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# LARVAHS: Predicting clam larval dispersal and recruitment using habitat suitability-based particle tracking model

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## ABSTRACT

We herein explore the potential larval dispersal and recruitment patterns of *Ruditapes decussatus* and *Ruditapes philippinarum* clams, influenced by larval behavior and hydrodynamics, by means of a particle-tracking model coupled to a hydrodynamic model. The main contribution of this study is that a habitat suitability-based (ENFA, Environmental Niche Factor Analysis) settlement–recruitment submodel was incorporated into the larval dispersal model to simulate settlement behavior and post-settlement mortality. For this purpose, a specific study was carried out in the Bay of Santander (Northern Spain), a well-mixed shallow water estuary where shellfishery of both species is carried out. The model was fed with observed winds, freshwater flows and astronomical tides to obtain predictions during the clams spawning period. Dispersion of larvae from seven spawning zones was tracked, subjected to three-dimensional advection, vertical turbulent diffusion and imposed vertical migration behavior parameterized from existing literature. Three simulation periods (Spring, Summer and Autumn) and two initial releases (spring/neap tide) were combined in six different modeling scenarios. The LARVAHS model proved to be a powerful approach to estimating recruitment success, highlighting the role of habitat suitability, larval swimming behavior, planktonic duration, season (i.e. predominating winds) and spawning ground location on recruitment success together with the effect of the tidal phase at spawning. Moreover, it has proven to be a valuable tool for determining major spawning and nursery grounds and to explore the connectivity between them, having important implications for restoration strategies and shellfisheries as well as aquaculture management.

## 1. Introduction

In intertidal and subtidal marine environments, many species are sessile or highly sedentary as adults, with dispersal occurring predominantly during a planktonic larval stage (Siegel et al., 2003). The supply of larvae, considered as the number of planktonic larvae available near suitable settlement sites (e.g. Minchinton and Scheibling, 1991; Gaines and Bertness, 1993), is the determinant of the stability of the benthic populations that depend upon the settlement and recruitment of planktonic larvae to balance the adult mortality losses (e.g. Rodriguez et al., 1993). Therefore, knowledge of the larval dispersal patterns between benthic habitat patches is critical to understanding the connectivity and persistence of marine populations (e.g. Botsford et al., 2001; Pineda et al., 2007). Thus, in recent decades, predicting the dispersion and supply of larvae has been one of the major goals of population ecology (e.g. Roughgarden et al., 1988), especially in fisheries management and restoration activities (e.g. North et al., 2009; Savina et al., 2010; Kim et al., 2012). The population dynamic of exploited species can be more sensitive to recruitment dynamics, since besides weather and oceanographic conditions, larval supply is linked to adult or spawning biomass, which in turn depends on the fishery (Bakun, 1996; Hsieh et al., 2006).

The prediction of the larval supply needs to encompass (i) spawning stock abundance (e.g. Myers, 1997; Ye, 2000), (ii) larval dispersion, which depends largely on the swimming behavior of the larvae, the duration of the planktonic stage and the hydrodynamic conditions (e.g. Roegner, 2000; Pineda et al., 2007) and (iii) settlement, which refers to where and when larvae find a suitable habitat to metamorphose (Pineda et al., 2007; North et al., 2008). The final recruitment success (i.e. the number of individuals reaching a juvenile nursery area) (North et al., 2009) is influenced by the previous settlement and early post larval mortality (Hunt and Scheibling, 1997).

Biophysical models integrating these factors are increasingly being used to predict larval transport and explore the role of different biological and physical factors on larval dispersal and settlement of marine benthic species (Metaxas and Saunders, 2009). Most of the developed larval dispersal models (LDMs) draw on information from hydrodynamics (i.e. water flow) and simplify the

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larval behavior as a passive tracer (e.g. Borsa and Millet, 1992; Incze and Naimie, 2000; Miyake et al., 2009). They seem to be promising because they can yield detailed connectivity matrices and also resolve dispersal trajectories, although they do not solve an adequate level of detail in flow structures (Largier, 2003). In the last decade, important steps have been made to integrate larval behavior into these models, such as age-dependent vertical migration or behavioral cues (Hinckley et al., 2001; North et al., 2008; Banas et al., 2009). Estuaries, lagoons and bays have proven to be excellent systems to apply these numerical models in order to study the influence of biological and physical processes on larval supply. These systems provide important nursery grounds and adult habitats for benthic invertebrates with pelagic larval stages and their enclosed morphology, which together with the predictable nature of their tidal flows and salinity variations, makes them ideal locations to easily measure physical processes and larval trajectories (Thompson, 2011).

Therefore, taking into account the above mentioned aspects, the larvae of exploited benthic invertebrate species in estuaries or bays should be, potentially, highly suitable to model, and the results can support decision making in fisheries management, aquaculture activities and conservation strategies. However, few studies have been conducted to predict larval dispersion and settlement patterns of benthic commercial invertebrates' within these systems. Commercial and widely distributed mollusks such as clams, oysters or abalones and crabs or fishes have been the main objective species of biophysical models. Larval dispersion of these species have been modeled assuming to behave as passive tracers of currents (Hinata and Tomisu, 2005; Hinata and Furukawa, 2006; Stephens et al., 2006; Miyake et al., 2009), incorporating larvae behavior (Herbert et al., 2012) and, in the absence of a settlement submodel, to have a competent period for settlement after planktonic larval duration was completed, or over the last three days of life. Recently, other authors have integrated settlement submodels in LDM and assumed the presence of adult oysters (North et al., 2008) or proximity of crabs to the coast (Roughan et al., 2011) as indicators of suitable zones for settlement, which by default accounted for habitat suitability. Hinrichsen et al. (2009) assumed a minimum requirement of a unique environmental variable (i.e. oxygen saturation) for cod (*Gadus morhua*) settlement and recruitment success.

