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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 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 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 (SDI). Regarding the population-based approaches, growth and abundance-at-age analyses highlighted a lasting signal of population structure, with three population subunits. Regarding the individual-based approaches, genetic analysis highlighted low but significant genetic differentiation between the three subunits over an evolutionary time scale. Besides, a mark-recapture study demonstrated a low level of exchange between these subunits. Finally, an analysis of otolith shape pinpointed spatial variation between the three subunits. Overall, the SDI = 0.93 suggested evidence of spatial structure. The misalignment of the current stock definition with the underlying biological metapopulation now requires the improvement of the assessment-management to ensure its sustainable exploitation.

Keywords

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

1. Introduction

Despite the stock concept is being central to fisheries science, several definitions could be adopted, depending on the scientific question and methods used (Begg *et al.*, 1999a; Abaunza *et al.*, 2008; Cadrin, 2020). From a fisheries management perspective, the stock is basically defined as a working unit for assessment models and management decisions (Kerr *et al.*, 2017; Cadrin, 2020). Ihssen *et al.* (1981) defined the stock as a monospecific group of individuals mating randomly to display spatiotemporal group integrity. The stock spatial unit is supposed to fit with the underlying biological population, stock assessment and management being provided at the population scale. Stock assessment models suppose that a population is closed and well mixed (Cadrin, 2020) and that 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.*, 2014; Mahé *et al.*, 2016), inducing a misalignment between the stock and the biological population (Hawkins *et al.*, 2016; Kerr *et al.*, 2017). In the early 2000's, around 50 out of about 150 stocks were misaligned with underlying populations (Stephenson, 2002). Such mismatches could lead to a "myopic view" of productivity across the stock (Orensanz and Jamieson, 1998), to biases in stock assessment (Archambault *et al.,* 2016) and to unsuitable exploitation of subunits having different productivity dynamics (Fu and Fanning, 2004; Cadrin and Secor, 2009; Goethel and Berger, 2017).

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). Marine connectivity is more complex to assess but is considered higher than in the terrestrial realm because the marine environment is more open (Carr *et al.*, 2003). Through the exchange of individuals that links populations (Secor, 2015), marine connectivity is involved in population structure (Parrish, 1989) at various spatial scales (Waples and Gaggiotti, 2006; Reiss *et al.*, 2009; Ciannelli *et al.*, 2013; Costello and Connor, 2019). Degrees of connectivity vary from panmixia (i.e. 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, metapopulation (i.e. a set of subpopulations connected by dispersal; Kritzer and Sale, 2010) may display a more or less consistent spatial structure (Waples and Gaggiotti, 2006). Moreover, the increasing habitat fragmentation and worldwide degradation and environmental shifts induced by 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 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 approaches are recommended to capture the prevailing stock structure (Welch *et al.*, 2015). To do so, the first step consists of gathering all available information of the stock identity into a holistic approach. The holistic understanding of population structure is currently considered as the best practice to draw robust conclusions regarding the stock structure (Begg and Waldman, 1999; Waldman, 1999; Abaunza *et al.*, 2008; Cadrin *et al.*, 2014). Indeed, population structure is induced by processes ranging from ecological to evolutionary time scales (i.e. time scales over which the ecological or genetic process happen; Gingerich, 2019). Bringing together spatial variations in phenotypic and genetic characteristics can help to elucidate the stock identity (Cadrin and Secor, 2009; Cadrin *et al.*, 2014). Moreover, combining different methods allows increasing the likelihood of identifying the "true" population structure since one tracer can detect a signal where another fails to do so (Begg and Waldman, 1999; Abaunza *et al.*, 2008; Zemeckis *et al.*, 2014; Pita *et al.*, 2016). The identification of complex marine population structure and associated uncertainty found through a holistic approach (Kerr *et al.*, 2017) allows for further evaluation of the consequences of assessment and management strategies regarding biological, economic and social purposes.

