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 7 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 2 initial releases (spring / neap tide) were combined in 6 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.

Keywords: Ruditapes decussatus, Ruditapes philippinarum, larvae, particle-tracking model, habitat suitability, ENFA, swimming behavior, recruitment, connectivity,

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. Rodríguez 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. Rougharden 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 (LDM) draw on information from hydrodynamics (i.e. water flow) and simplify the 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 *R. decussatus* and the introduced *R.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 modelling 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. Material 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 (Figure 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 Figure 1b) and (2) seasonally differentiated wind currents (see seasonal patterns in Figures 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 (*Ruditapes decussatus*) and the introduced Manila clam (*Ruditapes philippinarum*). Moreover, a Manila clam farming site covering 1 hectare 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.

Figure 1

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 (*Ruditapes decussatus*) and the nonindigenous Manila clam (*Ruditapes 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 x 298 cells, each measuring 51x51 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 and García et al., 2010a). This quasi three-dimensional model takes into account the different structure over the depth of horizontal velocities along the depth, due to wind action (Koutitas, 1988). A similar implementation, i.e. the same code, same forcing data and similar domain, has been previously calibrated and validated by López et al. (2013) against observed water levels, current velocities and salinities, covering a full phase of spring and neap tides.

2.2.2. Larval dispersal model: LARVAHS

LARVAHS was developed from a particle-tracking model designed to predict the movement of particles based on advection, sub-grid scale turbulence and larval swimming behavior. Moreover, it was designed to predict larval settlement and recruitment based on previous habitat-suitability raster-based maps obtained using ENFA by Bidegain et al. (2012) and Bidegain (2013) in the Bay of Santander.

Particle-tracking model

The model uses a particle-tracking approach to simulate larval advection and diffusion. Advection is computed by solving equation 1 for each particle:

$$dr / dt = q \qquad (1)$$

where r is the position vector of the particle and q is the current vector solved in components u and v along the x and y axes. Currents are obtained by running a hydrodynamic model in advance. As a consequence, the evaluation of the tidal advective transport of larvae is very fast and is not limited by the Courant Friedrich Levy criterion (Kowlik & Murty, 1993). Because horizontal and vertical diffusivity were constant in the hydrodynamic model, three-dimensional diffusion of the turbulent particle is simulated using a random walk method (Proctor et al., 1994a; Hunter, 1987; Periáñez and Elliott, 2002, Periáñez, 2004). The maximum sizes of the horizontal and vertical steps, D_h and D_v respectively, are:

$D_h = \sqrt{12 K_h \Delta t}$

$D_v = \sqrt{2 K_v \Delta t}$

where K_h and K_v are the horizontal and vertical diffusion coefficients respectively. The model included an external time step of 10 minutes, which is the recording time step of hydrodynamic model results, and an internal time-step of 30 seconds, which is the time interval of particle movement. Because of the hydrodynamic model resolution (51 m x 51 m), a given particle may take several time steps to move across a grid cell. Hence the predicted currents were interpolated in both space and time to provide 3D fine-resolution fields for advecting clam larvae according to the hydrodynamic model outputs. For particle movement due to current velocities in the x, y, and z directions, a 4th order Runge-Kutta scheme was implemented. The 4th order Runge-Kutta scheme provides the most robust estimate of the trajectory of particle motion in water bodies with complex fronts and eddy fields (Dippner 2004) like the Bay of Santander.

Regarding particle movement, different boundary conditions were imposed to the particle-tracking. First, if a particle passed through the surface or bottom boundary due to turbulence or vertical advection, the particle was placed back in the model domain at the previous time step location. Second, if a particle passed through the surface or bottom due to swimming behavior (see Behavior sub-model) it was placed just below the surface or above the bottom (i.e. it stopped near the boundary). Third, if a particle intersected a horizontal boundary, it was reflected off the boundary at an angle of reflection that equaled the angle of approach to the boundary.

Behavior sub-model

The behavior sub-model considers the larval ability to swim vertically during its life cycle, following comments and results obtained by North et al. (2006;2008), Ishii et al. (2005) Kuroda

(2005), and Suzuki et al (2002) for oysters such as *C. virginica or C. ariakensis* ,or Manila clam. This sub-model tries to mimic the vertical movement of larvae towards intermediate and surface water layers at early stages (trocophore, D and U larvae) and to the sea-bottom, when transition to pediveliger occurs. In the simulations, for the European clam, the planktonic larval phase is considered for a period of 21 days (Chícharo and Chícharo, 2001b; Vela and Moreno, 2005). Meanwhile, for the Manila clam, the planktonic larval stage is defined for a period of 15 days (Young-Baek et al., 2005; Hinata and Furukawa, 2006). Table 1 summarizes the behavioral considerations of the two species that were implemented into the behavior sub-model.

