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Invited feature

Using a spatially structured life cycle model to assess the influence of multiple stressors on an exploited coastal-nursery-dependent population

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ABSTRACT

Exploited coastal-nursery-dependent fish species are subject to various stressors occurring at specific stages of the life cycle: climate-driven variability in hydrography determines the success of the first eggs/larvae stages; coastal nursery habitat suitability controls juvenile growth and survival; and fisheries target mostly adults. A life cycle approach was used to quantify the relative influence of these stressors on the Eastern English Channel (EEC) population of the common sole (*Solea solea*), a coastal-nursery-dependent flatfish population which sustains important fisheries. The common sole has a complex life cycle: after eggs hatch, larvae spend several weeks drifting in open water. Survivors go on to metamorphose into benthic fish. Juveniles spend the first two years of their life in coastal and estuarine nurseries. Close to maturation, they migrate to deeper areas, where different subpopulations supplied by different nurseries reproduce and are exploited by fisheries. A spatially structured age-and stage-based hierarchical Bayesian model integrating various aspects of ecological knowledge, data sources and expert knowledge was built to quantitatively describe this complex life cycle. The model included the low connectivity among three subpopulations in the EEC, the influence of hydrographic variability, the availability of suitable juvenile habitat and fisheries. Scenarios were designed to quantify the effects of interacting stressors on population renewal. Results emphasized the importance of coastal nursery habitat availability and quality for the population renewal. Realistic restoration scenarios of the highly degraded Seine estuary produced a two-third increase in catch potential for the adjacent subpopulation. Fisheries, however, remained the main source of population depletion. Setting fishing mortality to the maximum sustainable yield led to substantial increases in biomass (+100%) and catch (+33%) at the EEC scale. The approach also showed how climate-driven variability in hydrography is likely to interact with human pressures, *e.g.*, overfishing increased the sensitivity to unfavourable conditions. Our results provided insights into the dynamics of numerous exploited coastal-nursery-dependent species while paving the way toward more robust advice for sustainable management of these resources.

1. Introduction

Marine fish populations are under the influence of multiple environmental and anthropogenic pressures (Halpern et al., 2008). Hydrographic variability (Lehodey et al., 2006), climate cycles (Francis et al., 1998) and long-term climate change (Brander, 2007) impact fish populations. The increasing concentration of human activities along coastal waters affects the quality of essential fish habitat (especially coastal and estuarine ecosystems; Halpern et al., 2008), through physical destruction and pollution (Beck et al., 2001; Peterson et al., 2003). Finally, fisheries (Christensen et al., 2003) affect populations through fishing mortality as well as indirect consequences, such as the reduction of genetic variability linked to selection pressure and the related demographic changes (Conover, 2007) and the perturbations of habitat structure (Turner et al., 1999). These stressors have their respective highest impact at different stages of the life cycle. Climate-driven hydrographic variability controls the success of eggs/larval development and

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survival (Bakun, 1996), *i.e.*, early stages recruitment success. Habitat availability and quality mostly impacts the critical growth and development phase of juveniles, especially for Coastal-Nursery-Dependent species (CND; *i.e.*, species for which nearshore habitat serves as a nursery for juveniles and contributes disproportionately to the size and numbers of adults relative to other juvenile habitats; Gibson, 1994; Beck et al., 2001). Fishing targets mostly adults (Hilborn, 2011).

Quantifying the impact of these stressors on population dynamics and renewal can offer insights on the ecology of populations needed to support sustainable management schemes. A considerable number of studies addressed the impact of each of these stressors individually. A large body of work has focused on the consequences of climate variability on early stages (review in Houde, 2008). The impact of habitat suitability on juveniles also has been well studied (Brown et al., 2000; Lindholm et al., 2001), especially for CND species (Beck et al., 2001; Vasconcelos et al., 2014). The assessment of fishing impacts on populations has driven the development of fisheries models in the last century (Beverton and Holt, 1957; Hilborn and Walters, 1992) and their wide use for stock assessment (Hilborn, 2011). However, life cycle approaches integrating impacts of these multiple stressors all along the life cycle remain rare. Also, less attention has been paid to the quantitative assessment of how the spatial structure of populations and patterns of connectivity along the life cycle interact with spatially structured stressors (Cianelli et al., 2013) such as coastal nursery habitat degradation (Rabalais, 2015) or spatially non-homogenous fishing effort.

