method for deriving the variance of a function of asymptotically normal random variables (Casella and Berger, 2002).

We qualitatively examined L_{10} trends per sex and subunit to evaluate the appearance, maintenance or disappearance of spatial patterns of growth over the time series.

2.3.3. Spatial synchrony in time series of growth parameters

We tested the spatial synchrony of time series (cohort year) of L_{10} to investigate the covariation in time trends among subunits. Covariations were assessed using multivariate time series analysis with the MARSS package in R (Holmes et al., 2013). This package allows for fitting time series models with (or without) covariates to a set of multivariate time series data. Given a set of $i = 1, \dots, m$ time series of data of length $t = 1, \dots, T$ (17 different cohorts are considered, $T = 17$) denoted $y_{i,t}$, the overarching model comprises a state process (Eq. 2), that defines the time series model including covariation between the m time series, and an observation process (Eq. 3), including observation errors in the data.

$$x_t = x_{t-1} + u + w_t, \text{ where } w_t \sim \text{MVN}(0, Q) \quad (2)$$

$$y_t = Z_t x_t + v_t, \text{ where } v_t \sim \text{MVN}(0, R) \quad (3)$$

with $x_t = x_{i,t}$, $i = 1, \dots, m$ the vector of size m of the state at any time step t , u a vector of size m accounting for any systematic trend in the time series x_t and w_t the multivariate Normal (MVN) process error with Q an $m \times m$ matrix describing the correlation between process deviations. y_t is the vector of observations at any time step t and v_t is the MVN observation error with $m \times m$ covariance matrix R . Process and observation errors inform on model reliability.

This general framework was applied to estimate the spatial covariations in the time series (cohorts) of $L_{10i,t}$ previously estimated from the VB growth model, where i defines the indices of spatial subunits and t the cohort. There were twice as many time series m as subunits (separate females and males). The linear time trend u and covariation matrix Q were estimated without constraints. The covariance matrix of observation errors R was constrained to be diagonal (no covariation in observation errors), with all variance parameters on the diagonal to be equal (same observation error variance for all of the time series).

The variance-covariance matrix Q was transformed into a correlation matrix using the *covtocor()* function of the *hapsim* package and visualized using the function *corrplot()* of the *corrplot* package in R.

2.4. Assessing the consistency in the variation of densities within subunits

In this analysis, we assessed to what extent variations of density-at-age across time propagate through a cohort at successive fish ages, and how the strength of this statistical signal changes given our hypotheses on the spatial structure of the stock (Table 1). High consistency in cohort's density throughout age classes within a spatial unit would be an indication of isolation of this subunit.

2.4.1. Anomalies of density-at-age time series

We used data on number of individuals in Table 2 to build abundance indices at age, per cohort, per sex and for each spatial unit considered in Table 1. Based on the density-at-age dataset (i.e., age 1–5, from cohort 1989 to 2010), we first calculated the density per sex, age, cohort and subunit, as the abundance relative to the trawled surface (Eq. 4):

$$\text{Density}_{\text{Sex,Subunit,Age,Cohort}} = \frac{\text{Abundance}_{\text{Sex,Subunit,Age,Cohort}}}{\sum (\text{Surface trawled}_{\text{Sex,Subunit,Cohort} + \text{Age}})} \quad (4)$$

The decline in abundance with age resulting from both natural and fishing mortality is strong. This decline could blur the statistical signal of covariations in abundance among age classes throughout a cohort. To avoid such limitation, we first standardized density indices from BTS surveys into anomalies using average density at age (Eq. 5):

$$\text{Anomaly}_{\text{Sex,Subunit,Age,Cohort}} = \frac{\text{Density}_{\text{Sex,Subunit,Age,Cohort}} - \text{Mean}(\text{Density}_{\text{Sex,Subunit,Age}})}{\sigma(\text{Density}_{\text{Sex,Subunit,Age}})} \quad (5)$$

