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Use of Lagrangian simulations to hindcast the geographical position of propagule release zones in a Mediterranean coastal fish

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ABSTRACT

The study of organism dispersal is fundamental for elucidating patterns of connectivity between populations, thus crucial for the design of effective protection and management strategies. This is especially challenging in the case of coastal fish, for which information on egg release zones (i.e. spawning grounds) is often lacking. Here we assessed the putative location of egg release zones of the saddled sea bream (*Oblada melanura)* along the south-eastern coast of Spain in 2013. To this aim, we hindcasted propagule (egg and larva) dispersal using Lagrangian simulations, fed with species-specific information on early life history traits (ELTs), with two approaches: 1) back-tracking and 2) comparing settler distribution obtained from simulations to the analogous distribution resulting from otolith chemical analysis. Simulations were also used to assess which factors contributed the most to dispersal distances. Back-tracking simulations indicated that both the northern sector of the Murcia region and some traits of the North-African coast were hydrodynamically suitable to generate and drive the supply of larvae recorded along the coast of Murcia in 2013. With the second approach, based on the correlation between simulation outputs and field results (otolith chemical analysis), we found that the oceanographic characteristics of the study area could have determined the pattern of settler distribution recorded with otolith analysis in 2013 and inferred the geographical position of main *O. melanura* spawning grounds along the coast. Dispersal distance was found to be significantly affected by the geographical position of propagule release zones. The combination of methods used was the first attempt to assess the geographical position of propagule release zones in the Mediterranean Sea for *O. melanura*, and can represent a valuable approach for elucidating dispersal and connectivity patterns in other coastal species.

1. Introduction

The study of causes and consequences of organism dispersal is crucial from both ecological and evolutionary perspectives (Burgess et al., 2015). It provides vital information on demographic processes, species responses to environmental variability and anthropogenic stresses and on gene flow among populations, which, in turn, affect meta-population dynamics and species local adaptation (Burgess et al., 2015). In the case of fish, dispersal plays a major role in determining the spatial scale over which populations interact genetically and ecologically (i.e. connectivity) and how they should be managed (Grüss et al., 2011; Green et al., 2014). In spite of its great importance, the quantification of dispersal is still a challenging issue. Direct measures of dispersal are made hard by the difficulty to track individuals throughout their life cycle, especially during early developmental stages (Barbee and Swearer, 2007; Cowen, 2007; Calò et al., 2013). Most marine coastal fish species have a complex life cycle including a pelagic propagule (egg and/or larva) phase, that ends with the settlement in benthic habitats, followed by a demersal juvenile/adult phase (Leis et al., 2011). For these fishes, post-settlement stages are considered relatively site attached, so it is the propagule phase that contributes mostly to species dispersal capacity (Leis, 2015), although, in some cases, movement by juveniles (Di Franco et al., 2015) and adults (Aspillaga et al., 2016) can significantly contribute to population connectivity. In this context, a major issue for fish ecologists is the lack of knowledge of the locations where eggs are released (i.e. spawning

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grounds) (Thorrold et al., 2007). This, together with the minuscule dimension of eggs and larvae, makes it impractical to track propagules from their origins to their destination (i.e. settlement sites) and obtain an exhaustive measure of connectivity during the pelagic phase (Thorrold et al., 2001). The location of egg release zones is only possible through direct observations of spawning events or using acoustic methods, or indirectly through traditional and/or local ecological knowledge (e.g. fisherman knowledge about zones of fish massive catches) (Heyman et al., 2004; Boomhower et al., 2007).

In the last decades, modelling tools based on outputs of water circulation models were developed to simulate particle dispersal. Assuming that propagules are advected and diffused similarly to water particles (Cowen, 2007), Lagrangian-based, spatially-explicit individual-based models (IBMs) have been recognized as powerful tools to track pelagic particles from potential release zones to settlement habitats (Werner et al., 2007; Watson et al., 2010). IBMs have been used both to hindcast and forecast patterns of propagule transport and address challenging ecological questions such as: the assessment of the potential impact of climate change on propagule dispersal (Lett et al., 2010; Andrello et al., 2015b) or to support the design of MPA networks and in their future management (Andrello et al., 2015a, 2017). IBMs have been also used to understand how dispersal and connectivity can be influenced by spatial and temporal variability of different physical and biological factors (Andrello et al., 2013; Ospina-Álvarez et al., 2013; Ospina-Álvarez et al., 2015; Tanner et al., 2017), providing crucial information on the factors that drive fish settlement variability and giving support to the development of effective fishery management strategies (Ospina-Álvarez et al., 2015). Model simulations were also used to corroborate results or test hypotheses on propagule dispersal based on complementary methodologies such as genetic analysis or chemical analysis of calcified structures [see Calò et al. (2013) for studies carried out in the Mediterranean Sea.