The common sole (*Solea solea*) of the Eastern English Channel (EEC; ICES division VIId; **Fig.1**), a substantively harvested flatfish species, has been overexploited over the last decades and is managed as a unique homogeneous population (ICES, 2017b, 2019). The drop in spawning biomass has led to a critical exploitation status over the last years. At the same time, a metapopulation structure of the EEC stock has been hypothesized (Rochette *et al.*, 2012), with potential consequences for stock dynamics and sustainable levels of exploitation (Archambault *et al.*, 2016, 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 distinct from the adjacent Western English Channel (ICES division VIIe) and the North Sea (ICES division IVc) stocks (**Fig.1**; Diopere *et al.*, 2018). However, misunderstanding regarding the internal EEC stock structure remained (Rochette *et al.*, 2013; Archambault *et al.*, 2016; ICES, 2019). Reproduction takes place in early spring on three distinct spawning grounds (**Fig.1**; Rochette *et al.*, 2012). After hatching, pelagic larvae drift passively towards shallow coastal and estuarine nursery grounds (**Fig.1**; Grioche, 1998; Rochette *et al.*, 2012) where individuals metamorphose and settle as juveniles for about 2.5 years before joining as mature soles spawning areas in deeper waters (Riou *et al.*, 2001; Rochette *et al.*, 2010). Larval and juvenile-induced connectivity between nurseries and spawning grounds are low at the scale of the EEC stock. Biophysical modelling highlighted that larvae are mostly advected towards the nearest nursery grounds (Rochette *et al.*, 2012). Then, juveniles display very moderate movements away from their nursery habitats and high sedentariness upon local nursery grounds (Riou *et al.*, 2001). However, the sub-adult (i.e. juveniles leaving their nurseries before the first reproduction) and adult-mediated connectivity are still poorly known despite of their potentially high importance in population structuring (Mullon *et al.*, 2002; Frisk *et al.*, 2014).

Focusing on sub-adult and adult stages, recent studies have investigated the structure of the EEC stock of sole using a large range of approaches, from population-based (abundances and growth; Randon *et al.*, 2018) to individual-based approaches (mark recapture; Lecomte *et al.*, 2020; genetics and otolith shape; Randon *et al.,*2020). The present study aims at (1) synthetizing all the available information regarding the stock structure and (2) discussing alternative assessment and management 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 approach (Kerr *et al.*, 2017) the various population- and individual-based analyses that previously provided information on the stock structure.

2. Material and methods

2.1. Current delineation of the Eastern English Channel stock of sole and the 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**).

