

# A holistic investigation of tracers at population and individual scales reveals population structure for the common sole of the Eastern English Channel

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A holistic investigation of tracers at population and 1 individual scales reveals population structure for the 2 common sole of the Eastern English Channel 3 4 5 **RANDON** Marine<sup>1\*</sup>, **REVEILLAC** Elodie<sup>2</sup> and **Le Pape** Olivier<sup>3</sup> 6 7 <sup>1</sup>: Statistical and Actuarial Science Department, Simon Fraser University, 8888 University Drive, 8 9 Burnaby, BC V5A 2S6, Canada 10 <sup>2</sup>: LIENSs, Littoral, Environnement et Societés, La Rochelle University, 2 rue Olympe de Gouges, 17000 La Rochelle, France 11 <sup>3</sup>: ESE, Ecologie et Santé des Ecosystèmes, Agrocampus Ouest, INRAE, 65 rue de Saint-Brieuc, 35042 12 13 Rennes Cedex, France 14 15 \*: corresponding author: marine randon@sfu.ca 16

# 17 Abstract

The sustainable exploitation of sea resources is based on the understanding of population distribution, structure and functioning. The mismatch between stock units and fish populations can dramatically bias the assessment and lead to irrelevant or even detrimental management measures. The common sole of the Eastern English Channel (EEC; ICES division VIId) is a flatfish species of high interest that has been overexploited over the last decades. Low connectivity induced by early life stages across the stock was previously known, but gaps remained regarding the role of adults in population connectivity and spatial structure. In this study we have filled these gaps by (1) gathering 25 all the information on stock identity through five population- and individual-based approaches, and (2) combining this information in a semi-quantitative framework, i.e. the Stock Differentiation Index 26 (SDI). Regarding the population-based approaches, growth and abundance-at-age analyses 27 highlighted a lasting signal of population structure, with three population subunits. Regarding the 28 29 individual-based approaches, genetic analysis highlighted low but significant genetic differentiation 30 between the three subunits over an evolutionary time scale. Besides, a mark-recapture study 31 demonstrated a low level of exchange between these subunits. Finally, an analysis of otolith shape 32 pinpointed spatial variation between the three subunits. Overall, the SDI = 0.93 suggested evidence 33 of spatial structure. The misalignment of the current stock definition with the underlying biological 34 metapopulation now requires the improvement of the assessment-management to ensure its 35 sustainable exploitation.

#### 36 Keywords

37 Stock – Metapopulation – Flatfish – Multi-tracer – Assessment – Management

38

# 39 1. Introduction

40 Despite the stock concept is being central to fisheries science, several definitions could be 41 adopted, depending on the scientific question and methods used (Begg et al., 1999a; Abaunza et al., 42 2008; Cadrin, 2020). From a fisheries management perspective, the stock is basically defined as a 43 working unit for assessment models and management decisions (Kerr et al., 2017; Cadrin, 2020). 44 Ihssen et al. (1981) defined the stock as a monospecific group of individuals mating randomly to 45 display spatiotemporal group integrity. The stock spatial unit is supposed to fit with the underlying 46 biological population, stock assessment and management being provided at the population scale. 47 Stock assessment models suppose that a population is closed and well mixed (Cadrin, 2020) and that

48 vital rates and productivity are homogeneous across the stock (Cadrin et al., 2013; Bosley et al., 2019). However, the stock delineation is frequently unclear (Cadrin et al., 2010; Zemeckis et al., 49 2014; Mahé et al., 2016), inducing a misalignment between the stock and the biological population 50 (Hawkins et al., 2016; Kerr et al., 2017). In the early 2000's, around 50 out of about 150 stocks were 51 52 misaligned with underlying populations (Stephenson, 2002). Such mismatches could lead to a 53 "myopic view" of productivity across the stock (Orensanz and Jamieson, 1998), to biases in stock 54 assessment (Archambault et al., 2016) and to unsuitable exploitation of subunits having different 55 productivity dynamics (Fu and Fanning, 2004; Cadrin and Secor, 2009; Goethel and Berger, 2017).

56 Delineating marine populations is complex because aquatic species are rarely observed directly ("Counting fish is like counting trees except you can't see them and they move"; John Sheperd). 57 58 Marine connectivity is more complex to assess but is considered higher than in the terrestrial realm 59 because the marine environment is more open (Carr et al., 2003). Through the exchange of 60 individuals that links populations (Secor, 2015), marine connectivity is involved in population 61 structure (Parrish, 1989) at various spatial scales (Waples and Gaggiotti, 2006; Reiss et al., 2009; 62 Ciannelli et al., 2013; Costello and Connor, 2019). Degrees of connectivity vary from panmixia (i.e. 63 random mating of individuals; Bailleul et al., 2018) to complete isolation of populations (e.g. Smedbol and Wroblewski, 2002; Abaunza et al., 2008; Cadrin et al., 2010). Between those two situations, 64 metapopulation (i.e. a set of subpopulations connected by dispersal; Kritzer and Sale, 2010) may 65 66 display a more or less consistent spatial structure (Waples and Gaggiotti, 2006). Moreover, the 67 increasing habitat fragmentation and worldwide degradation and environmental shifts induced by 68 climate change are shaping new distribution areas and are challenging the definition of marine populations (Link et al., 2010). Uncertainties regarding the spatial scope of stocks and populations 69 70 thus arise from multiple factors that need to be considered in stock assessment and management.