The common sole (*Solea solea*, L.) population in the Eastern English Channel (EEC, Fig. 1) is an ideal case study (Riou et al., 2001) to quantitatively assess the relative influence of various stressors on fish population dynamics. In the EEC, pelagic larval stages successfully transported to coastal areas (Rochette et al., 2012) metamorphose and settle to the shallow-water demersal habitats of coastal and estuarine nursery grounds (Rochette et al., 2010) before moving to deeper areas when reaching adult stages oduce (Horwood, 1993). The low connectivity along the successive stages of the life cycle (*i.e.*, (i) larval retention within spawning regions (Rochette et al., 2012); (ii) spatial segregation of juveniles inside separated coastal and estuarine nursery grounds (Coggan and Dando, 1988; Riou et al., 2001); and (iii) limited individual movement at the adult stages (Kotthaus, 1963)) suggests a metapopulation structure with partial segregation of three

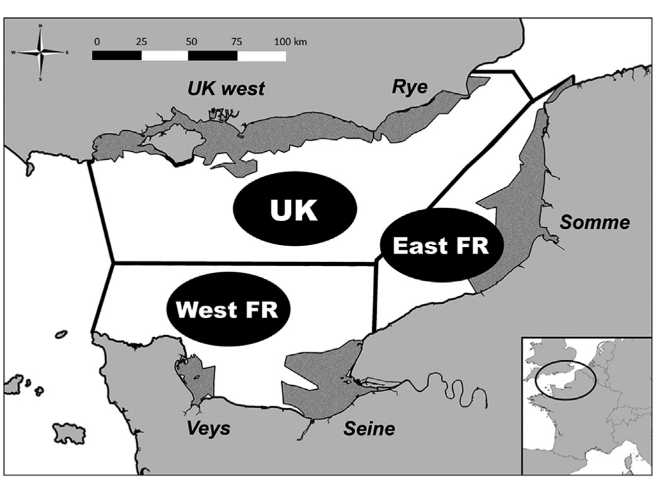

Fig. 1. Study area with the three components of the Eastern English Channel sole population (white text in black circles) and the five coastal and estuarine nursery sectors (coastal areas in dark greys with the adjacent related name in italic). In the bottom right corner: general location of the study area in Western Europe.

subpopulations (UK, East FR, and West FR; Fig. 1). Multiple pressures impact the life cycle in the EEC: climate-driven hydrographic variability on survival of pelagic eggs and larvae (Rochette et al., 2012); substantial habitat loss and degradation of the quality of remaining habitats in coastal and estuarine nursery grounds, especially in the Seine estuary (Le Pape et al., 2007; Rochette et al., 2010); high fishing mortality at adult stages (*i.e.*, higher than fishing mortality at Maximum Sustainable Yield; F_{MSY}; ICES, 2013). Based on the modelling framework developed by Rochette et al. (2013), Archambault et al. (in review) have built an integrated spatially structured life cycle model for this population in a Bayesian hierarchical modelling framework (Parent and Rivot, 2012), which proved successful in integrating ecological knowledge, heterogeneous sources of data and expert information. In this present work, the model structure and parameterization proposed by Archambault et al. (in review) was used to run simulations based on scenarios designed to assess the relative influence of the different stressors (*i.e.*, hydrographic variability; quantity/quality of nursery habitat; fisheries exploitation) on the survival during the life cycle and the productivity of the population. This study not only evaluated the respective impact of each of these stressors on the life cycle but also examined their possible interactions. Because no consistent data exist to quantify adult-mediated connectivity (Archambault et al., in review), the model was also used to qualitatively assess how the patterns of adult connectivity among the three subpopulations may interact with the influence of the different stressors.

2. Materials and methods

2.1. Operating model for the population dynamics

The spatial structure of the EEC sole populations (Fig. 1) was based on the three subpopulations previously identified (UK, East FR and West FR; Archambault et al., in review). Five coastal and estuarine nursery grounds, each associated with one of the three subpopulations (Veys and Seine in West FR, UK West and Rye in UK, Somme in East FR; Fig. 1) were considered. The life cycle model was based on an extensive data set presented in detail by Archambault et al. (in review) which included: (i) the outputs of a biophysical larval drift model which provided annual egg and larval survival and allocation from spawning areas to the five nursery sectors; (ii) annual juvenile (ages 0 and 1) abundance indices over the five nursery sectors; (iii) annual catch-at age and abundance indices from the ICES stock assessment working groups, also defined at the scale of the three subpopulations using ancillary data. The main processes and key parameters of the life cycle are given in the following model structure (Fig. 2, with matching numbering). All parameters were derived from the Bayesian fitting procedure developed by Archambault et al. (in review).

(1) Each year (subscript y from 1982 to 2007), eggs and larvae were transported from each of the three spawning areas (subscript r from 1 to 3) and eventually died or settled in one of the 5 identified nursery sectors (subscript i from 1 to 5). The probability for an egg from an egg pool $\omega_{y,r}$ to reach a nursery i was given by an allocation and survival matrix $Key_{y,r,i}$. Values of the allocation and survival matrix were sampled in a time series of 26 years (1982–2007) available from previous work (Rochette et al. (2012), upgraded by Savina et al., in press). The number of larvae L reaching a given nursery sector at year y was calculated from Eq. (1):

$$L_{y,i} = \sum_{r} \omega_{y,r} \times Key_{y,r,i} \quad (1)$$