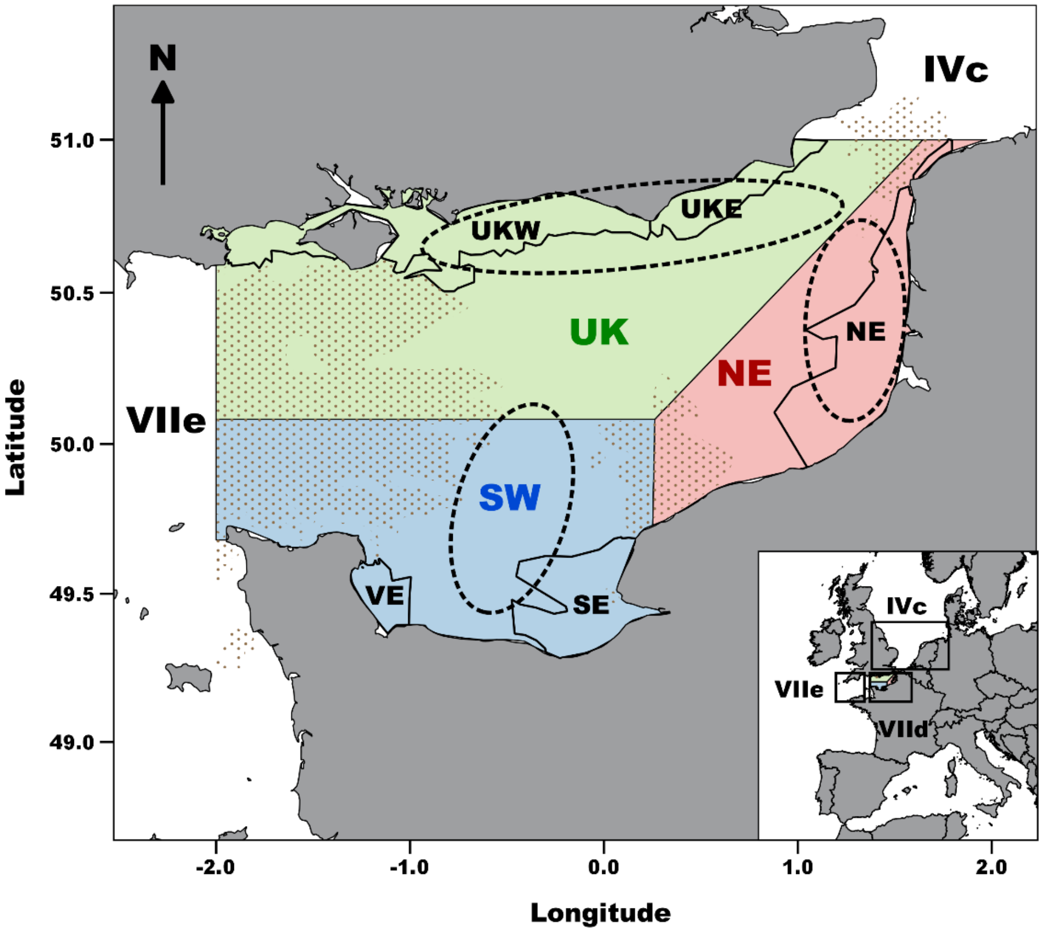


Figure. 1 Map of the EEC stock of common sole (ICES division VIId) and the three putative subunits (SW, NE and UK). Light grey dots represent rocky reefs. Coastal and estuarine nursery grounds (25 m

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.

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.

2.2. Gathering information obtained through population- and individual-based approaches

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

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.

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

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).

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.

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.

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

2.2.2. Individual-based approaches

Mark-recapture

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

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

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 mark-recapture studies since genetic analyses informed the stock genetic structure over the broader evolutionary time scale.

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.

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:

$$\boldsymbol{SDI = \sum DV \,/\, Count\ DV}$$

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

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).

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-recapture	Genetics	Otolith shape	Pairwise SDI
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

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

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.

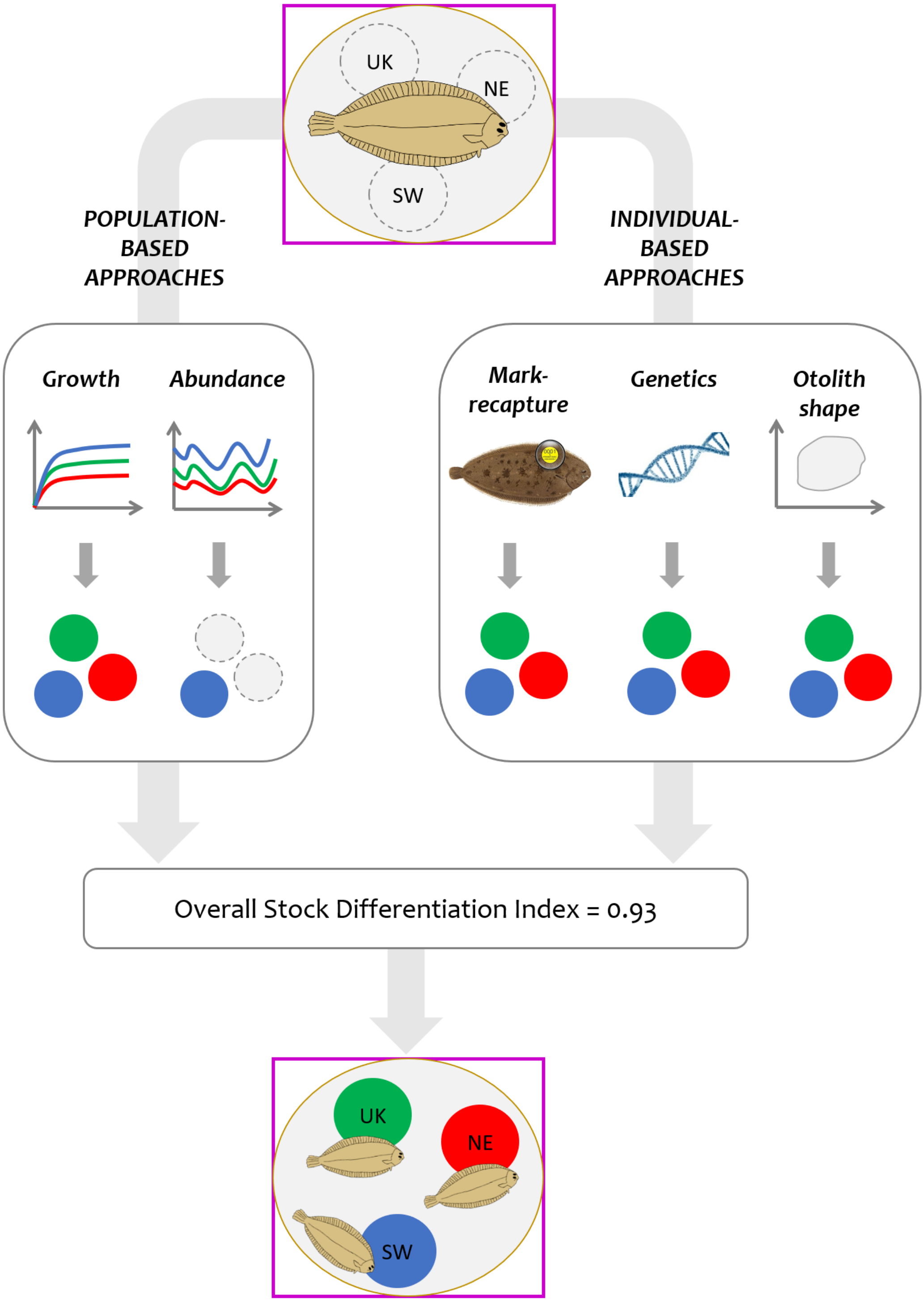
4.1. Mismatch between the common sole (meta)population and the EEC stock

