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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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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 VIIId) 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
26 (2) combining this information in a semi-quantitative framework, i.e. the Stock Differentiation Index
27 (SDI). Regarding the population-based approaches, growth and abundance-at-age analyses
28 highlighted a lasting signal of population structure, with three population subunits. Regarding the
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.*,
49 2019). However, the stock delineation is frequently unclear (Cadrin *et al.*, 2010; Zemeckis *et al.*,
50 2014; Mahé *et al.*, 2016), inducing a misalignment between the stock and the biological population
51 (Hawkins *et al.*, 2016; Kerr *et al.*, 2017). In the early 2000's, around 50 out of about 150 stocks were
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
57 ("Counting fish is like counting trees except you can't see them and they move"; John Sheperd).
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
64 and Wroblewski, 2002; Abaunza *et al.*, 2008; Cadrin *et al.*, 2010). [Between those two situations,](#)
65 [metapopulation](#) (i.e. a set of subpopulations connected by dispersal; Kritzer and Sale, 2010) [may](#)
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
69 populations (Link *et al.*, 2010). Uncertainties regarding the spatial scope of stocks and populations
70 thus arise from multiple factors that need to be considered in stock assessment and management.

71 Challenging such issues, Kerr *et al.* (2017) evidenced the need for adapting fisheries exploitation
72 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
94 underlying population (ICES, 2017a). The EEC stock of common sole was found to be genetically
95 distinct from the adjacent Western English Channel (ICES division VIle) 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
115 Differentiation Index (SDI; Welch *et al.*, 2015; Izzo *et al.*, 2017), was applied to collate in a holistic
116 approach (Kerr *et al.*, 2017) the various population- and individual-based analyses that previously
117 provided information on the stock structure.

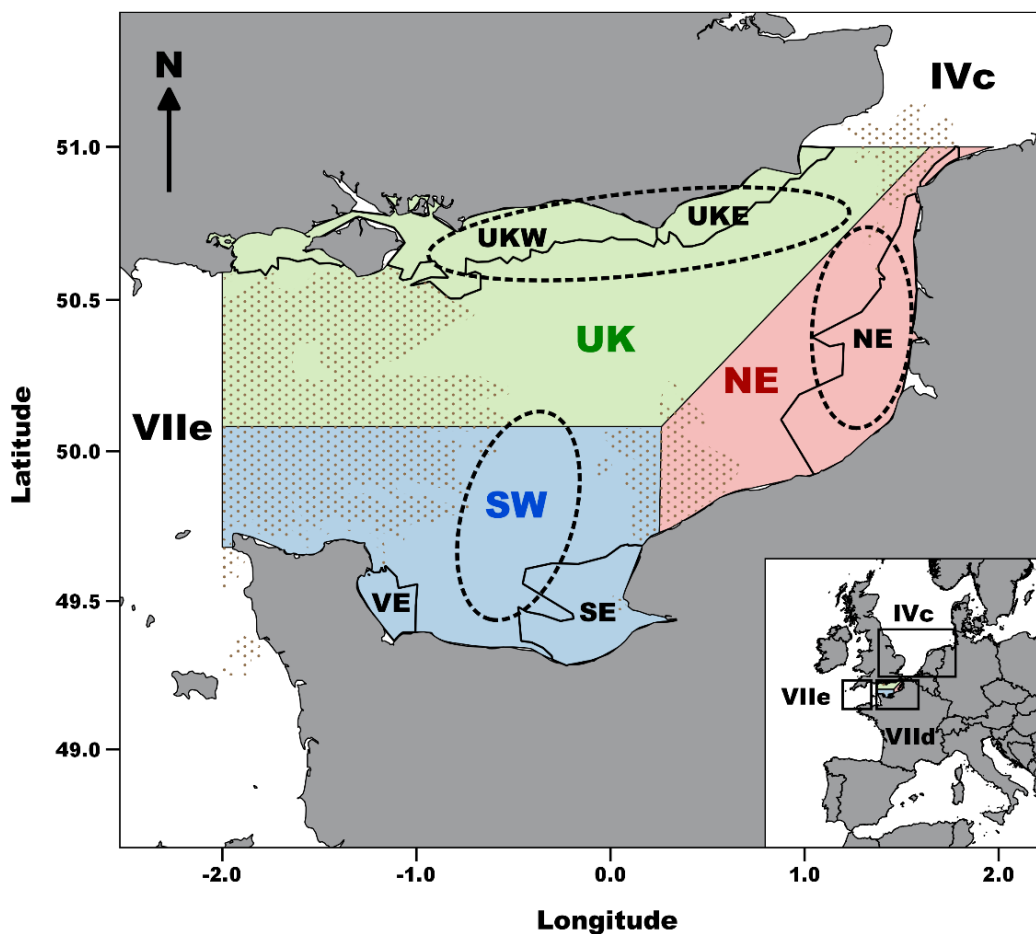
118

119 2. Material and methods

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

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

127



128

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

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

134

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

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

143

144 2.2. Gathering information obtained through population- and individual-based 145 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 synthesizing
154 results in a holistic approach allowed increasing the likelihood of detecting spatial structure and the

