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

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A B S T R A C T

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

1. Introduction

According to Ihssen et al. (1981), a stock is a monospecific group of individuals that randomly mate and displays spatiotemporal group integrity. Accurate delineation of stocks is a prerequisite for setting appropriate fisheries management measures (Kutkuhn, 1981; Smith et al., 1990; Begg et al., 1999a). However, the existence of population structure at different geographic scales and life stages is common (Waples and Gaggiotti, 2006; Reiss et al., 2009; Ames and Lichter, 2013; Ciannelli et al., 2013), and should be considered in stock assessments (Carson et al., 2011; Petitgas et al., 2013; Frisk et al., 2014). Inaccurate representation of the spatial structure of (meta-)population, e.g. by ignoring the existence of independent subunits, or of connectivity and exchanges with other stocks, biases estimates of population vital rates (i.e., growth, maturity and mortality) (Cadrin et al., 2013; Kerr et al., 2017). When the understanding of stock structure and delineation is limited (Cadrin et al., 2010; Zemeckis et al., 2014; Mahe et al., 2016), current practice assumes homogeneous vital rates without contrasts between putative subunits (Cadrin et al., 2013). This can induce a mismatch between the management unit and ecological connectivity (Hawkins et al., 2016; Kerr et al., 2017), resulting in the overexploitation of less productive subunits and underexploitation of more productive ones (Fu and Fanning, 2004; Cadrin and Secor, 2009; Ying et al., 2011; Goethel and Berger, 2017).

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

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

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

For decades, stock assessments of the common sole (*Solea solea*, L.), a commercial species of main interest (ICES, 2017b), have considered three independent stocks in the English Channel-North Sea Region: the North Sea (ICES division IVc), the Eastern English Channel (EEC; ICES division VIId) and the Western English Channel (ICES division VIIe) stocks (Fig. 1). This separation is in accordance with patterns of isolation by distance (Diopere et al., 2017). In the EEC, reproduction occurs in early spring on relatively coastal spawning grounds (Rochette et al., 2012). Once hatched, pelagic larvae drift for almost 2 months towards shallow estuarine and coastal nursery grounds (Grioche, 1998; Savina et al., 2010; Rochette et al., 2012). After metamorphosis, juveniles grow on these shallow nursery grounds for about two years before moving to deeper offshore adult foraging grounds (Riou et al., 2001; Rochette et al., 2010). Uncertainty remains regarding the spatial unity of the stock (Rochette et al., 2013; Archambault et al., 2016; ICES, 2017a). Larval connectivity is low since spawning areas directly feed adjacent coastal and estuarine nursery grounds (Rochette et al., 2012). Besides, very moderate movements of juvenile fish at small scales (< 10 km; Le Pape and Cognez, 2016) and their strong dependence upon local nursery habitats (Riou et al., 2001) result in low juvenile connectivity (Coggan and Dando, 1988). However, connectivity among subunits as a result of adult movement, a potentially important driver of population segregation (Mullon et al., 2002; Frisk et al., 2014) still remains partially unknown (Burt and Millner, 2008; Archambault et al., 2016). Based on several lines of evidence, three subunits of the stock appeared a realistic hypothesis in the EEC (Rochette et al., 2012; Archambault et al., 2016): the Bay of Seine (southwest subunit, SW), the Northern French coast (northeast subunit, NE) and the English coast (English subunit, UK) (Fig. 1). Natural barriers with unsuitable habitats for adult sole (i.e., large and deep gravel grounds in the middle of Eastern Channel, wide rocky reefs from shallow to deep areas; Rochette et al., 2012; Archambault et al., 2016) separate these subunits. Considering metapopulation dynamics among these potential subunits in the EEC would drastically change inferences on population dynamics and stock assessment (Archambault et al., 2016).

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

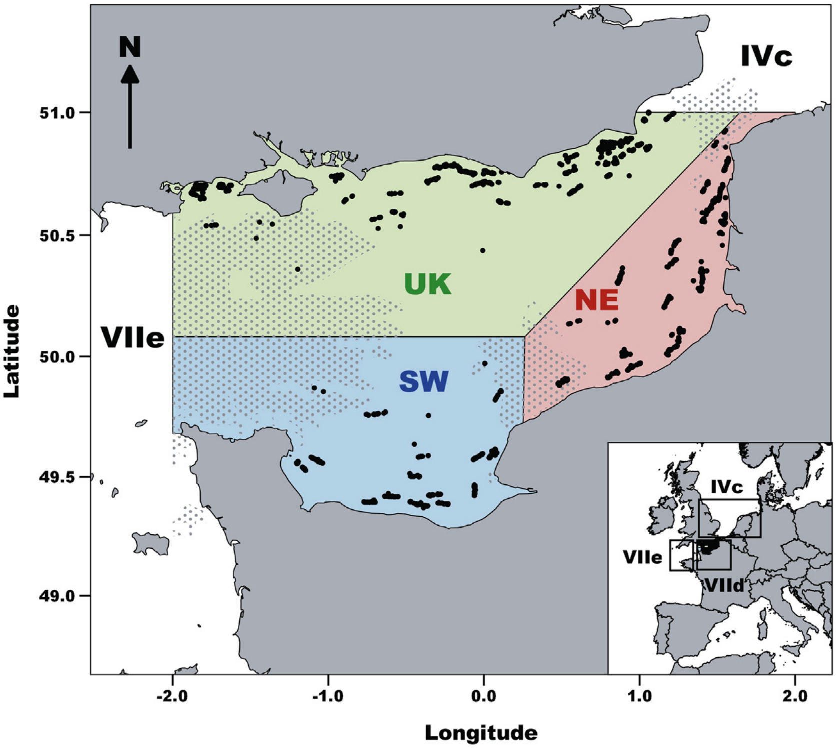

Fig. 1. Map of the Eastern English Channel common sole stock (ICES division VIId) including the three putative subunits tested for in this study (UK, NE and SW). Light grey dots indicate rocky reefs. Black dots correspond to the location of the UK-BTS sampling stations from 1989 to 2015.