Challenging such issues, Kerr *et al.* (2017) evidenced the need for adapting fisheries exploitation
to the underlying population structure. In order to identify accurate management units, integrated

73 approaches are recommended to capture the prevailing stock structure (Welch et al., 2015). To do 74 so, the first step consists of gathering all available information of the stock identity into a holistic 75 approach. The holistic understanding of population structure is currently considered as the best 76 practice to draw robust conclusions regarding the stock structure (Begg and Waldman, 1999; 77 Waldman, 1999; Abaunza et al., 2008; Cadrin et al., 2014). Indeed, population structure is induced by 78 processes ranging from ecological to evolutionary time scales (i.e. time scales over which the 79 ecological or genetic process happen; Gingerich, 2019). Bringing together spatial variations in 80 phenotypic and genetic characteristics can help to elucidate the stock identity (Cadrin and Secor, 81 2009; Cadrin et al., 2014). Moreover, combining different methods allows increasing the likelihood of 82 identifying the "true" population structure since one tracer can detect a signal where another fails to 83 do so (Begg and Waldman, 1999; Abaunza et al., 2008; Zemeckis et al., 2014; Pita et al., 2016). The 84 identification of complex marine population structure and associated uncertainty found through a 85 holistic approach (Kerr et al., 2017) allows for further evaluation of the consequences of assessment 86 and management strategies regarding biological, economic and social purposes.

87 The common sole (Solea solea) of the Eastern English Channel (EEC; ICES division VIId; Fig.1), a 88 substantively harvested flatfish species, has been overexploited over the last decades and is 89 managed as a unique homogeneous population (ICES, 2017b, 2019). The drop in spawning biomass 90 has led to a critical exploitation status over the last years. At the same time, a metapopulation 91 structure of the EEC stock has been hypothesized (Rochette et al., 2012), with potential 92 consequences for stock dynamics and sustainable levels of exploitation (Archambault et al., 2016, 93 2018). In 2017, a benchmark pinpointed the potential misalignment of the EEC stock with the underlying population (ICES, 2017a). The EEC stock of common sole was found to be genetically 94 95 distinct from the adjacent Western English Channel (ICES division VIIe) and the North Sea (ICES 96 division IVc) stocks (Fig.1; Diopere et al., 2018). However, misunderstanding regarding the internal 97 EEC stock structure remained (Rochette et al., 2013; Archambault et al., 2016; ICES, 2019). 98 Reproduction takes place in early spring on three distinct spawning grounds (Fig.1; Rochette et al.,

99 2012). After hatching, pelagic larvae drift passively towards shallow coastal and estuarine nursery 100 grounds (Fig.1; Grioche, 1998; Rochette et al., 2012) where individuals metamorphose and settle as 101 juveniles for about 2.5 years before joining as mature soles spawning areas in deeper waters (Riou et 102 al., 2001; Rochette et al., 2010). Larval and juvenile-induced connectivity between nurseries and 103 spawning grounds are low at the scale of the EEC stock. Biophysical modelling highlighted that larvae 104 are mostly advected towards the nearest nursery grounds (Rochette et al., 2012). Then, juveniles 105 display very moderate movements away from their nursery habitats and high sedentariness upon 106 local nursery grounds (Riou et al., 2001). However, the sub-adult (i.e. juveniles leaving their nurseries 107 before the first reproduction) and adult-mediated connectivity are still poorly known despite of their 108 potentially high importance in population structuring (Mullon et al., 2002; Frisk et al., 2014).

109 Focusing on sub-adult and adult stages, recent studies have investigated the structure of the EEC 110 stock of sole using a large range of approaches, from population-based (abundances and growth; 111 Randon et al., 2018) to individual-based approaches (mark recapture; Lecomte et al., 2020; genetics 112 and otolith shape; Randon et al., 2020). The present study aims at (1) synthetizing all the available 113 information regarding the stock structure and (2) discussing alternative assessment and management 114 strategies for the stock of sole of the EEC. To do so, a semi-quantitative approach, the Stock Differentiation Index (SDI; Welch et al., 2015; Izzo et al., 2017), was applied to collate in a holistic 115 116 approach (Kerr et al., 2017) the various population- and individual-based analyses that previously 117 provided information on the stock structure.

118

119 2. Material and methods

120 2.1. Current delineation of the Eastern English Channel stock of sole and the121 alternative structure hypothesis

The EEC stock of sole is currently assessed and managed as one single stock (**Fig.1**), but the existence of three putative subunits has been hypothesized (Rochette *et al.*, 2013; Archambault *et al.*, 2016): the southwest subunit (SW; along the southwestern French coast of the EEC), the northeastern subunit (NE; along the northern French coast of the EEC) and the English subunit (UK; along the southern English coast of the EEC) (**Fig.1**).

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Figure. 1 Map of the EEC stock of common sole (ICES division VIId) and the three putative subunits
(SW, NE and UK). Light grey dots represent rocky reefs. Coastal and estuarine nursery grounds (25 m

isobaths) and spawning areas (Rochette *et al.*, 2012) are delineated by solid and dotted lines,
respectively. VE = Bay of Veys, SE = Bay of Seine, NE = Bay of Somme, UKE and UKW = the Eastern
and Western parts of the UK coasts.