Table 1

Disappearance sub-model

The disappearance sub-model associates first-order decay to each simulated particle in order to reflect the egg and larval mortality induced by natural causes (predation, starvation, etc.) (Morgan, 1995). We assumed egg duration of 1 day (Table 1) and a natural egg mortality of 99% for both species, considering that the percentage of fertilized eggs in low population densities is 1% (Levitan, 1995). During the planktonic larval duration (Table 1), we assumed a natural larval mortality of 98% for both species, adapting results obtained by several authors (e.g. Carriker, 1961; Chícharo and Chícharo, 2001b; Zhang and Yan 2006).

$$dN/dt = -kN$$

where N is the number of eggs released, t is the specific life cycle duration (see Table 1) in seconds and k is the considered egg or larval mortality rate (s^{-1}) to obtain the assumed natural mortality percentages.

Settlement-recruitment sub-model

We used a habitat-suitability (HS) raster-based grid to determine if a pediveliger-stage larvae encountered a suitable habitat to settle and recruit. Each cell of the grid had a HS index (HSI) which ranged from 0 to 100, with higher values being more suitable for recruitment and zero being completely unsuitable. This grid was obtained from the ecological niche factor analysis (ENFA) conducted by Bidegain et al. (2012) and Bidegain (2013) for each of the studied species in the Bay of Santander obtaining reasonably good model validation results (see Figure 2a). Different topographic (depth), physical (salinity, current velocity and sediment characteristics such as percentage of sand, gravel and silt) and chemical environmental variables (organic matter content in sediment), assumed as meaningful to the ecology and distribution of these species (e.g. Laing and Child, 1996; Vincenzi et al., 2006, Cannas, 2010) were considered, together with presence data to perform this analysis. The integration of habitat suitability grids in the model grid was automatic since the extent of the study area and the cell size used were identical.

The minimum HSI value considered for recruitment to occur was 25, assuming a HSI value from 0 to 25 to be an unsuitable habitat for recruitment (see Figure 2a,b). For every internal time step (30 s), each pediveliger-stage particle was tested to determine if it was at the sea-bottom. When it was at the bottom, the sub-model checked if the HSI on this cell was greater than 25 and in that case, the particle settled, or stopped moving. When the HSI was lower than 25, the particle continued swimming. Finally, if the particle did not encounter a cell of HSI > 25 at the end of the pediveliger-stage, the particle dies.

Once a given particle settled in a cell, the HSI value of this cell was assumed as the survival probability of the particle. To perform the larval recruitment, the model generated a random number between 0 and 100. If this random number was lower than the survival probability of the particle (the HSI), the settled particle survived and it was successfully recruited. On the contrary, if the random number was greater than the survival probability of the particle, the settled particle died.

2.3. Initial conditions and scenarios

2.3.1. Spawning zones

Initial conditions for the simulations were defined for the major spawning areas in the Bay of Santander. Spawning areas were considered those defined as highly suitable (HSI > 75) for both species by Bidegain et al. (2012) and Bidegain (2013) using ENFA (see Figures 2a,b), assuming a higher density and reproductive efficiency of adults in these areas. Thus, using this criterion we determined 6 spawning grounds for *R. decussatus* and 7 for *R. philippinaurm* (Figures 2c,d).

Figure 2

2.3.2. Number of particles (eggs) released

The number of particles released in each spawning zone and scenario was proportional to the density of female adult clams and the area of the spawning ground. It was calculated by multiplying (1) ½ of adult density (individuals/m^2) in the spawning ground considering a 1:1 male/female ratio by (2) the number of cells within the area, and (3) the area of each cell (51 x 51 m) and (4) the number of eggs produced by each female adult clam. Considering previous estimations of the broodstock conditioning of this species (Yap, 1977; Chung et al., 2001; Park and Choi, 2004; Matías et al., 2009) we assumed a total of 0.6 x 10^6 eggs released by each female clam for both species (i.e. 100,000 in each scenario). A maximum of ~1 million particles were released from the most productive spawning zone due to computational constraints. Therefore, each released particle represented 1 x 10^5 eggs, in order to achieve the assumed egg production per female. Note that in Elechas, for the two cells where the Manila clam farming area is located (1 hectare), a density of 100 adult clams/m^2 was assumed (Data provided by the Regional Fisheries Administration).