In 2013, otoliths of juvenile individuals of the saddled sea bream (*Oblada melanura*) were analysed chemically to identify the number of potential natal sources along the Mediterranean south-eastern coast of Spain (Murcia region). A set of release zones were found to supply a series of coastal sites spread along ~180 km of coastline (Calò et al., 2016). Otolith analysis, however, does not allow to assess the geographical position of natal origins. In this context, dispersal simulations could be used to hindcast the position of the previously identified sources of propagules.

In the present study we implemented a biophysical IBM to investigate the putative geographical position of propagule release zones of *Oblada melanura* previously discriminated with otolith chemical analysis, along the south-eastern coast of Spain in 2013. Dispersal simulations were also used to assess the factors more likely to influence propagule dispersal distances in the region. We used local species-specific information on early life history traits (ELTs), i.e. spawning dates, pelagic larval duration and settlement dates, of the selected species. This information was gathered in the same spatial and temporal context of the oceanographic data implemented for the simulations. Apart from their ecological importance in the geographic context considered, the results of the study can provide useful insights for the development of new approaches to investigate the location of fish spawning areas.

2. Material and methods

2.1. Hydrodynamic model

The Western Mediterranean OPerational forecasting system (WMOP; Juza et al., 2016), developed at the Balearic Islands Coastal Observing and Forecasting System (www.socib.es), is based on a regional ocean configuration of the ROMS model implemented over the Western Mediterranean Sea. The ROMS is a free-surface split-explicit model, solving the hydrostatic primitive equations using terrain-following curvilinear vertical coordinates, employing the Arakawa-C horizontal and vertical grid staggering (Shchepetkin and McWilliams, 2005). The WMOP has a horizontal resolution of around 2 km and 32 sigma-levels in the vertical dimension, with a spatial coverage from Gibraltar strait to Sardinia Channel (6°W, 9°E, 35°N, 44.5°N). The model is forced by high-resolution atmospheric forcing (5 km, 3 h) from HIRLAM model simulations produced by the Spanish Meteorological Agency. The simulation used in this study is a sample over the period June-July 2013 of a 7-year-long free run simulation of WMOP model starting in September 2008. Initial and boundary conditions were provided by the CMEMS Mediterranean model (Simoncelli et al., 2014). The WMOP model was selected in this study since it was providing, at the time of writing this article, the finest resolution simulation available in the region, driven by the finest resolution atmospheric forcing, which is the dominant driver for the coastal surface circulation affecting propagule dispersion close to the coast. During the study period, satellite Sea Surface Temperature data reveald the presence of a relatively warm coastal band (around 15 km wide) along the coast of Murcia, which is also represented in the simulation, associated with the coastal southward current illustrated in Fig. 7. Similarly to altimeter data, an anticyclonic eddy is present in the model between Cartagena and the African Coast, yet with a south-westward shift of the centre of the eddy around 60 km compared to altimetry.

2.2. Larval dispersal model

Daily outputs of three-dimensional velocities fields simulated by WMOP were used to simulate *Oblada melanura* larval dispersal using the software Ichthyop 3.2 (Lett et al., 2008). The time step of larval transport was set to 100 s in order to keep it lower than the ratio of cell size to maximum current velocity, so that propagules do not cross more than one cell boundary in a single time step (Courant–Friedrichs–Lewy condition). Little information on larval active swimming is available for the saddled sea bream. Larvae of *O. melanura* in the Mediterranean Sea are mainly concentrated in the upper layer of the water column (between 0 and 10 m), with very limited to negligible diel vertical migration (Olivar and Sabatés, 1997). Propagules were therefore forced to remain on a fixed depth level of 5 m (i.e. the mean of the depth range where larvae of the species are commonly found; Olivar and Sabatés, 1997), thus accounting for larval active movements. Propagules were set to have a 'bouncing' coastline behaviour (i.e. a reflective condition along the coast). A horizontal dispersion scheme following Peliz et al. (2007) was also implemented in the forward simulations. Diffusion could not be implemented in backward simulations as it is not a time-reversible process.

2.3. Putative natal origins and settler distribution of Oblada melanura

To locate the major natal origins of *O. melaura* identified along the study area in 2013, two different approaches were used: 1) backtracking propagule dispersal simulations and 2) the comparison between settler distributions obtained from forward model simulations and the pattern recorded from post-settler otolith chemistry by Calò et al. (2016) (see Supplementary Material).

Running the larval dispersal model in backtracking mode allow to explore the areas of origin for the pre-settler individuals sampled in 2013. The dispersal duration used for the backtracking simulation was 13.5 days, i.e. the sum of the mean “days after hatching” (DAH = 11.5 days) plus 2 days accounting for egg phase duration (Antolović et al., 2010) (see Supplementary Material for further details). The choice to use a shorter measure of larval duration was made in order to exclude the last days of larval life (i.e. the competency phase) in which behavioural and movement capabilities are thought to be more developed than in the previous larval phases (Leis, 2007). In backward simulations, particles released from a backward-time-release-zone started their ‘virtual life’ with a positive age (i.e. 13.5 days) and became