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The three subunits have been hypothesized based on several lines of evidence: (1) the low connectivity induced by early life stages (i.e. larval advection towards the nearest nurseries and low movements of juveniles after settlement) and (2) the natural barriers with unsuitable habitats for the common sole, benthic after metamorphosis, such as rocky reefs (**Fig.1**) and a deep gravel covered central channel (Rochette et al., 2012; Archambault et al., 2016).

The null hypothesis (H0) considered the EEC as a single stock (i.e. the current assessment and management unit), while the alternative hypothesis (H1) assumed the stock to be partitioned into three subunits.

143

144 2.2. Gathering information obtained through population- and individual-based145 approaches

146 Five different approaches were developed recently to analyze potential structure in the EEC stock 147 of common sole (Table 1). Abundance-at-age throughout the cohorts and growth aimed at 148 estimating differences at the population scale. Individual-based approaches focused on the estimate 149 of individual movements or inter-individual differences in phenotypic and/or genotypic 150 characteristics. Based on the assumption that a well-mixed stock should present homogeneous 151 spatial patterns of demographic, genetic and phenotypic variables (Cadrin, 2020), population- and 152 individual-based approaches aimed at detecting spatial differences in these variables to reveal 153 population structure. Each approach had its own spatiotemporal scale (Table 1) so that synthetizing 154 results in a holistic approach allowed increasing the likelihood of detecting spatial structure and the

reliability of the assessment (Waldman, 1999; Abaunza *et al.*, 2008; Cadrin *et al.*, 2014; Tanner *et al.*,
2016).

157

**Table 1.** Reference studies dealing with the spatial stock structure of the common sole of the EEC
(ICES division VIId). Spatial and temporal scales represent the resolution of tracers. Temporal scales
in brackets represent the extent of the data used in each study.

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Focus	Type of tracer	Spatial scale	Temporal scale	Reference
Population-based	Abundance-at-age	VIId	Generational (1990-2015)	Randon <i>et al.</i> (2018)
approach	Growth			
Individual-based	Mark-recapture	VIId + VIIe +IVc	Individual lifespan (1970-2018)	Lecomte <i>et al.</i> (2020)
annroach	Genetics	VIId	Evolutionary (2017-2018)	Pandon et al. (2020)
	Otolith shape	VIId	Individual lifespan (2016-2018)	Kandon <i>et ul</i> . (2020)

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163

### 164 2.2.1. Population-based approaches

Analyzing spatiotemporal patterns of growth and abundance-at-age, Randon *et al.*, (2018) tested for a long-lasting signal (**Table 1**) of spatial structure inside the EEC stock of sole. They retrieved length-at-age data from the UK Beam Trawl Survey (UK-BTS) and estimated both von Bertalanffy growth parameters and synchrony (*i.e.* correlation) between trends in density-at-age throughout cohorts, to be used as structure markers (Begg *et al.*, 1999b; Cope and Punt, 2009; Erlandsson *et al.*, 2017; Walter *et al.*, 2017).

171 *Growth* 

Heterogeneous growth parameters across the stock suggested population structure (Randon *et al.*, 2018). The hypothesis of three subunits was supported (H1). In spite of congruent decreasing trends over the time series in each subunit, higher asymptotic length was found in the SW compared to the UK and NE subunits.

#### 176 Abundance-at-age

The asynchrony (i.e. different patterns) in density-at-age throughout the cohorts between subunits also evidenced spatial stock structure. High synchrony among time series was observed in the SW subunit, suggesting high spatiotemporal integrity inside this subunit and potential isolation from the rest of the EEC stock.

181 Combining analyses of growth and abundance-at-age over two decades, Randon *et al.* (2018) 182 highlighted a long-lasting signal of stock structure. This study of life history traits provided an 183 overview of stock structure over generations.

184

### 185 2.2.2. Individual-based approaches

#### 186 Mark-recapture

187 Investigation of post-larval dispersal was evaluated through a mark-recapture study covering the 188 three putative subunits of the EEC stock and the adjacent North Sea (ICES division IVc) and Western 189 English Channel (ICES division VIIe) stocks (Lecomte *et al.*, 2020). Adult connectivity was estimated 190 using a state-space mark-recovery model that integrated mark-recapture (i.e. external Petersen tag 191 disks; Latour, 2005) data from multiple release experiments over three decades (**Table 1**).

192 Results suggested very low movements of soles between the three subunits of the EEC and with 193 adjacent stocks, supporting the hypothesis of segregated subunits (H1) within the EEC. This markrecapture analysis at the scale of the fish lifespan over decades of experiments was not redundantwith previous population-based approaches.

#### 196 Genetics

Using up-to-date genetic markers (Single Nucleotide Polymorphism; SNPs), population structure was interrogated over an evolutionary time scale (Randon *et al.*,2020). Focusing on adult individuals on spawning grounds, this analysis aimed at understanding potential segregation across the stock. Spatial variations in genetic features were expected to reveal reproductive isolation.

Results indicated that genetic differentiation was low but significant between subunits within the EEC stock, reinforcing the hypothesis (H1) of stock structure of the common sole across the EEC. Information of stock structure was not redundant with information of life history traits or markrecapture studies since genetic analyses informed the stock genetic structure over the broader evolutionary time scale.

#### 206 Otolith shape

A large data set of otolith shape descriptors was investigated in order to test for potential spatial variations (Randon *et al.*,2020). Since the shape of the otolith results from a combination of ontogenetic (i.e. development stage), environmental and genetic factors (Cardinale *et al.*, 2004; Vignon, 2015), spatial differences may indicate population segregation and internal stock structure.