155 reliability of the assessment (Waldman, 1999; Abaunza *et al.*, 2008; Cadrin *et al.*, 2014; Tanner *et al.*,
 156 2016).

157

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

161

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

162

163

164 2.2.1. Population-based approaches

165 Analyzing spatiotemporal patterns of growth and abundance-at-age, Randon *et al.*, (2018) tested
 166 for a long-lasting signal (**Table 1**) of spatial structure inside the EEC stock of sole. They retrieved
 167 length-at-age data from the UK Beam Trawl Survey (UK-BTS) and estimated both von Bertalanffy
 168 growth parameters and synchrony (*i.e.* correlation) between trends in density-at-age throughout
 169 cohorts, to be used as structure markers (Begg *et al.*, 1999b; Cope and Punt, 2009; Erlandsson *et al.*,
 170 2017; Walter *et al.*, 2017).

171 **Growth**

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

176 ***Abundance-at-age***

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

194 recapture analysis at the scale of the fish lifespan over decades of experiments was not redundant
195 with previous population-based approaches.

196 **Genetics**

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

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

206 **Otolith shape**

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

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

215

216 2.2.3. Stock Differentiation Index calculation

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

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

$$228 \quad \quad \quad \mathbf{SDI = \sum DV / Count DV}$$

229
230 where $\sum DV$ corresponds to the sum of DVs for one pair of subunits and $Count DV$ is the total
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 (H_0) 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, $0.33 \leq SDI \leq 0.66$ provides moderate
237 evidence of spatial structure and $SDI > 0.66$ would highlight strong evidence of stock spatial
238 structure.

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

242

243 3. Results

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

248

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

		Tracers					Pairwise SDI
		Abundance	Growth	Mark-recapture	Genetics	Otolith 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

251

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

254

255 4. Discussion

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

261

262 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
265 ecological scales. Here, the SDI calculation was used as a semi-quantitative holistic approach (Welch
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.