No universal quantitative method exists to combine the results of population- and individual-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 *et al.*, 2015; Izzo *et al.*, 2017). Even though the SDI could be viewed as an inflexible method, it presents the main advantages to be easily understood and to integrate various approaches into a single framework. SDI is a simplification of the status of the stock structure because it does not consider complex biological and ecological processes. However, the SDI is relevant to feed the 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?



Yes – Three subpopulations inside the 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.

4.2. Practical consideration regarding alternative assessment and management strategies

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.

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 incorporating data on spatial structure (e.g. tagging data), a spatial assessment improves the estimates of biological reference points (Goethel and Berger, 2017), particularly when growth varies spatially (Punt, 2019), which is the case in the EEC stock of common sole (Du Pontavice *et al.*, 2018; Randon *et al.*, 2018). Despite unanimous appreciation of spatially explicit models to estimate the bias in assessment when spatial structure is ignored, they are still not broadly adopted because they require large data sets (the data must match with the new spatial resolution and thus, it might increase cost of monitoring from both fishery-dependent and -independent data collection) to provide unbiased estimates (Goethel *et al.*, 2015). Furthermore, institutional inertia is probably the most limiting point (Punt, 2019) and could explain that no spatially explicit models have been used to manage stocks in North Atlantic fisheries, to date (Kerr *et al.*, 2017). Indeed, changing the assessment model would require the assessment working group to develop a new complex model that would be fed by large and potentially new data sets. These limitations constitute institutional inertia and might explain why, in most cases, the stock assessment process does not change. A Bayesian spatial integrated life cycle model has explored the exploitation of the common sole of the EEC under a three subunits hypothesis to assess the impact of stock structure on the estimates of reference points and productivity (Archambault *et al.*, 2016). Exploitation was far above MSY (Maximum Sustainable Yield; F/F_{MSY} = 1.8) considering a single well-mixed stock (H0), but with contrasted patterns when considering three subunits; the NE and UK subunits exploited above MSY (i.e. F/F_{MSY} = 2 and 1.9, respectively) and the SW subunit approaching full exploitation (F/F_{MSY} = 1.05). Thus, considering a metapopulation structure would undoubtedly help in providing unbiased estimates of reference points for the stock of sole of the EEC. Although it would be relevant to modify the current 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 evaluated through MSE prior to changing the current assessment and management process.

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