2.4.2. Spatial synchrony of density-at-age anomalies

The MARSS package allowed for assessing the strength of the correlation in the variation of densities (anomalies) across ages and cohorts within a spatial unit. Thus, referring to notations introduced in Section 2.3.3., we assessed the covariations among m ($i = 1, \dots, m$) series $y_{i,t}$ where $y_{i,t}$ denote the anomalies of density of the cohort t ($t = 1, \dots, T$; 19 different cohorts are considered here, $T = 19$) and i denotes the combination of age classes (5) and spatial units considered (Table 1). For instance, under hypothesis H0 (no spatial structure), $m = 5$ as only 5 series of abundance at age 1 to 5 are considered. Under the hypothesis H1 (3 subunits), $m = 15$ as 5 time series of density-at-age (ages 1 through 5) are considered for each of the 3 subunits.

We performed separate analyses for each of the 5 alternative hypotheses regarding spatial stock structure (Table 1), for males and females independently because no information allows for considering that they have the same dynamics. The linear time trend and covariation matrix were estimated without constraints. The covariance matrix of observation errors was constrained to be diagonal, with equal variance parameters on the diagonal. The variance-covariance matrices were transformed into correlations matrices using the *covtocor()* function then plotted with the *corrplot()* function.

3. Results

3.1. Spatiotemporal patterns of growth parameters

3.1.1. Model selection

The “sex”, “cohort” and “subunit” effects were first tested on K , L_∞ and L_1 separately and then simultaneously. Models that simultaneously included effects on the three parameters systematically outperformed models that considered effects on each parameter separately (not presented). The following models therefore considered the sequential introduction of effects on the three parameters simultaneously.

As expected, preliminary results showed that the variable “sex” captured the greatest part of the variability, followed by “cohort” and “subunit” (Table 3). In other words, models including sex and cohort effects always outperformed models without sex or cohort effects, regardless of the spatial structure considered. Finally, regarding AIC weights, results showed that the best model (having the higher conditional probability among models) agreed with hypothesis H1 (Table 3). This model showed no violations of normality or homoscedasticity in the data (Fig. S1).

3.1.2. Spatiotemporal trends in growth

Growth parameters K , L_∞ and L_1 were estimated from the best

Table 3
Akaike Information Criterion (AIC) and AIC weights of each model tested considering different spatial structure hypotheses (the null hypothesis H0 and 4 alternative hypotheses H1, H2, H3 and H4). Sex, cohort and subunit effects on the three parameters of the von Bertalanffy growth function were included simultaneously. H0 = single stock, H1 = NE, SW and UK subunits, H2 = (NE + SW) and UK subunits, H3 = (UK + SW) and NE subunits, H4 = (UK + NE) and SW subunits.

Structure hypotheses	Effects on parameters L_{∞} , L_1 and K	AIC	Akaike Weights
H0	Sex	109,924	0
	Sex, Cohort	102,762	0
H1	Sex, Cohort, Subunit	101,149	1
H2	Sex, Cohort, Subunit	101,347	0
H3	Sex, Cohort, Subunit	101,925	0
H4	Sex, Cohort, Subunit	102,514	0

model for each sex, cohort and spatial subunits (H1). The parameter L_{10} was then calculated from K , L_{∞} and L_1 for each sex, cohort and subunit (Fig. 2; see the related growth curves in Fig. S2).

The spatial synchrony analysis of growth parameters yielded negative values for vectors u (Table S1), with L_{10} exhibiting a generally decreasing trend among cohorts from 1989 to 2008, regardless of sex and subunit (Fig. 2). Over this period, females' L_{10} declined by 35, 53 and 54 mm in the UK, NE and SW subunits, respectively (Fig. 2a), corresponding to a loss of 10 to 14% in size. For males (Fig. 2b) L_{10} decreased by 19, 56 and 35 mm in the UK, NE and SW subunits respectively, representing a loss of 7 to 18%.

