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Sole larval supply to coastal nurseries: Interannual variability and connectivity at interregional and interpopulation scales

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ABSTRACT

Simulating fish larval drift helps assess the sensitivity of recruitment variability to early life history. An individual-based model (IBM) coupled to a hydrodynamic model was used to simulate common sole larval supply from spawning areas to coastal and estuarine nursery grounds at the meta-population scale (4 assessed stocks), from the southern North Sea to the Bay of Biscay (Western Europe) on a 26-yr time series, from 1982 to 2007. The IBM allowed each particle released to be transported by currents, to grow depending on temperature, to migrate vertically depending on development stage, to die along pelagic stages or to settle on a nursery, representing the life history from spawning to metamorphosis. The model outputs were analysed to explore interannual patterns in the amounts of settled sole larvae at the population scale; they suggested: (i) a low connectivity between populations at the larval stage, (ii) a moderate influence of interannual variation in the spawning biomass, (iii) dramatic consequences of life history on the abundance of settling larvae and (iv) the effects of climate variability on the inter-annual variability of the larvae settlement success.

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1. Introduction

A majority of marine fish species produce a high number of eggs with a low and variable probability of survival, i.e., survival rates close to 1/1000 from spawning to the end of larval stages (Juanes, 2007; Le Pape and Bonhommeau, 2015). The high sensitivity of larval survival to hydrodynamics and environmental conditions causes large variations in recruitment (Daewel et al., 2011) and largely explain the lack of significant stock-recruitment relationships for marine exploited fish (Vert-Pre et al., 2013; Cury et al., 2014; Szuwalski et al., 2015). Indeed, most of the recruitment variability of marine fishes is explained by variations in larval survival rates (Levin and Stunz, 2005; Houde, 2008).

The recruitment variability is lower in populations with large density-dependent effects at juvenile stage (Iles and Beverton, 2000), in which case the capacity of nursery habitats has a significant effect (Johnson, 2007). This is the case for pleuronectiforms (Archambault et al., 2014). However these species also have an r-oriented strategy at larval stages (an order of magnitude of 10^{-3} for survival rate at larval stages for various populations of pleuronectiforms, similar than for other marine fish orders; Le Pape and Bonhommeau, 2015) and their

recruitment relies on processes generating high variability during their pelagic life, before metamorphosis and transfer to benthic habitats (van der Veer et al., 2000). The predictive power of the stock-recruitment relationship is very weak for flatfish and this weakness is partly linked to variability at larval stages (Archambault et al., 2014).

With regards to their large influence on recruitment at settlement stages for flatfish, a better understanding of larval processes would help to estimate the number of larvae successfully reaching nursery grounds, to identify the factors generating the associated spatio-temporal variability and their consequences for recruitment (Stige et al., 2013), as well as to improve knowledge on population structure (Buckley et al., 2008; Wilber et al., 2013).

However, as short term variations associated with mortality and advection are high, reliable in situ data are scarce and the use of larval drift model appears especially appropriate (Gallego et al., 2012). Indeed, larval drift individual based models (IBM) have proved useful to investigate the influence of hydrodynamics on ecology of flatfish larvae. They have been used to study the effects of spawning dynamics (Rochette et al., 2012), hydrodynamics and larval behaviour (Fox et al., 2006; Sentchev and Korotenko, 2007; Bolle et al., 2009), dispersal kernels (Koutsikopoulos et al., 1991; Sentchev and Korotenko, 2005) or connectivity within a population (Rochette et al., 2012) or a meta-population (Savina et al., 2010). However, most of these studies were conducted

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on relatively short periods of time and/or limited spatial scales. The use of numerical simulations over longer time series, at large scale covering several populations, could provide useful tools to study spatio-temporal variability in dispersal at larval stages and settlement success on suitable nursery habitats, and their consequences on recruitment dynamics and metapopulation structure.

The common sole (*Solea solea*, L.) is an important commercial flatfish resource with a large range of distribution, from North Western Africa and Mediterranean Sea to the Baltic Sea (Wheeler, 1978). With variations along its latitudinal range, the common sole spawns from winter to spring, pelagic larvae dwell during several weeks (\approx 1–2 months; Rochette et al., 2012) and newly metamorphosed individuals settle in coastal and estuarine areas, which act as exclusive nursery grounds for about 2 years, before sexual maturity (Dorel et al., 1991; Riou et al., 2001). Recruitment variability, although moderate with regard to many marine fish species, is high for the common sole (Le Pape et al., 2003a, b), with a high influence of hydro-climate on larval transport and larval supply (Savina et al., 2010; Rochette et al., 2012).

To explore the potential effects of hydrodynamics from spawning to metamorphosis of sole larvae over nurseries and the associated large scale spatio-temporal variability, larval supply was simulated using a three dimensional hydrodynamic model. The aim was to simulate sole larval supply in coastal and estuarine nursery areas on a wide scale covering four fished sole stocks–populations (ICES, 2014a, b), from the Bay of Biscay to the southern North Sea over a long period of time (1982–2007). An individual based particle-tracking module was used to simulate larval drift and survival under realistic biological processes from egg to benthic settlement on estuarine and coastal areas. Patterns of spawning, larval settlement success and dispersal, and sensitivity to hydrodynamics variability, were assessed at population scale, and the consequences on recruitment dynamics and metapopulation structure were analysed.