2.3.3. Simulation scenarios and environmental conditions

Three spawning seasons were tested within the identified spawning period for both species (April-November, Rodriguez-Moscoso et al., 1992; Rodríguez-Moscoso and Arnaiz, 1998; Urrutia et al., 1999; Ojea et al., 2005): Spring, Summer and Autumn 2010. In each season two egg releases were tested: 15/04 and 25/04 (Spring), 12/08 and 20/08 (Summer), and 09/10 and 16/10 (Autumn) in 2010. The first date of release in each season coincided with neap tide and the second one with spring tide. Tidal-river and wind currents during simulation periods are presented in Figure 1. The seawater circulation pattern due to tidal and river forcing is presented as mean annual currents (Figure 1b) considering that the tidal force is similar for all seasons and river outputs were low in general (< 2 m^3/s) and not significantly different between seasons (Bidegain et al., 2013). Regarding winds, each season was mainly characterized by a predominating wind: SW winds in Spring, NE winds in Summer and W winds in Autumn, resulting in northward/offshore (Figure 1c), southward/inshore (Figure 1d) and eastward wind currents (Figure 1e) respectively. Thus, 6 scenarios were tested from each spawning zone and species, corresponding to different tidal phases and seasons.

2.4. LARVAHS model evaluation

A preliminary evaluation of the LARVAHS model to predict recruitment of clams was conducted in two nursery grounds (Elechas and Raos) by comparing predictions with observed data. Moreover, two variations of this model were also evaluated in order to analyze the role of larval behavior and habitat suitability in recruitment: (1) a LARVAHS model with no behavior submodel (NO BEHAVIOR model) and (2) a LARVAHS model with no habitat suitability based recruitment submodel, obtaining settled larvae (NO HS model). The evaluation grounds were selected because (i) they are located near each other and thus allows for the sampling of both grounds during the same tide and (ii) shellfishing activity is minimal since they are located far from the coastline or out of the permitted shellfishing zones. Hence, the potential mortality of early recruiters associated with this activity (raking or pressing the sediment) was minimal.

Predicted densities were compared with observed densities of early recruiters and the strength of the correlation was analyzed by Spearman's rank correlation coefficient. Predicted recruitment density was calculated by dividing the number of individuals successfully recruited in each nursery ground at each season (adding larvae coming from different spawning grounds at both tidal scenarios) by the nursery ground area. To obtain the observed early recruiters density, four sediment samples of 50 cm^2 to a depth of 15 cm were collected in each nursery ground on the 29th of June, the 23rd ofOctober and the 12th of December, i.e. after each spawning season modeled in the study (Spring, Summer, Autumn). All samples were passed through a 1 mm sieve and clam lengths were measured to the nearest 0.1 mm. Individuals larger than 1 mm but smaller than 3 mm for *R. decussatus* and 5 mm for *R. philippinarum* were considered as early recruiters. This selection criterion was based on differential growth patterns described for these clam species (Arnal and Fernández-Pato, 1977, 1978; Spencer et al., 1991; Solidoro et al., 2000; Chessa et al., 2005) as well as the desire to avoid counting early recruiters of the previous spawning season.

2.5. Data analysis

2.5.1. Simulation results and model sensitivity

For each spawning zone in each tidal and seasonal scenario the percentage of the total eggs released which resulted in successfully recruited clams was calculated for *R. decussatus* and *R. philippinarum* by running simulations using the LARVAHS, the NO BEHAVIOR model and the NO HS model. Normality and homogeneity of variance were examined by Shapiro-Wilk and Levene tests, respectively, and data were transformed if these assumptions for a parametric analysis were violated. An ANOVA- test and post-hoc Tukey's HSD –test were applied to the recruitment data to find out if differences exist between the model results and to examine the model sensitivity to larval behavior and habitat suitability incorporation. A t-test was also performed to determine if recruitment success was significantly different between species for each variation of the model.

2.5.2. Influential factors on recruitment success

Recruitment success, calculated as the percentage of the total eggs released that were retained in the Bay and successfully recruited, was used as a response variable to compare the results obtained from different runs. A t-test was performed to determine if recruitment success was significantly different between the studied species with differing larval phase durations. In addition, to analyze the single and interactive effects of the location of the spawning site, the tidal amplitude and the season on recruitment success, a multifactorial ANOVA was conducted.