Over the whole time-series, common sole growth, estimated from L_{10} , was generally lower in the NE than in the SW subunit. The situation was more complex along the UK coast where growth was comparable to estimates for the NE subunit for the first half of the time series, but declined less rapidly than in the two other subunits and was closer to growth estimates in the SW since around 2000. However, in the SW subunit, L_{10} presented high inter-cohort variability (Fig. 2).

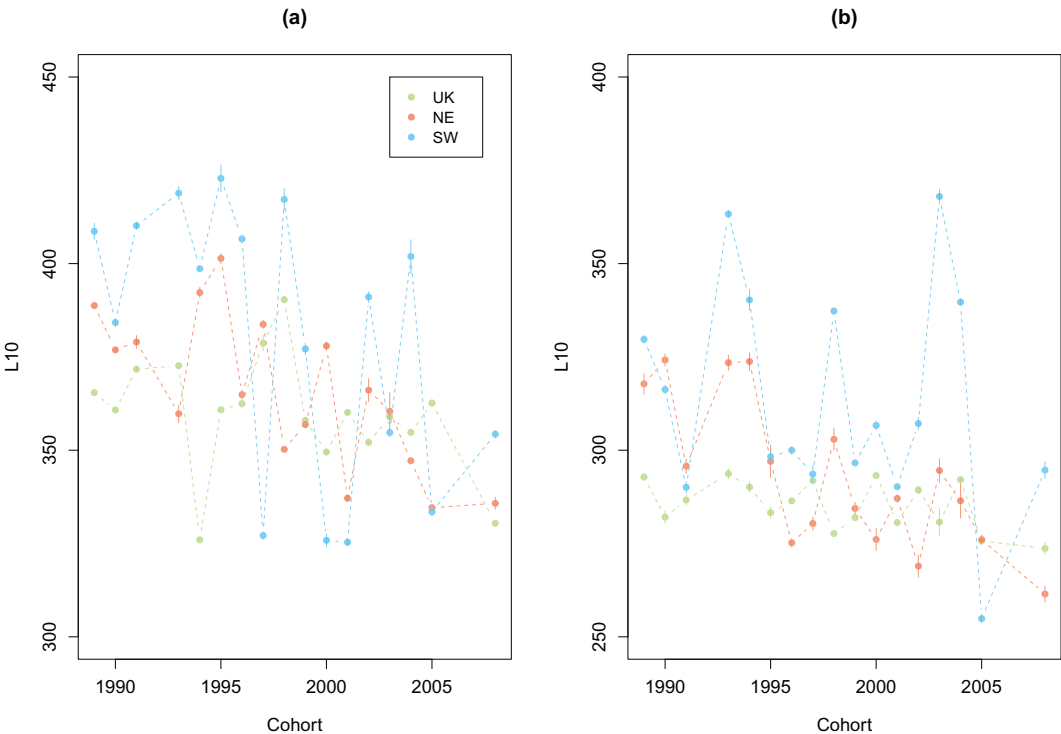


Fig. 2. L_{10} time series for females (a) and males (b) within each subunit (UK, NE and SW) with their associated standard-errors.

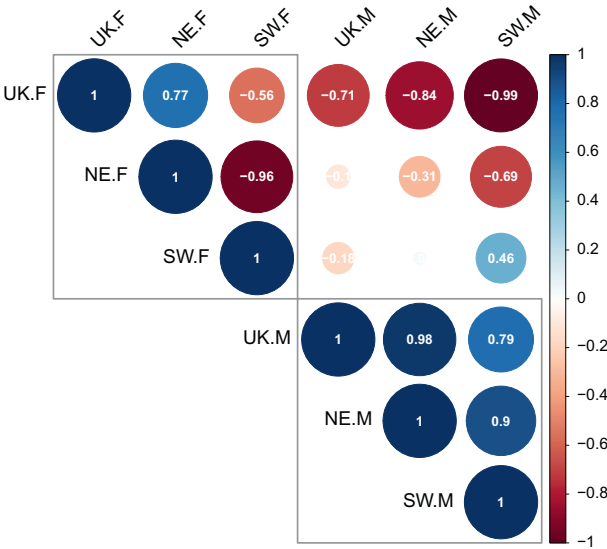


Fig. 3. Pair-wise correlation matrix between L_{10} time series by sex and subunit. F and M refer to female and male time series. UK, NE and SW are the three subunits considered (hypothesis H1). The colors and sizes of the circles indicate the direction (positive or negative) and strength of the correlation. Grey squares separate females and males' spatial correlations.