Shape indices were significantly different between subunits, particularly between the SW and NE subunits, detecting a signal of stock structure. Information was not redundant with life history trait, mark-recapture or genetic analyses since otolith shape variations translated a combination of environmental and/or genetic differentiation, integrated throughout the fish lifespan.

### 216 2.2.3. Stock Differentiation Index calculation

To integrate the previous findings on the EEC stock structure of common sole into a holistic approach (Kerr *et al.*, 2017), the Stock Differentiation Index (Welch *et al.*, 2015; Izzo *et al.*, 2017) was used to combine tracers in a synthetic manner regardless of their spatial and temporal resolutions (Begg and Waldman, 1999; Waldman, 1999). As mentioned above, information of the selected tracers were not redundant, therefore the calculation of SDI was not biased or amplified through redundancy.

The SDI is a semi-quantitative method that aims at underlying spatial structure inside a stock (Welch *et al.*, 2015). When a tracer reveals spatial differences between two subunits, a binary difference value DV = 1 is assigned to the pairwise comparison. However, when a tracer fails to detect spatial differences between two subunits, a binary difference value DV = 0 is assigned. Subsequently, pairwise SDI is calculated as:

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$$SDI = \sum DV / Count DV$$

229

where  $\sum DV$  corresponds to the sum of DVs for one pair of subunits and Count DV is the total 230 231 number of tracers used. The overall SDI (i.e. across the stock) measures the relative differences 232 among subunits. SDI ranges between 0 and 1, 0 indicating no spatial structure and 1 suggesting 233 maximal spatial differences between subunits. As suggested by Welch et al. (2015), the null 234 hypothesis (H0) has to be retained when the overall SDI = 0, even if there is no clear evidence of a 235 single stock. Thresholds have been defined (Izzo et al., 2017) to evaluate the strength of the spatial 236 segregation. SDI < 0.33 may indicate a weak spatial structure,  $0.33 \le$  SDI  $\le 0.66$  provides moderate 237 evidence of spatial structure and SDI > 0.66 would highlight strong evidence of stock spatial 238 structure.

Three pairwise comparisons among subunits were examined through pairwise SDI calculations (i.e. SW vs NE, SW vs UK and NE vs UK). The five tracers (**Table 1**) were weighted equally in the calculation of the SDI since they were not redundant.

242

# 243 3. Results

Pairwise SDI were calculated between each pair of subunits and provided strong evidence of spatial separation, particularly between the SW and the rest of the stock (**Table 2**). These highest values of SDI between the SW and the two other subunits were due to the differences found with the abundance-at-age analysis (cf. 2.2.1).

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Table 2. Difference values (DV) between pairs of subunits of the EEC regarding the five available
 tracers applied to the common sole.

		Tracers					
		Abundance	Growth	Mark-	Genetics	Otolith	Pairwise SDI
				recapture		shape	
Pairwise subunits	SW vs NE	1	1	1	1	1	1
	SW vs UK	1	1	1	1	1	1
	NE vs UK	0	1	1	1	1	0.8
		-	-	-	-	-	0.0

251

Finally, the overall SDI = 0.93 across the EEC stock of common sole indicated strong evidence of spatial structure (**Fig. 2**).

254

### 4. Discussion

This holistic approach filled the gap in the knowledge on the population structure of common sole stock of the EEC by focusing on sub-adult and adult stages. The present synthesis of available information on the EEC stock structure and the use of a semi-quantitative SDI provided evidence of spatial structure and isolation of subunits for the common sole of the EEC. These findings call for changes of the assessment-management process.

261

### 4.1. Mismatch between the common sole (meta)population and the EEC stock

263 No universal quantitative method exists to combine the results of population- and individual-264 based approaches despite the interest to pool their contrasted resolutions, from evolutionary to ecological scales. Here, the SDI calculation was used as a semi-quantitative holistic approach (Welch 265 266 et al., 2015; Izzo et al., 2017). Even though the SDI could be viewed as an inflexible method, it 267 presents the main advantages to be easily understood and to integrate various approaches into a 268 single framework. SDI is a simplification of the status of the stock structure because it does not 269 consider complex biological and ecological processes. However, the SDI is relevant to feed the 270 discussion between scientists and stakeholders.

The synergy of information from various tracers and the strength of the overall SDI (i.e. largely above the threshold of 0.66 fixed by Izzo *et al.*, 2017) highlighted a strong and long-lasting signal of spatial structure inside the common sole stock of the EEC (**Fig. 2**). Spatial structure was indeed found at the evolutionary (genetics; Randon et al., 2020), generational (population growth and abundances; Randon *et al.*, 2018) and individual lifespan (otolith shape and mark-recapture; Randon et al., 2020; Lecomte *et al.*, 2020) scales.

Therefore, based on previous studies and the overall SDI, the common sole population of the EEC has to be considered as a metapopulation. Moderate larval dispersal and nursery fidelity of juveniles act over relatively small distances (Riou *et al.*, 2001; Rochette *et al.*, 2012) and could have

contributed to shape a metapopulation. Moreover, the sub-adult and adult-mediated connectivity is
low, inducing a strong spatial structure inside the EEC stock. Considering the low connectivity
throughout the lifespan and natural barriers (e.g. rocky reefs, deep central Channel) for this benthic
flatfish species, the metapopulation structure made of three subunits appeared a realistic hypothesis
that must be considered in the stock assessment-management process.