2.5.3. Determination of major spawning and nursery grounds

We calculated, for the eggs released in each spawning ground (i.e. HSI > 75), the proportion of larvae recruited in the whole Bay (i.e. HSI >25) and defined as the most successful spawning grounds those from where, after larval release and dispersal, the highest total recruitments or percentages were obtained.

Delimitation of nursery grounds by cells HSI > 25 (i.e. where recruitment occurs in the model) was not viable if we were to analyze recruitment spatial patterns, since most of the nursery grounds overlapped using this criterion (see Figures 2a,b). Therefore, we decided to consider the nursery grounds as being identical to the spawning grounds (i.e. highly suitable areas, HSI > 75) in order to have them clearly separated from each other, facilitating the analysis and interpretation of results regarding the determination of major nursery grounds and/or connectivity between grounds. To determine major nursery grounds, recruitment density was calculated in each ground by adding together larvae coming from different spawning grounds at different tidal and seasonal scenarios and dividing the number of individuals by the nursery ground area (= spawning ground area).

2.5.4. Connectivity between spawning and nursery grounds

Connectivity matrices were created for each spawning season and tidal scenario. The connectivity matrices, adapted from Savina et al. (2010) indicate which proportion of the total larvae recruited in a given nursery zone (x-axis) comes from each spawning zone (y-axis). Attending these proportions, the robustness between spawning and nursery grounds connections and the isolation and self-recruitment of grounds was analyzed.

3. Results

3.1. LARVAHS model evaluation

The LARVAHS model estimations were evaluated in two zones (Raos and Elechas) and for the three studied seasons (Spring, Summer, Autumn) revealing that the predicted recruitment density values were lower than the mean observed values in general, for both species and all seasons (see black circles in Figure 3), except in the summer scenario in Raos. The generalized underestimation of the LARVAHS model was not significantly different between species considering that when underestimation occurred it was 3.62 (± 1.47) (± SD) individuals/m^2 for *R. decussatus* (Figures 3a,b) and 3.28 (± 2.09) individuals/m^2 for *R. philippinarum* (Figures 3c,d). Figure 3 shows that the seasonal variability in recruitment patterns was detected by the LARVAHS model, obtaining significant correlation values between observed and predicted recruitment density for *R. decussatus* (Spearman’s R=0.89, n=6, t (n-2) = 4.1, p=0.0) and *R. philippinarum* (Spearman’s R=0.94, n=6, t (n-2) = 5.6, p=0.005) which involves a good qualitative fit of the model to the in situ measured data.

However, seasonal variability in recruitment was not detected by the two variations of the LARVAHS model and the correlation values obtained between predictions and observed data were not significant, neither for the NO BEHAVIOR model (*R. philippinarum,* R=0.07, n=6, t (n-2) = 0.14, p=0.89; *R. philippinarum,* R=0.70, n=6, t (n-2) = 1.94, p=0.12), nor for the NO HS model (*R. philippinarum,* R=0.46, n=6, t (n-2) = 1.05, p=0.35; *R. philippinarum,* R=0.430, n=6, t (n-2) = 0.95, p=0.40). Moreover, the NO BEHAVIOR model results underestimated the observed data more significantly than the LARVHAS model in all cases for both species, and using the NO HS model the overestimation was highly appreciable (Figure 3).

Figure 3

3.2. Simulation results data and model sensitivity

Results of the 78 runs, 36 runs for *R. decussatus* and 42 runs for *R. philippinarum* are presented in Table 2 for the LARVAHS model and the two described variations of this model: the LARVAHS model without the behavior submodel (NO BEHAVIOR) and the LARVAHS model without the habitat suitability based recruitment submodel (NO HS). For each spawning zone the particles released were different, according to the zone extension and the density of adults clams. Thus, for *R. decussatus* Cubas the Outer ground, with ~ 800000 x 10^5 eggs released, was the most "egg productive" spawning zone, followed by Astillero and Pedreña with ~ 188000 x 10^5 and ~ 164000 x 10^5 eggs released, respectively. Additionally, the Pedreña spawning zone, with 963000 x 10^5 eggs released was the most productive zone for *R. philippinarum*, followed by Elechas with ~ 333000 x 10^5 eggs released.