3.1.3. Spatial synchrony in growth parameter time series

The estimated correlation matrix did not reveal spatial synchrony in the L_{10} time series between the three subunits (Fig. 3).

We found high correlations (> 0.79) in L_{10} time series among the three subunits for males (Fig. 3), indicating high growth synchrony. However, female growth exhibited strong negative correlation (< -0.90) between the NE and SW subunits (Fig. 3), and a positive correlation between the UK and NE subunits. Interannual variations in growth was asynchronous between the SW and the other subunits.

However, these results have to be interpreted with caution since

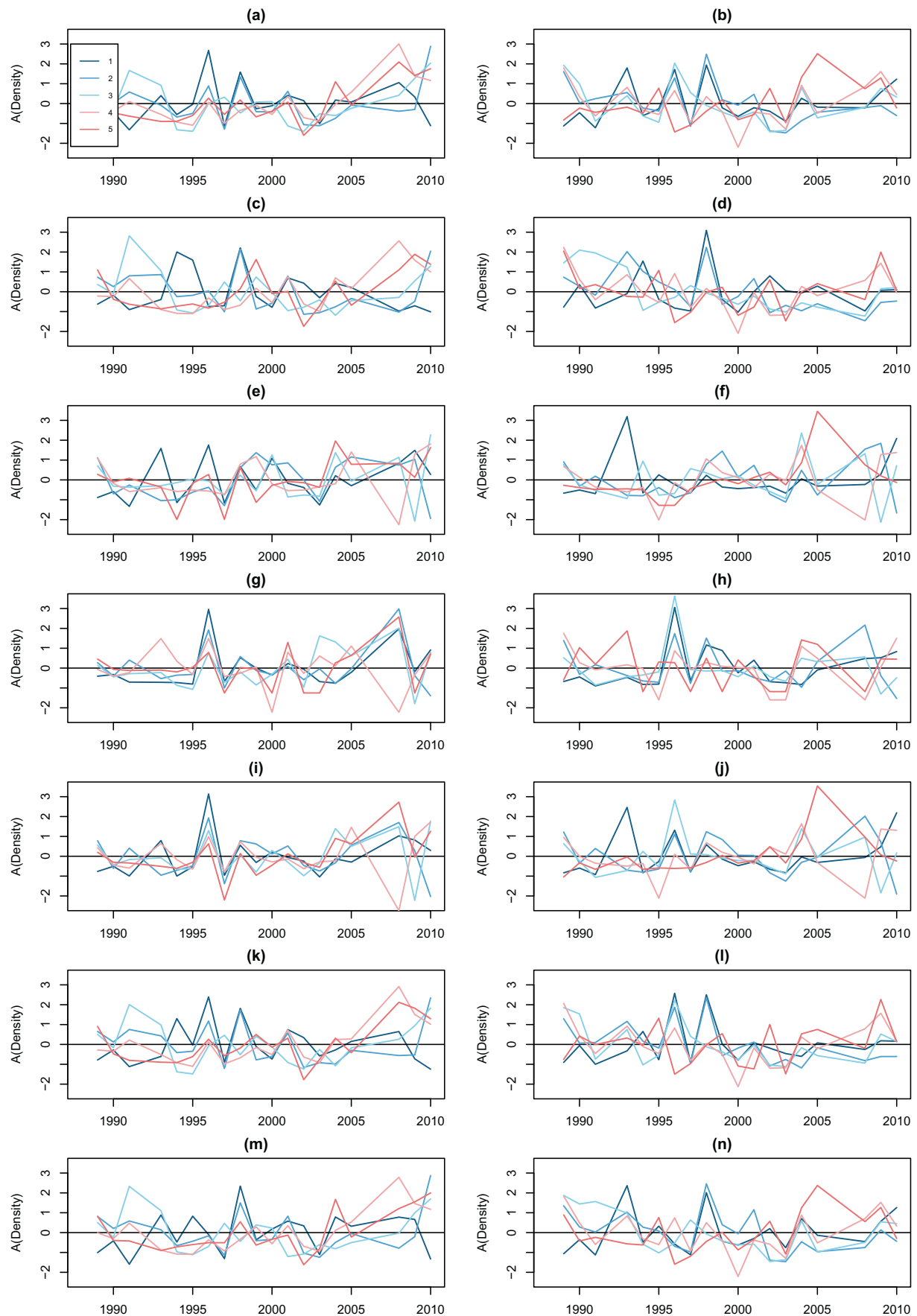


Fig. 4. Times series of density anomalies for common soles of age 1 to 5 in the Eastern English Channel for cohorts between 1990 and 2010. Left and right panels correspond to females and males, respectively. Individual panels correspond to the different spatial structure hypotheses tested. Single stock (a,b); UK (c,d); NE (e,f); SW (g,h); NE + SW (i,j); UK + SW (k,l); UK + NE (m,n).