Mismatch between population and stock unit?



Figure. 2. Overview of the holistic investigation of population structure of common sole inside the Eastern English Channel stock. Grey circles indicate that the tracer did not highlight differences between subunits.

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4.2. Practical consideration regarding alternative assessment and managementstrategies

As suggested by Kerr *et al.* (2017), after contributing to a synthetic view of the stock (e.g. through the SDI), the following steps consist of proposing alternative assessment and management options and evaluating their limitations. With regards to the metapopulation structure, different options could be proposed to improve the assessment and management of the stock.

297

### 298 4.2.1. Assessment of three independent subunits

The first option could be a change in stock unit boundaries by considering the three subunits as independent and assessing them separately. This option is probably not the simplest alternative to answer the issues of the misalignment (Kerr *et al.*, 2017; Cadrin, 2020) since it would imply a higher amount of work for stock assessment (i.e. three independent stock assessment). Moreover, the SW, NE and UK subunits have been found to form a metapopulation, which means that exchanges may occur between these components. Assessing each subunit separately would ignore the metapopulation functioning and may lead to an inappropriate stock assessment.

A possibly more realistic option might be the implementation of a spatially structured stock assessment (Cadrin and Secor, 2009; Berger *et al.*, 2017; Punt, 2019; Cadrin, 2020). Spatially explicit models incorporate population structure and connectivity information to reveal the outcomes of ignoring spatial structure (Kerr and Goethel, 2014; Goethel *et al.*, 2016). In other words, spatially explicit models analyze how detrimental it would be to ignore the existing stock spatial structure. By 311 incorporating data on spatial structure (e.g. tagging data), a spatial assessment improves the 312 estimates of biological reference points (Goethel and Berger, 2017), particularly when growth varies 313 spatially (Punt, 2019), which is the case in the EEC stock of common sole (Du Pontavice et al., 2018; 314 Randon et al., 2018). Despite unanimous appreciation of spatially explicit models to estimate the bias 315 in assessment when spatial structure is ignored, they are still not broadly adopted because they 316 require large data sets (the data must match with the new spatial resolution and thus, it might 317 increase cost of monitoring from both fishery-dependent and -independent data collection) to 318 provide unbiased estimates (Goethel et al., 2015). Furthermore, institutional inertia is probably the 319 most limiting point (Punt, 2019) and could explain that no spatially explicit models have been used to 320 manage stocks in North Atlantic fisheries, to date (Kerr et al., 2017). Indeed, changing the assessment 321 model would require the assessment working group to develop a new complex model that would be 322 fed by large and potentially new data sets. These limitations constitute institutional inertia and might 323 explain why, in most cases, the stock assessment process does not change. A Bayesian spatial 324 integrated life cycle model has explored the exploitation of the common sole of the EEC under a 325 three subunits hypothesis to assess the impact of stock structure on the estimates of reference 326 points and productivity (Archambault et al., 2016). Exploitation was far above MSY (Maximum 327 Sustainable Yield; F/F<sub>MSY</sub> = 1.8) considering a single well-mixed stock (H0), but with contrasted 328 patterns when considering three subunits; the NE and UK subunits exploited above MSY (i.e. F/F<sub>MSY</sub> = 329 2 and 1.9, respectively) and the SW subunit approaching full exploitation ( $F/F_{MSY} = 1.05$ ). Thus, 330 considering a metapopulation structure would undoubtedly help in providing unbiased estimates of 331 reference points for the stock of sole of the EEC. Although it would be relevant to modify the current 332 assessment model, other alternative strategies focusing on local management must be considered.

4.2.2. Assessment of one single stock and management of three subunits

Instead of considering the assessment of three distinct subunits, an alternative strategy might be to assess the stock as a single stock (i.e. the current practice) and to retrospectively adapt the management to local productivities.

This might be translated into adjusting the exploitation to the lowest productivity among the three subunits. In the EEC stock of common sole, productivities are contrasted with the SW subunit being the least productive and the NE subunit being the most productive one (Archambault *et al.*, 2016). This strategy would prevent the stock from being overharvested. Another option could be a spatial management of fishing effort to adapt the exploitation level to local productivities. Finally, an alternative option might be to allocate the quota relatively to local productivities (e.g., regarding the respective survey-based estimate of biomass in the subunits of the stock; Bosley *et al.*, 2019)

Therefore, local management strategies might be interesting and feasible options (Cadrin *et al.*, 2010; Wright *et al.*, 2019) and have to be evaluated relatively to the data and method requirements, but also social, economic and institutional limitations (Punt, 2019).

Quantitative evaluation of the outcomes of alternative management options should be performed through MSE (Management Strategy Evaluation). MSE is currently viewed as the state-of-the-art management decision-making since it evaluates both biological and economic consequences of a range of management strategies (Sainsbury *et al.*, 2000; Bunnefeld *et al.*, 2011; Kerr *et al.*, 2017). Evaluation of management options is an interface between biology/ecology, fishery and management and should therefore improve the assessment-management of the common sole of the EEC.

To conclude, this study argued for the integration of the common sole metapopulation structure into the EEC stock assessment process. A misalignment between the biological and the stock units was pinpointed by compiling all the available information on the population structure focusing on the adult stage. Different strategies might be considered for adapting the stock management and assessment. The biological and economic consequences of those strategies should be evaluatedthrough MSE prior to changing the current assessment and management process.