Table 2

The recruitment percentages were very low for the LARVAHS model and also for the two variations of the model, due mainly to high natural mortality rates and low retention of larvae within the Bay, or to settlement in unsuitable zones. Recruitment success was significantly higher for *R. philippinarum* than for *R. decussatus* (see Table 3) for LARVAHS (df=76, t=-3.38, p=0.001) and also for the two model variations (No Behavior, df= 76, t=-2.45, p=0.01; No HS, df= 76, t=-4.48, p=0.0003). The analysis of the variance of recruitment success between models showed significant differences between all of the models for both species, with thesignificantly highest recruitment for the NO HS model and the lowest recruitment percentages for the NO BEHAVIOR model (Table 3).

Table 3

3.3. Larval dynamics

The assumed vertical behavior of *R. decussatus* and *R. philippinarum* larvae adapted from literature (see Table 1) was correctly simulated (see Figure 4 and Video S1, supplementary information). During the trocophore phase, we found all larvae at the surface (Figure 4a) while D and early Umbo-stage larvae were found at surface to intermediate depths (Figure 4b). Late Umbo and early Pediveliger-stage larvae were found uniformly distributed at all depths (Figure 4c), while late Pediveliger larvae were observed close to the bottom (Figure 4d). Regarding spatial dynamics, Video S2 (see supplementary information) helps to visualize larval pool movements and shows the plume of larvae alternatively flushed in and out of the Bay with the tidal currents, and a differentiated retention of larvae depending on the zone of spawning. Nevertheless, final recruitment spatial patterns occurring after larval dispersal and influential factors are described in later sections.

Figure 4

3.4. Influential factors on recruitment and connectivity between grounds

Recruitment data (i.e., the percentage of the total released eggs successfully recruited) were first log-transformed to achieve normality and homogeneity of variance. The factorial ANOVA results presented in Table 4 shows that season (i.e. predominating winds) and the location of the spawning zone have significant effects on the final recruitment success of both clam species. The location of spawning zone contributed more importantly to the overall variance. Additionally, the tidal phase (spring or neap) at the spawning moment had no significant effect on the recruitment of either of the two species. However, the interaction between these two factors had a significant effect for *R. decussatus* (Table 4) and a tidal effect on connection patterns between spawning and nursery grounds can be appreciated (Figure 8).

Table 4

Season and winds

Regarding spawning season, the highest recruitments of both species' larvae were observed in summer, with predominating NE winds (Figure 1d) which aided the retention of larvae in the western and southern flats of the Bay (Figures 5b,e). These wind currents in summer also helped to generate more frequent connections between the northwestern spawning grounds and the southwestern nursery grounds (Figure 6). Regarding these connections between grounds, the most robust ones (i.e. more than 30 % of the total larvae recruited in a given nursery ground originating from a given spawning site, green and black rectangles) occurred more frequently for *R. philippinarum* than for *R. decussatus* and particularly in summer at neap tides. Conversely, a limited recruitment was observed in spring (northward currents) (Figures 5a,d) and in Autumn (eastward currents) (Figures 5c,f) corresponding to weaker connections between grounds, particularly at spring tides (Figure 6).

Figure 5

Figure 6

Spawning zones

Regarding zones, for *R. decussatus* larvae released from the western and southern zones of the Bay, Raos and Astillero respectively, showed the highest proportions of recruited individuals, particularly in summer (Figure 7a). This higher retention within the Bay when spawning occurs in southern zones is demonstrated in Video S2 (see supplementary information) as mentioned above. Moreover, although Cubas Outer, in the north, was not a very successful spawning ground it was significant in terms of absolute values of larvae recruited, owing to the high number of eggs released (Table 2). For this species, the interaction between the spawning zone and tides was significant. Thus, for instance, when eggs were released in Cubas Outer, the final recruitment was significantly higher at spring tide than at neap tide, while when spawning occurred in southern zones (Astillero or Elechas) recruitment was higher at neap tide than at spring tide (Table 2). For *R. philippinarum,* larvae released from the southern Bay (Astillero and Solía-Tijero) showed the highest recruitment rates (Figure 7b) and these were also the major spawning grounds in terms of the number of individuals recruited. Moreover, this species showed similar patterns regarding tide-zone effect (although not statistically significant) (Table 2 and Table 4), together with a significantly higher number and the most robust connections, which occurred at neap tides (Figure 6).