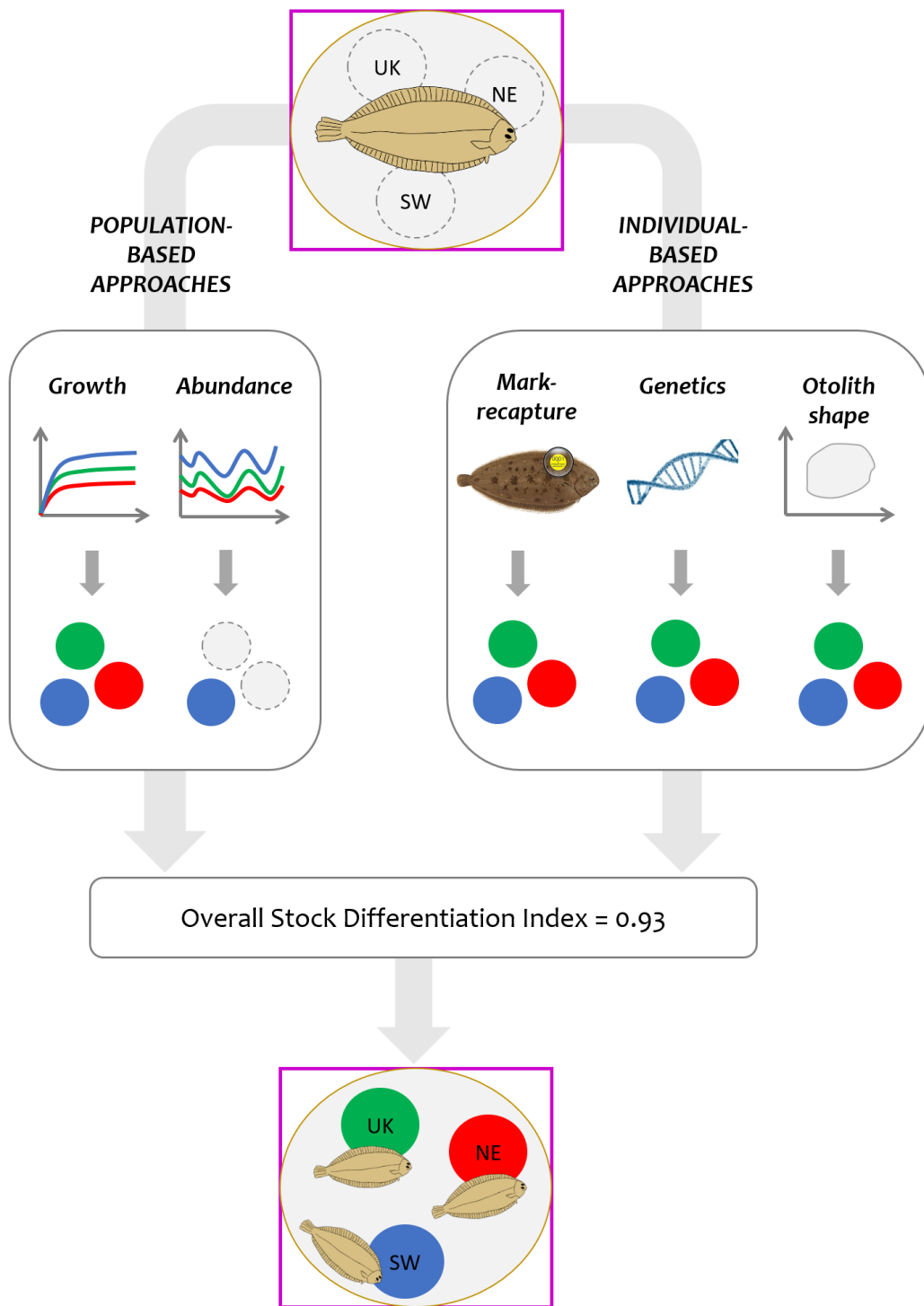
271 The synergy of information from various tracers and the strength of the overall SDI (i.e. largely
272 above the threshold of 0.66 fixed by Izzo *et al.*, 2017) highlighted a strong and long-lasting signal of
273 spatial structure inside the common sole stock of the EEC (**Fig. 2**). Spatial structure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

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

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

285

Mismatch between **population** and **stock unit**?



Yes – Three **subpopulations** inside the **stock unit**

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

290

291 4.2. Practical consideration regarding alternative assessment and management 292 strategies

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

297

298 4.2.1. Assessment of three independent subunits

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

306 A **possibly** more realistic option might be the implementation of a spatially structured stock
307 assessment (Cadrin and Secor, 2009; Berger *et al.*, 2017; Punt, 2019; Cadrin, 2020). Spatially explicit
308 models incorporate population structure and connectivity information to reveal the outcomes of
309 ignoring spatial structure (Kerr and Goethel, 2014; Goethel *et al.*, 2016). In other words, spatially
310 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; $F/F_{MSY} = 1.8$) considering a single well-mixed stock (H_0), but with contrasted
328 patterns when considering three subunits; the NE and UK subunits exploited above MSY (i.e. $F/F_{MSY} =$
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.

333

334 4.2.2. Assessment of one single stock and management of three subunits

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

338 This might be translated into adjusting the exploitation to the lowest productivity among the
339 three subunits. In the EEC stock of common sole, productivities are contrasted with the SW subunit
340 being the least productive and the NE subunit being the most productive one (Archambault *et al.*,
341 2016). This strategy would prevent the stock from being overharvested. Another option could be a
342 spatial management of fishing effort to adapt the exploitation level to local productivities. Finally, an
343 alternative option might be to allocate the quota relatively to local productivities (e.g., regarding the
344 respective survey-based estimate of biomass in the subunits of the stock; Bosley *et al.*, 2019)

345 Therefore, local management strategies might be interesting and feasible options (Cadrin *et al.*,
346 2010; Wright *et al.*, 2019) and have to be evaluated relatively to the data and method requirements,
347 but also social, economic and institutional limitations (Punt, 2019).

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

355 To conclude, this study argued for the integration of the common sole metapopulation structure
356 into the EEC stock assessment process. A misalignment between the biological and the stock units
357 was pinpointed by compiling all the available information on the population structure focusing on
358 the adult stage. Different strategies might be considered for adapting the stock management and

359 assessment. The biological and economic consequences of those strategies should be evaluated
360 through MSE prior to changing the current assessment and management process.

361

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369

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