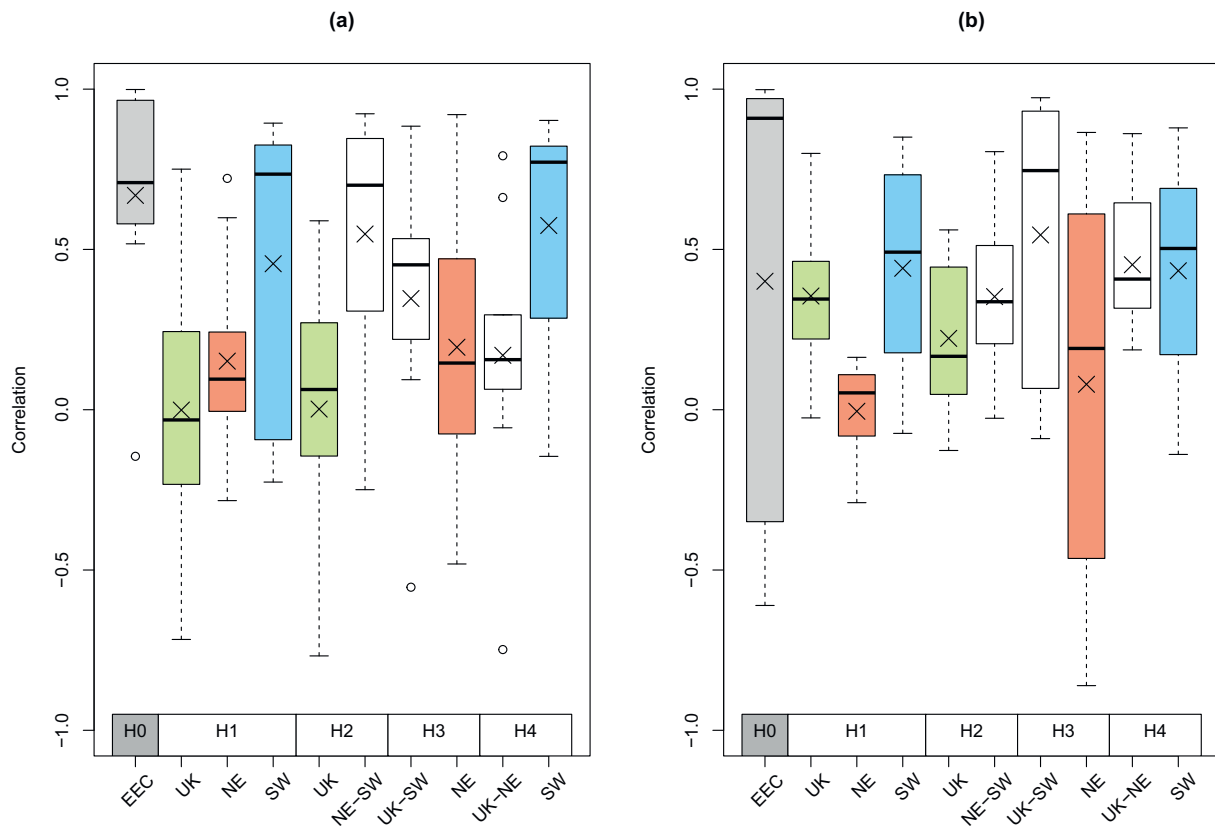


Fig. 5. Distributions of the correlations between density-at-age time series (ages 1–5, 10 pairwise correlations in each boxplot, cross indicates the mean) for each subunit and spatial structure hypothesis, for females (a) and males (b). Colors represent the subunits considered (in white when 2 subunits are pooled). H0 = single stock, H1 = 3 subunits (UK, NE and SW); 2 subunits for H2 = UK and (NE + SW), H3 = NE and (UK + SW) and H4 = SW and (UK + NE).

observation and process errors were high, especially in the SW subunit for both sexes. Process error was > 1000 in the SW subunits whereas it varied between 6 and 100 in other subunits.

3.2. Spatiotemporal patterns of densities-at-age anomalies

We did not find any trend in the time series of density-at-age anomalies regardless of the subunits and sex considered (Fig. 4). These results were supported by vector u estimates from the MARSS models (not presented).

Correlation matrices between density-at-age time series per subunit for each hypothesis (Fig. S3) are synthesized on Fig. 5. Whatever the hypothesis, process errors were close to 1 (between 0.02 and 2.1), allowing for interpretations.

For both sexes, the strength of the synchrony across density-at-age time series was high considering the null hypothesis, i.e. no spatial structure (Fig. 5). Regarding females, the null hypothesis presented the highest level of synchrony among the structure hypotheses (Fig. 5a). Regarding males, the strength of the synchrony considering H0 was also high (Fig. 5a), but was not the highest. These results indicated that the null hypothesis, (i.e. no spatial structure) was credible for both sexes and that mixing across the EEC stock could be important.

However, the existence of spatial structure was also probable for both sexes since the synchrony between density-at-age time series were also high within the SW subunit (H1 and H4, Fig. 5). Mixing between putative subunits appeared higher for other subunits, with low synchrony across density-at-age time series, especially in the UK subunit for females (H1 and H2; Fig. 5a), and in the NE subunit for males (H1 and H3; Fig. 5b).