Figure 7

Major nursery grounds and connectivity with spawning grounds

The predicted major current nursery grounds in the Bay of Santander were (1) Cubas Outer in the northeastern grounds of the estuary with ~80 recruiters/m^2 and Raos (17 recruiters/m^2) in the central western flats for *R. decussatus* and (2) Solía-Tijero in the southern inner zones of the Bay (240 recruiters/m^2) and Cubas Outer in the northeastern area of the bay and Astillero grounds with 50 and 40 recruiters/m^2, respectively, for *R. philippinarum* (Figure 8). The predicted recruitment density for the whole Bay in highly suitable areas (i.e. the sum of individuals recruited in cells with habitat suitability index (HSI) >75 divided by the total area of the nursery grounds) was considerably higher for *R. philippinarum* with 50 recruiters/m^2 than for *R. decussatus* with 17 recruiters/m^2, as a result of a higher retention of larvae within the Bay and a smaller area of highly suitable habitat for recruitment for *R. philippinarum* (317 Hectares) compared with *R. decussatus* (407 Hectares) (see Figure 2 and Bidegain, 2013).

Figure 8

Regarding the most important nursery grounds estimated in this study (Figure 8), for *R. decussatus* Cubas Outer nursery ground can be considered a self-recruitment ground in spring at spring tide, while it received "allochthonous" larvae from Cubas Inner in this season at neap tides and also in Autumn at spring tides (Figure 6a).Additionally, Raos also exhibited self-recruitment behavior, except in Summer and Autumn at neap tide. For *R. philippinarum*, Solía-Tijero and Astillero displayed self-recruitment behavior although they received recruiters from several zones, particularly at neap tide when retention within the Bay is higher (Figure 6b). Also, for this species, Cubas Outer received significant amounts of larvae coming from Cubas Inner and Elechas in Summer and Autumn. Finally, the most isolated nursery was Cubas Inner for both species, considering that it did not recruit larvae from any of the spawning sites.

4. Discussion

The incorporation of habitat suitability modelling results obtained by ENFA has proven to be a powerful approach to creating larval dispersal models (LDM) with cues which stimulate larval settlement and including an estimator of recruitment success (Turner et al. 1994, Tamburri et al. 1996). This advance follows the recommendations, of the relevant ICES working group, to couple LDM with additional spatial information in order to delineate the source populations, as well as the recruitment habitat, along the path of an individual particle (North et al., 2009). The LARVAHS model, incorporating habitat suitability as well as swimming behavior, was reasonably suitable in its ability to qualitatively forecast seasonal variability of recruitment, and the obtained predictions significantly correlated with observed data (Figure 3). Moreover, estimated spatial recruitment patterns considerably agree with those found in this estuary by Juanes et al. (2012), finding higher densities in northern open zones for *R.decussatus* and in southern inner zones for *R. philippinarum*.

Swimming behavior and habitat suitability

In order to analyze the role of swimming behavior and habitat suitability submodels in recruitment predictions we considered it necessary to compare estimations obtained by the LARVAHS model with those obtained by two variations of the model (i.e. a NO HS model, using settled larvae without a habitat suitability- recruitment submodel and (ii) a NO BEHAVIOR model, a passive behavior model   that ignores swimming ability. This comparative analysis showed that these two variations of the LARVAHS model did not adequately forecast seasonal patterns and no significant correlations were observed with field data. On one hand, the absence of habitat suitability led to a strong overestimation of recruitment, since the important post settlement mortality associated with recruitment of benthic invertebrates (Hunt and Scheibling, 1997) was not integrated in the NO HS model and, consequently, all larvae settled within the Bay survived. On the other hand, the NO BEHAVIOR model with a passive behavior of larvae underestimated the observed recruitment more significantly than the LARVAHS model. This result suggests that the incorporation of swimming behavior favored larvae retention within the Bay, influencing their encounter with a suitable habitat for recruitment (Table 3). According to Kuroda (2005), this vertical-down "migration" is essential to prevent all larvae from being dragged into offshore areas at ebb tide. This finding is consistent with recent observations by Herbert et al. (2012) for *R. philippinarum,* and such vertical swimming behavior also has a major impact on the distribution in tidal estuaries of other species which broadcast larvae, such as crustaceans (Zeng and Naylor, 1996) and other bivalves (North et al., 2008).