361

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# 370 References

- Abaunza, P., Murta, A. G., Campbell, N., Cimmaruta, R., Comesaña, A. S., Dahle, G., García
   Santamaría, M. T., *et al.* 2008. Stock identity of horse mackerel (*Trachurus trachurus*) in the
   Northeast Atlantic and Mediterranean Sea: Integrating the results from different stock
   identification approaches. Fisheries Research, 89: 196–209.
- Archambault, B., Le Pape, O., Baulier, L., Vermard, Y., Véron, M., and Rivot, E. 2016. Adult-mediated
   connectivity affects inferences on population dynamics and stock assessment of nursery dependent fish populations. Fisheries Research, 181: 198–213.
- Archambault, B., Rivot, E., Savina, M., and Le Pape, O. 2018. Using a spatially structured life cycle
   model to assess the influence of multiple stressors on an exploited coastal-nursery dependent population. Estuarine, Coastal and Shelf Science, 201: 95–104.

- Bailleul, D., Mackenzie, A., Sacchi, O., Poisson, F., Bierne, N., and Arnaud-Haond, S. 2018. Large-scale
  genetic panmixia in the blue shark (*Prionace glauca*): A single worldwide population, or a
  genetic lag-time effect of the "grey zone" of differentiation? Evolutionary Applications, 11:
  614–630.
- Begg, G. A., Friedland, K. D., and Pearce, J. B. 1999a. Stock identification and its role in stock
  assessment and fisheries management: an overview. Fisheries Research, 43: 1–8.
- Begg, G. A., and Waldman, J. R. 1999. An holistic approach to fish stock identification. Fisheries
  Research, 43: 35–44.
- Begg, G. A., Hare, J. A., and Sheehan, D. D. 1999b. The role of life history parameters as indicators of
  stock structure. Fisheries Research, 43: 141–163.
- Berger, A. M., Goethel, D. R., Lynch, P. D., Quinn, T., Mormede, S., McKenzie, J., and Dunn, A. 2017.
  Space oddity: The mission for spatial integration. Canadian Journal of Fisheries and Aquatic
  Sciences, 74: 1698–1716.
- Bosley, K. M., Goethel, D. R., Berger, A. M., Deroba, J. J., Fenske, K. H., Hanselman, D. H., Langseth, B.
- J., *et al.* 2019. Overcoming challenges of harvest quota allocation in spatially structured
   populations. Fisheries Research, 220: 105344.
- Bunnefeld, N., Hoshino, E., and Milner-Gulland, E. J. 2011. Management strategy evaluation: a
   powerful tool for conservation? Trends in Ecology & Evolution, 26: 441–447.
- Cadrin, S. X., and Secor, D. H. 2009. Accounting for Spatial Population Structure in Stock Assessment:
  Past, Present, and Future. *In* The Future of Fisheries Science in North America, pp. 405–426.
  Ed. by R. J. Beamish and B. J. Rothschild. Springer Netherlands.
- 402 Cadrin, S. X., Bernreuther, M., Daníelsdóttir, A. K., Hjörleifsson, E., Johansen, T., Kerr, L., Kristinsson,
- 403 K., *et al.* 2010. Population structure of beaked redfish, *Sebastes mentella*: evidence of 404 divergence associated with different habitats. ICES Journal of Marine Science, 67: 1617–
- 405 1630.

- Cadrin, S. X., Kerr, L. A., and Mariani, S. 2013. Stock Identification Methods: Applications in Fishery
  Science. Academic Press. 589 pp.
- Cadrin, S. X., Kerr, L. A., and Mariani, S. 2014. Chapter Twenty Two Interdisciplinary Evaluation of
  Spatial Population Structure for Definition of Fishery Management Units. *In* Stock
  Identification Methods (Second Edition), pp. 535–552. Ed. by S. X. Cadrin, L. A. Kerr, and S.
  Mariani. Academic Press, San Diego.
- 412 Cadrin, S. X. 2020. Defining spatial structure for fishery stock assessment. Fisheries Research, 221:
  413 105397.
- Cardinale, M., Doering-Arjes, P., Kastowsky, M., and Mosegaard, H. 2004. Effects of sex, stock, and
   environment on the shape of known-age Atlantic cod (*Gadus morhua*) otoliths. Canadian
   Journal of Fisheries and Aquatic Sciences, 61: 158–167.
- Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., and Largier, J. L. 2003. Comparing
   Marine and Terrestrial Ecosystems: Implications for the Design of Coastal Marine Reserves.
   Ecological Applications, 13: 90–107.
- Ciannelli, L., Fisher, J. A. D., SkernMauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., and
  Bailey, K. M. 2013. Theory, consequences and evidence of eroding population spatial
  structure in harvested marine fishes: a review. Marine Ecology Progress Series, 480: 227–
  243.
- 424 Cope, J. M., and Punt, A. E. 2009. Drawing the lines: resolving fishery management units with simple
  425 fisheries data. Canadian Journal of Fisheries and Aquatic Sciences, 66: 1256–1273.
- 426 Costello, M. J., and Connor, D. W. 2019. Connectivity Is Generally Not Important for Marine Reserve
  427 Planning. Trends in Ecology & Evolution, 34: 686–688.
- 428 Diopere, E., Vandamme, S. G., Hablützel, P. I., Cariani, A., Van Houdt, J., Rijnsdorp, A., Tinti, F., et al.
- 429 2017. Seascape genetics of a flatfish reveals local selection under high levels of gene flow.430 ICES Journal of Marine Science.