4. Discussion

The understanding of population structure is of major importance for the management of marine species (Kerr et al., 2010a,b; Ciannelli et al., 2013). Inconsistencies between population structure and stock units may bias stock assessment results and the quantification of risks for sustainable fisheries management (Kerr et al., 2017). In the EEC stock of common sole, the existence of spatial structure was evidenced for larvae (Rochette et al., 2012) and juveniles (Riou et al., 2001; Le Pape and Cogné, 2016). For adults, the existence of spatial structure was also suggested by Du Pontavice et al., (2018), considering recent spatial contrasts in growth between the UK, NE and SW subunits. Herein, we expanded this study by assessing two different analyses of long-term growth and densities to inform on this spatial structure.

4.1. Growth analysis revealed long-term stock structure

The von Bertalanffy growth modelling exhibited spatial stock structure for the common sole between the three predefined subunits in the EEC. This was consistent with Du Pontavice et al., (2018), who found higher length-at-age in the SW than in the NE and the UK subunits over the recent period 2010–2015, for both sexes. Herein, the analysis of long-term time series (1989–2015) highlighted a global decreasing trend of L_{10} over the last two decades, whatever the sex and subunit. This finding corroborates the decreasing length-at-age trends in commercial landings since 2004 (ICES, 2017a). L_{10} in the SW remained the highest among subunits all along the study period, with dramatically higher inter-cohort variability. The common soles from the UK subunit presented similar L_{10} values as from the NE subunit before 2000, and higher values after 2000.