Regarding specific differences, recruitment of larvae within the Bay was significantly higher for *R. philippinarum* with all the models (Table 3). In the case of the LARVAHS model, this outcome was remarkable, since we considered larger areas of suitable habitat for recruitment of *R. decussatus* compared with *R. philippinarum* (see Figure 2 and Bidegain, 2013). This suggests that retention of larvae might be a more critical determinant of final recruitment than the difference in suitable habitat surface area between species. When we modeled larvae dispersal without incorporating habitat suitability, the differences in recruitment between species were more significant (i.e. higher t-statistic values) than for the LARVAHS or NO BEHAVIOR models, suggesting that specific differences in post larval mortality associated with differences in highly suitable surface areas has a stronger effect on recruitment than specific differences in planktonic larval duration (PLD) (or each larval phase duration).

Planktonic larval duration

Results obtained with the NO BEHAVIOR (or passive swimming) model showed that the PLD had an effect on larvae retention and final recruitment within the estuary. A longer PLD of *R. decussatus* has a significant negative effect on larval retention, resulting in higher mortality rates and lower recruitment success than *R. philippinarum*. Thus, the longer PLD of *R. decussatus* over *R. philippinarum* seems to be the main reason for the higher larval dispersion and lower recruitment rates for this species. This result is consistent with the outcomes of the few biophysical models that have tested for it and found significant effects of PDL on larval transport (Edwards et al., 2007). For example, increasing the PLD significantly of brittle star (echinoderms) decreases the larval retention in the natal region and increases the larval mortality (Lefebvre et al., 2003). Moreover, a reduction in the PDL of scallop larvae decreases their displacement distance (Tremblay et al., 1994).

Season, spawning ground location and tidal effect

The results suggest that the location of the source populations and wind-induced currents have significant effects on the recruitment of both species (Table 4). The complex configuration of the Bay of Santander with both inner/narrower areas and more open tidal flats, where spawning grounds are located, appears to have the greatest impact on the success of larval retention and recruitment, explaining ~60-70 % of the total variance of recruitment. Herbert et al. (2012) found similar results when modelling *R. philippinarum* larval transport in Pool Harbour (England) which contains different embayments. Hinckley et al. (2001) highlighted the importance of spawning location and timing to successful walleye pollock *Theragra chalcogramma* larval transport to nursery areas. Moreover, Rigal et al. (2010) demonstrated that the interaction between spawning location and hydrodynamics have important effects on retention of the gastropod *Crepidula fornicata* within a coastal bay. Wind advection has been considered to have important effects in larval distribution in large (~1000 km^2) and vertically stratified bays (Hinata and Tomisu, 2005) and open coastal areas (e.g. Bas et al., 2009; Ayata et al., 2010) where wind-induced currents are usually important together with water movements due to tides. Therefore, although initially it may be assumed that in a small estuary like the Bay of Santander this wind effect would not be important, our results suggest that wind-induced hydrodynamics is a factor to be considered, being responsible for the ~ 8 – 14 % of the total variance of recruitment. Other studies have also shown that wind effects are important in larval distribution (Suzuki et al., 2002; Leis, 2006; Ayata et al., 2010) and under some conditions the wind-induced physical structure could be an important mechanism of retention of invertebrate larvae (Epifanio et al., 1989; Verdier-Bonnet et al., 1997).

The interaction between spawning zone location and tidal phase at the spawning moment showed an effect on final recruitment, being statistically significant for *R. decussatus* and explaining 22 % of the total variance. Recruitment was higher at spring tides in the outer zone of Cubas, probably due to the return of larvae to the mouth of estuary helped by tides, and higher at neap tides in the inner southern zones since neap tides limited flushing larvae out of estuary. Similarly, recruitment of larvae retention of crabs or clam larvae is higher when spawning occurs at neap tides than at spring tides (Forward, 1987, Gove and Paula, 2000; Chícharo and Chícharo, 2000:2001a) and the ingress of crab larvae in a estuary and settlement is higher at times, ranging from several days after spring tide to near the neap tide (Roegner et al., 2007).

Major spawning and nursery zones

The models ability to identify major spawning and nursery grounds could support shellfishery management strategies such as restoration, cultivation and creation of “sanctuaries” or protected areas, with the potential of supplementing populations outside the protected area both under normal conditions and in the cases of unforeseen events or decline of populations (Allison et al., 1998; Peterson, 2002; Jones, 2006). However, the results obtained in this study should be taken with caution since the selection of a high HSI threshold (i.e. 75) to define spawning or nursery grounds is a simplification of the reality in easily delimitated grounds, adopted in order to avoid overlapping and facilitate interpretation and analysis of results. Lower thresholds may lead to larger grounds but with lower estimations of average spawner adult densities or recruitment rates. Therefore, depending on the management needs, a combination of detection of the main hot spot(s), delimitation of larger sanctuaries and interpretability of results should be considered in order to select the appropriate HSI threshold.