Du Pontavice, H., Randon, M., Lehuta, S., Vermard, Y., and Savina-Rolland, M. 2018. Investigating
 spatial heterogeneity of von Bertalanffy growth parameters to inform the stock structuration
 of common sole, *Solea solea*, in the Eastern English Channel. Fisheries Research, 207: 28–36.

Erlandsson, J., Östman, Ö., Florin, A.-B., and Pekcan-Hekim, Z. 2017. Spatial structure of body size of
European flounder (*Platichthys flesus* L.) in the Baltic Sea. Fisheries Research, 189: 1–9.

Frisk, M. G., Jordaan, A., and Miller, T. J. 2014. Moving beyond the current paradigm in marine
population connectivity: are adults the missing link? Fish and Fisheries, 15: 242–254.

Fu, C., and Fanning, L. P. 2004. Spatial Considerations in the Management of Atlantic Cod off Nova
 Scotia, Canada. North American Journal of Fisheries Management, 24: 775–784.

Gingerich, P. D. 2019. Evolutionary Time. *In* Rates of Evolution: A Quantitative Synthesis, Cambridge:
Cambridge University Press, pp. 53–63.

Goethel, D. R., Legault, C. M., Cadrin, S. X., and Wilberg, M. 2015. Testing the performance of a
spatially explicit tag-integrated stock assessment model of yellowtail flounder (*Limanda ferruginea*) through simulation analysis. Canadian Journal of Fisheries and Aquatic Sciences,
72: 582–601.

Goethel, D. R., Kerr, L. A., and Cadrin, S. X. 2016. Incorporating spatial population structure into the
assessment-management interface of marine resources. Management science in fisheries: an
introduction to simulation based methods. Edited by CTT Edwards and DJ Dankel. Routledge,
New York: 319–347.

Goethel, D. R., and Berger, A. M. 2017. Accounting for spatial complexities in the calculation of
 biological reference points: effects of misdiagnosing population structure for stock status
 indicators. Canadian Journal of Fisheries and Aquatic Sciences, 74: 1878–1894.

Hawkins, S. J., Bohn, K., Sims, D. W., Ribeiro, P., Faria, J., Presa, P., Pita, A., *et al.* 2016. Fisheries
stocks from an ecological perspective: Disentangling ecological connectivity from genetic
interchange. Fisheries Research, 179: 333–341.

- 456 ICES. 2017a. Report of the Benchmark Workshop on the North Sea stocks (WKNSEA). ICES CM
  457 2017/ACOM:34. Copenhagen, Denmark.
- 458 ICES. 2017b. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea
  459 and Skagerrak. ICES HQ. ICES CM 2017/ACOM:21.
- 460 ICES. 2019. ICES WGNSSK Report Sole in Division7d (Eastern English Channel).
- 461 Ihssen, P. E., Booke, H. E., Casselman, J. M., McGlade, J. M., Payne, N. R., and Utter, F. M. 1981. Stock
  462 Identification: Materials and Methods. Canadian Journal of Fisheries and Aquatic Sciences,
  463 38: 1838–1855.
- Izzo, C., Ward, T. M., Ivey, A. R., Suthers, I. M., Stewart, J., Sexton, S. C., and Gillanders, B. M. 2017.
   Integrated approach to determining stock structure: implications for fisheries management
   of sardine, *Sardinops sagax*, in Australian waters. Reviews in Fish Biology and Fisheries, 27:
- 467 267–284.
- Kerr, L. A., and Goethel, D. R. 2014. Simulation Modeling as a Tool for Synthesis of Stock
  Identification Information. *In* Stock Identification Methods, pp. 501–533. Elsevier.

470 Kerr, L. A., Hintzen, N. T., Cadrin, S. X., Clausen, L. W., Dickey-Collas, M., Goethel, D. R., Hatfield, E. M.

- 471 C., et al. 2017. Lessons learned from practical approaches to reconcile mismatches between
- biological population structure and stock units of marine fish. ICES Journal of Marine Science,
  74: 1708–1722.
- 474 Kritzer, J. P., and Sale, P. F. 2010. Marine Metapopulations. Academic Press. 573 pp.
- 475 Latour, R. J. 2005. Chapter 4. Tagging methods and associated data analysis. *In* Management
  476 techniques for elasmobranch fisheries, pp. 45–61. Academic Press, Burlington.
- 477 Lecomte, J.-B., Le Pape, O., Baillif, H., Nevoux, M., Vermard, Y., Savina-Rolland, M., Veron, M., et al.
- 478 2020. State-space modeling of multi-decadal mark-recapture data reveals low adult dispersal
- 479 in a nursery-dependent fish metapopulation. Canadian Journal of Fisheries and Aquatic480 Sciences.