2. Methods

The approach combined a hydrodynamic model with a particle-tracking module including previously described eggs and larval behaviour to simulate spawning and hatching of eggs, larval drift, growth and settlement on coastal and estuarine nursery grounds under realistic hydro-climatic conditions. Particles were released according to the spawning season and spatial distribution of eggs. The development (growth), swimming behaviour, benthic settlement and survival of each particle were modelled in parallel with its transport in the hydrodynamic model.

As the present model relies mainly on a previous approach on a restricted spatiotemporal scale in the Eastern English Channel (Rochette et al., 2012), the explanations about model structure and parametrization were summarized. Details are provided only when the model options have been modified, especially with regards to the extent of the study area and the input of new data. For further information please refer to the seminal approach of Rochette et al. (2012).

2.1. Hydrodynamic model

The three dimensional (3D) ocean circulation model MARS (hydrodynamic Model for Application at Regional Scale; Lazure and Dumas, 2008) was used to simulate hydrodynamics from the Bay of Biscay to the southern North Sea (Fig. 1) during 26 years. The model used a 4 km horizontal resolution with 30 vertical generalized sigma layers. A time step of about 2 minutes allowed the model to solve the strong tidal currents occurring in many parts of the continental shelf of Western Europe, with respect to stability criteria. Atmospheric forcing was extracted from the NCEP-CFSR database (Saha et al., 2010). River discharges were upgraded from those in Huret et al. (2010) and Rochette et al. (2012), and interannual variability at open boundaries for temperature and salinity was provided by a global circulation model solution ORCA from the OPA-NEMO model (Michel et al., 2009). The simulation

period 1982–2007 was the longest allowing for consistent available forcing conditions (river, open boundary and atmospheric).

2.2. Larvae model

A particle-tracking module was coupled on-line to the 3D hydrodynamic model as in Huret et al. (2010). This module simulates trajectories and life traits of released particles (Ayata et al., 2010), from spawning areas to nursery grounds (Rochette et al., 2012). A random walk was considered for vertical mixing following Visser (1997), using the vertical eddy diffusivity compiled by the hydrodynamic model and interpolated at the particle depth (see Huret et al., 2010 for additional details).

The spatio-temporal variability of spawning and the larvae natural mortality were implemented in a post-treatment analysis by applying a posteriori weighting factors to released particles (Fox et al., 2006):

- (1) Each particle released in a given point at a given date in a given year in the 3D model is a super-individual, representing a certain number of eggs having the same initial conditions.
- (2) The model simulates, for each particle, a trajectory, as well as a survival probability for the egg stages.
- (3) The number of surviving larvae is then calculated (post-processed) by taking into account: the number of eggs corresponding to each particle released in the model (post-processed), the survival probability throughout the different eggs stages (simulated), the survival probability throughout larval stages (post-processed), and the final position of the particle (i.e., inside or outside a suitable nursery area, simulated).

2.2.1. Initial conditions: spatial and temporal variability of egg release

Patches of particles (i.e., super individual) covering the soft bottom grounds of the entire study area were released every 4 km and every 2 weeks (i.e., on the 10th and 25th of each month at 23:00) during the whole spawning season (in compliance with the preliminary testing carried out in Rochette et al. (2012) on the influence of frequency and number of particles released and the trade-off with the constraints of computing time). Given the eggs buoyancy (Koutsikopoulos et al., 1991), particles were released at 5 metres depth. Around 9000 particles were released for each year simulated.

Each particle represented a number of eggs calculated on the basis of (i) the total number of eggs spawned each year and (ii) the spatio-temporal distribution of eggs within the year. For each stock (i.e., Bay of Biscay BoB, Western English Channel WC, Eastern English Channel EC, southern North Sea NS), the total number of eggs released each year (Fig. S1) was calculated from the number and age structure of adults in each population (ICES, 2014a, b), accounting for the female fraction, the number of eggs at age per female and the proportion of mature females (Rochette et al., 2012). Each patch of particles released every 15 days along the spawning period represented a proportion of the total number of eggs spawned in a year by one population and was distributed in space. The spatio-temporal weighting factors were the combination of time and space weighting factors, standardized to a sum of 1, and then multiplied by the number of eggs spawned that year in this population.

2.2.1.1. Time weighting factor. In the EC, the sole spawning period is correlated to sea surface temperature (van der Land, 1991). For each year, a dome shaped curve of spawning temporal dynamics was defined from a previously established model (ICES, 1992) and fitted on the temperature simulated by the 3D numerical model (Rochette et al., 2012). Fincham et al. (2013) estimated the timing of spawning in sole and its interannual variability and trends, including the WC and EC and the NS populations. Based on their analysis, a similar dome shaped spawning curve was set for the WC (i.e., the spawning peak occurring 15 days earlier than in the EC) and the NC (the spawning peak occurring

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