Growth is a phenotypic expression of genetic and environmental

factors (Swain et al., 2007; Cadrin et al., 2013). Disentangling the relative effects of these factors is difficult for wild populations (Sinclair et al., 2002). Growth is impacted by global change (Brunel and Dickey-Collas, 2010; Baudron et al., 2014); as increasing sea temperature advantages early maturation and smaller body size. For the common sole of the EEC, changes of growth in response to global warming may explain the general decreasing trend of L_{10} observed over the last two decades. Indeed, increasing trends of water temperature are homogeneous throughout the EEC (Gohin et al., 2010). Considering these homogeneous trends, contrasts in evolution of spatial growth between the UK and NE subunits could not be attributed to divergent environmental changes. Growth of the common sole is also impacted by intensity and size-selectivity of the fishery (Mollet et al., 2007) and fishery-induced evolution could have induced these contrasts in observed growth. Removing the larger individuals acts as a non-random genetic selection (Sinclair et al., 2002; Law, 2007; Enberg et al., 2012) and favor smaller size-at-age and early-maturation (Enberg et al., 2012). In the case of common sole of the EEC, contrasted size-selective fishing or exploitation rates between subunits could lead to spatial differences in growth trends (Mollet et al., 2013; Hunter et al., 2016) and is a relevant candidate mechanism to explain both the decreasing trend of length-at-age and the contrasted evolution of growth between subunits. Indeed, under the spatial hypothesis H1, Archambault et al., (2016) suggested contrasted estimates of fishing mortality between the UK, NE and SW subunits between 1980 and 2010: fishing mortality was the highest in the NE and the lowest in the SW subunit, with increasing difference between the UK and NE subunits after 2000. A lower fishing pressure in the SW could also have partly contributed to a lower selective pressure thus more variable growth potential and higher variability in growth in this area. Therefore, our findings may indicate a combined effect of global warming and fishery-induced evolution for the common sole of the EEC, although deep investigations about the relative contribution of environmental factors and exploitation rate are required.

Despite these various trends, spatial contrasts in growth remained large during the whole period, especially between the NE and SW, revealing a long-lasting signal of spatial structure between these subunits (Erlandsson et al., 2017). In addition to the analysis of spatiotemporal differences in growth parameters, we investigated the spatial structure through the synchrony analysis in L_{10} time series among subunits. Interpretation of differences in spatial synchrony of growth parameters was spurious because the observation and state process errors were high. Especially, process error was high in the SW subunit, with a probable link to the high inter-cohort variability of L_{10} . Besides, for growth parameters estimated on multiyear time span, environmental drivers have potentially synchronous inter-annual variations between the subunits (Moran, 1953) thus have similar impacts on different cohorts (inter-annual autocorrelation in growth). Thus, synchronous variations in growth parameter is not a reliable indicator of the lack of spatial structure.

4.2. Density-at-age analysis highlighted isolation of the SW subunit

The assessment of covariability between abundance at different locations highlighted the potential existence of spatial structure in the EEC and was thus particularly valuable to describe the dynamic structure of subpopulations (Bjørnstad et al., 1999; Botsford and Paulsen, 2000; Östman et al., 2017). Whatever the sex, the synchrony analysis of density-at-age revealed a synchronous signal at the stock scale, but also at the SW subunit scale, and demonstrated a lack of synchrony in the UK for females and NE subunits for both sex.