- 481 Link, J. S., Nye, J. A., and Hare, J. A. 2010. Guidelines for incorporating fish distribution shifts into a
  482 fisheries management context. Fish and Fisheries, 12: 461–469.
- Mahé, K., Oudard, C., Mille, T., Keating, J., Gonçalves, P., Clausen, L. W., Petursdottir, G., *et al.* 2016.
  Identifying blue whiting (*Micromesistius poutassou*) stock structure in the Northeast Atlantic
  by otolith shape analysis. Canadian Journal of Fisheries and Aquatic Sciences, 73: 1363–1371.
- 486 Mullon, C., Cury, P., and Penven, P. 2002. Evolutionary individual-based model for the recruitment of 487 anchovy (*Engraulis capensis*) in the southern Benguela. Canadian Journal of Fisheries and
- 488 Aquatic Sciences, 59: 910–922.
- Orensanz, J. L., and Jamieson, G. S. 1998. The assessment and management of spatially. *In* Proceedings of the North Pacific symposium on invertebrate stock assessment and
   management, p. 441. NRC Research Press.
- 492 Parrish, J. 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions.
  493 Marine Ecology Progress Series, 58: 143–160.
- Pita, A., Casey, J., Hawkins, S. J., Villarreal, M. R., Gutiérrez, M.-J., Cabral, H., Carocci, F., *et al.* 2016.
  Conceptual and practical advances in fish stock delineation. Fisheries Research, 173, Part 3:
  185–193.
- 497 Punt, A. E. 2019. Spatial stock assessment methods: A viewpoint on current issues and assumptions.
  498 Fisheries Research, 213: 132–143.
- Randon, M., Réveillac, E. & Le Pape, O. Complementarity and discriminatory power of genotype and
  otolith shape in describing the fine-scale population structure of an exploited fish, the
  common sole of the Eastern English Channel. *Submitted to PlosOne in August 2020*.
- Randon, M., Réveillac, E., Rivot, E., Du Pontavice, H., and Le Pape, O. 2018. Could we consider a single
   stock when spatial sub-units present lasting patterns in growth and asynchrony in cohort
- 504 densities? A flatfish case study. Journal of Sea Research, 142: 91–100.

- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine
  fish: mismatch between biological and fisheries management units. Fish and Fisheries, 10:
  361–395.
- Riou, P., Le Pape, O., and Rogers, S. I. 2001. Relative contributions of different sole and plaice
  nurseries to the adult population in the Eastern Channel: application of a combined method
  using generalized linear models and a geographic information system. Aquatic living
  resources, 14: 125–135.
- Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. 2010. Effect of nursery
  habitat degradation on flatfish population: Application to *Solea solea* in the Eastern Channel
  (Western Europe). Journal of Sea Research, 64: 34–44.
- Rochette, S., Huret, M., Rivot, E., and Le Pape, O. 2012. Coupling hydrodynamic and individual-based
   models to simulate long-term larval supply to coastal nursery areas: Modelling larval supply
   to coastal nurseries. Fisheries Oceanography, 21: 229–242.
- Rochette, S., Le Pape, O., Vigneau, J., and Rivot, E. 2013. A hierarchical Bayesian model for
  embedding larval drift and habitat models in integrated life cycles for exploited fish.
  Ecological Applications, 23: 1659–1676.
- 521 Sainsbury, K. J., Punt, A. E., and Smith, A. D. M. 2000. Design of operational management strategies 522 for achieving fishery ecosystem objectives. ICES Journal of Marine Science, 57: 731–741.
- 523 Secor, D. H. 2015. Migration Ecology of Marine Fishes. JHU Press. 305 pp.
- Smedbol, R. K., and Wroblewski, J. S. 2002. Metapopulation theory and northern cod population
   structure: interdependency of subpopulations in recovery of a groundfish population.
   Fisheries Research, 55: 161–174.
- 527 Stephenson, R. L. 2002. Stock structure and management structure: an ongoing challenge for ICES. *In* 528 ICES Marine Science Symposia, pp. 305–314.
- Tanner, S. E., Reis-Santos, P., and Cabral, H. N. 2016. Otolith chemistry in stock delineation: A brief
   overview, current challenges and future prospects. Fisheries Research, 173: 206–213.

- Vignon, M. 2015. Disentangling and quantifying sources of otolith shape variation across multiple
   scales using a new hierarchical partitioning approach. Marine Ecology Progress Series, 534:
   163–177.
- Waldman, J. R. 1999. The importance of comparative studies in stock analysis. Fisheries Research, 43:
  237–246.
- Walter, J. A., Sheppard, L. W., Anderson, T. L., Kastens, J. H., Bjørnstad, O. N., Liebhold, A. M., and
  Reuman, D. C. 2017. The geography of spatial synchrony. Ecology Letters, 20: 801–814.
- Waples, R. S., and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic
  methods for identifying the number of gene pools and their degree of connectivity: WHAT IS
  A POPULATION? Molecular Ecology, 15: 1419–1439.
- 541 Welch, D. J., Newman, S. J., Buckworth, R. C., Ovenden, J. R., Broderick, D., Lester, R. J. G., Gribble, N.
- 542 A., *et al.* 2015. Integrating different approaches in the definition of biological stocks: A 543 northern Australian multi-jurisdictional fisheries example using grey mackerel, 544 *Scomberomorus semifasciatus*. Marine Policy, 55: 73–80.
- Wright, P. J., Christensen, A., Régnier, T., Rindorf, A., and van Deurs, M. 2019. Integrating the scale of
   population processes into fisheries management, as illustrated in the sandeel, *Ammodytes marinus*. ICES Journal of Marine Science.
- 548Zemeckis, D. R., Martins, D., Kerr, L. A., and Cadrin, S. X. 2014. Stock identification of Atlantic cod549(Gadus morhua) in US waters: an interdisciplinary approach. ICES Journal of Marine Science,

551

550

71: 1490–1506.