In summary, only a few biophysical models include a habitat suitability approach in their settlement subroutines, which commonly do not consider a combination of environmental variables to define the suitable habitat conditions for survival of species. The subsequent aim, beyond determining larval dispersal and simplified settlement patterns, is to move towards including habitat suitability modeling to better understand recruitment success and post settlement mortality. In this context, we developed a particle-tracking model to study the larval transport, supply, and recruitment of the native clam *Ruditapes decussatus* and the introduced *Ruditapes philippinarum* in the Bay of Santander (Northern Spain, Gulf of Biscay), since they require taking an additional step in order to understand their recruitment patterns (Juanes et al., 2012). For this purpose, the model includes a larval behavior submodel and a settlement-recruitment submodel based on the habitat suitability resulting from ecological niche factor analysis (ENFA), a niche-based predictive habitat suitability modeling technique for presence-only data based on multivariate ordination. ENFA compares distributions of eco-geographical variables between the locations where the species is present and the whole area, extracting the range of environmental conditions of the locations that the species inhabits, or the niche width and habitat suitability maps based on a habitat suitability index (HSI) (Hirzel, 2001; Hirzel et al., 2002).

In this study we evaluate the model sensitivity to larval behavior and ENFA-based habitat suitability and try to answer the questions: "Where do the larvae settle?" and "Where did the settled larvae come from?" To address these two questions, the specific objectives of this study are (1) investigating the effect of the location of spawning zones and hydrodynamic variables (i.e. tide and wind) on larval dispersion and supply, (2) determining the most important spawning zones (i.e. the major suppliers of successful recruits) and nursery grounds and (3) assessing the potential connectivity between the spawning and nursery grounds.

## 2. Materials and methods

### 2.1. Study area

This study is focused on the Bay of Santander, the largest estuary on the northern coast of Spain (Gulf of Biscay) and the adjacent coast (Fig. 1a). The estuary, with 22.7 km$^2$ and relatively shallow waters with a mean depth of about 4.7 m, is morphologically complex and dominated by intertidal areas and tidal dynamics (Galván et al., 2010). The substratum of this area varies from sandy in the northern open areas to muddy sediments in the southern and inner areas (Bidegain, 2013). Hydrodynamic conditions are controlled by (1) a semidiurnal tidal regime and 3 m of mean tidal range, interacting with variable freshwater inputs coming mainly from the Miera river through the Cubas area (Puente et al., 2002) with a mean flow of 8 m$^3$/s (Galván et al., 2010) (see tidal-river currents in Fig. 1b) and (2) seasonally differentiated wind currents (see seasonal patterns in Fig. 1c–e). In the intertidal flats, comprising 67% of the Bay's surface, together with razor clams, the two most widely distributed commercial bivalves are the native carpet shell clam (*R. decussatus*) and the introduced Manila clam (*R. philippinarum*). Moreover, a Manila clam farming site covering 1 ha is located in the southeastern Elechas tidal flat. Both species' main spawning events usually occur from Spring to Autumn, according to previous studies in neighboring areas (Rodriguez-Moscoso et al., 1992; Rodríguez-Moscoso and Arnaiz, 1998; Urrutia et al., 1999; Ojea et al., 2005). According to the results obtained by Juanes et al. (2012) the higher recruitment intensity had occurred in the central and northern zones of the Bay for the carpet shell clam and in the central and innermost southern zones for the Manila clam.

### 2.2. Model description

The model was created by coupling a hydrodynamic model and a particle-tracking model, and including behavior, disappearance, and settlement–recruitment sub-models. This latter sub-model is based on the habitat suitability (HS) for the studied species, giving the LARVAHS acronym to the model. The LARVAHS model calculates the movement of particles that simulate larvae dynamics. In this study, it was implemented to adequately represent the larval dispersal of two clam species: the native European clam (*R. decussatus*) and the nonindigenous Manila clam (*R. philippinarum*). The model tracked the trajectories of larvae in three dimensions and then predicted settlement and recruitment success based on habitat suitability maps. The model was forced with tide, river and wind conditions which occurred from April to November 2010, in order to capture a range of environmental variability experienced by clam larvae during the considered spawning season. We examined whether specific larval swimming behavior and seasonal and tidal conditions could influence dispersal distance, encounter with suitable habitat and connectivity between grounds. The grid used in the model is defined by 244 × 298 cells, each measuring 51 m × 51 m.

#### 2.2.1. Hydrodynamic model

Tidal current velocities were calculated by means of a two-dimensional depth-averaged hydrodynamic coastal and estuarine circulation model (H2D model; see Bárcena et al., 2012a,b; García