Understanding the mechanisms behind spatial synchrony (environmental stochasticity versus dispersal) remains a great challenge in ecology (Liebhold et al., 2004). Spatial synchrony in population dynamics may arise from 2 mechanisms (Liebhold et al., 2004; Walter et al., 2017), (1) dispersal among populations, and (2) congruent

dependence of population dynamics on a synchronous exogenous factor. Dispersal among different subunits can lead to different levels of metapopulation structure, from very low connectivity between subunits to a single population (Östman et al., 2017). Distinct demographic changes (i.e., high synchrony within subunit and low synchrony between subunits) may result from low dispersal rates and fine scale environment processes, and synchronous demographic changes from high dispersal rates between subunits. In the case of the common sole of the EEC, concluding between a metapopulation and a single population from synchrony in cohort abundance was not possible although, the SW subunit appeared isolated from the others. The intra-subunit synchrony detected in the SW may result from low exchange rates with the other subunits of the EEC.

4.3. Congruence between analyses and perspectives

Stock identification methods may provide inconsistent results about the stock structure, some may detect stock structure where others fail to. Spatial level of stock structure could be changed with the method sensitivity and congruence between contrasting methods improves confidence (Cadrin et al., 2013; Izzo et al., 2017). A multiple approach is hence preconized (Begg and Waldman, 1999; Waldman, 1999; Cadrin et al., 2013) but remains underused (Pita et al., 2016).

Herein, we performed in parallel two distinct analyses of long-term life history parameters (growth and density-at-age) using survey data, underused for that purpose despite their easy access (Östman et al., 2017). Our analyses were partially consistent to detect a lasting signal of stock structure for common sole in the EEC. On the one hand, growth analysis highlighted the existence of long-term structure in three distinct subunits, previously defined (Rochette et al., 2012; Archambault et al., 2016). On the other hand, synchrony analysis of density-at-age time series underscored that two hypotheses of structure were probable, without concluding between the single stock hypothesis and spatial structuration, with pronounced segregation in the SW subunit. Therefore, consistent evidence of spatial structure emerged with relatively strong indications of isolation of the SW subunit from the rest of the EEC. The SW subunit is physically isolated from the NE subunit and from the Western English Channel (ICES division VIIe) by rocky reefs forming a natural barrier (Rochette et al., 2010; Fig.1), and a deep central Channel covered by gravels separates the UK and SW subunits (Rochette et al., 2012). These unsuitable habitats for the common sole limit the migration of sub-adults and adults and isolate fish in the SW subunit. In addition to the low connectivity induced at larval (Rochette et al., 2012) and juvenile stages (Riou et al., 2001; Le Pape and Cogné, 2016), our findings likely indicate low exchanges between the SW subunit and the rest of the EEC. For the two other subunits, isolation remains in question, suggesting higher exchange rates of sub-adults and adults between the UK and NE subunits, and potentially with the adjacent North Sea stock (ICES division IVc, Fig.1).

These assumptions need to be deeply investigated since a heterogeneous population dynamics among subunits could be inconsistent with the present assumption of the fishery assessment, which supposed a single stock. Archambault et al., (2016) examined the effect of a metapopulation structure on the estimates of reference point for the common sole of the EEC. They suggested that such structuration lead to contrasted sub-stock assessment, with full-exploitation of the SW subunit but over-exploitation of the UK and NE subunits. If further investigations confirm the sub-stock segregation, it would be necessary to integrate their outcomes to improve the management of common sole in the EEC (Ulrich et al., 2017) and to ensure the persistence capacity of populations (Heino et al., 1997). In the same time, the decreasing trend of length-at-age needs to be accounted for, since the consequences of smaller adult body length could reduce reproductive rates (Rijnsdorp et al., 2010) and decrease populations resilience (Hsieh et al., 2006).

Authors contribution

Each author significantly contributed to this article.

M. Randon: conceptualization, investigation, methodology, writing and statistical analyses

E. Réveillac: conceptualization, writing

E. Rivot: methodology, writing

H. Du Pontavice: methodology

O. Le Pape: conceptualization, methodology, writing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2018.09.012>.

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