Therefore, suitable sites for the application of these strategies for the native clam *R. decussatus* could be located in successful spawning zones in terms of final recruitment. However, for the introduced clam *R. philippinarum* sanctuaries should be located in grounds where dramatic retentions of larvae and widespread proliferation or domination would not occur. For this species, less successful spawning zones could be considered. In this regard, the limited proliferation and no general domination patterns of the nonindigenous clam may be related to the suitable location of this species cultivation zone in the not especially-successful spawning ground of Elechas (Figure 7).

The major nursery zones in the Bay of Santander, regarding the predicted recruitment density of larvae, were Solía-Tijero for *R. philippinarum* and Cubas Outer for *R. decussatus*. These predicted major nursery zones partially coincided with the density of adult clams (Figure 2) or the recruitment patterns estimated by Juanes et al. (2012). Non-coincidences can be easily explained by (1) the temporal recruitment variability, (2) the fact that the recruitment density was predicted only in highly suitable areas and (3) other factors which significantly influence the final density of adults not integrated in the habitat suitability model such as the differential predation occurring between recruitment zones. This last hypothesis is consistent with the high predation of clams by crabs and fishes found in the Bay (Bidegain and Juanes, 2013). Seasonal protection regimes for estimated major nursery zones could be also efficient supplements to more traditional fishery management practices.

Connectivity between spawning and nursery grounds

The model also provided theoretical outcomes concerning connectivity between grounds. Our results suggest that there are both isolated areas or “self-recruitment nursery grounds” and areas that are potentially well connected, where recruited larvae come from distant or nearby spawning grounds in several scenarios. In general, a considerably higher number of connections was observed for *R. philippinarum* than for *R. decussatus*. The shorter PLD and higher retention of *R. philippinarum* larvae may be one of the main reasons which explains this difference between species. In the same line, it seems that neap tides and dominating NE winds of summer favored connections between grounds, particularly for *R. philippinarum*. The connectivity between internal areas of the south with northern distant areas was less evident than between non distant zones or nearby inner grounds, being consistent with the fact that retention of larvae in inner nearby grounds is higher and connections between them could be more easily produced.

Overall, more self-recruitment cases were found for *R. decussatus* which is, consequently, the species with lower potential recruitment success. Self-recruitment nursery grounds, which notably do not receive larvae from other grounds, are more susceptible to recruitment declines when scenarios favoring the export of larvae from this given ground out of the Bay occur. Whereas well connected areas can compensate for the larvae deficit coming from a given spawning site with larvae pools from other sources.

5. Conclusions

The LARVAHS model may serve as a useful framework to guide quantitative investigations about settlement and recruitment predictions since it has an important focus in habitat suitability modelling-based recruitment estimations. The model predicted seasonal recruitment variability reasonably well although, like other similar models, it cannot reproduce the orders of magnitude variability since it does not include many important biological processes (e.g. specific larvae behavior, gamete fertilization success, larval mortality and growth, post-settlement mortality due to predation, etc.). Thus, future analyses should be conducted upon these results by assessing the potential contribution of these parameters. Moreover, it is essential to validate the results obtained using the model through comparison with new observed data such as larvae concentration at different levels of the water column and early recruiters (< 250 microns) density.

Model results have implications for shellfisheries and aquaculture management and also conservation programs. However, grid resolution constrains the applicability of predictions and, consequently, refined circulation predictions may be necessary to better guide the location of specific management and conservation strategies.

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References

Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine Reserves are Necessary but not Sufficient for Marine Conservation. Ecological Applications 8 (1), S79-S92

Arnal, J.I., Fernández-Pato, C., 1977. La croissance de la palourde, *Venerupis decussatu*s L., a la Baie de Santander (Espagne): premières resultats. Int. Counc. Exp. Sea CM 1977/K, 16.

Arnal, J.I., Fernández-Pato, C., 1978. La croissance de la palourde, *Venerupis decussatus* L., a la Baie de Santander (Espagne) dans des conditions naturelles. Int. Counc. Exp. Sea CM 1978/K, 28.

Ayata, S.-D., Lazure, P., Thiébaut, É., 2010. How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (northeast- Atlantic). Progress in Oceanography 87, 18–36.

Bakun, A., 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico. 323 pp.

Banas, N.S., McDonald, S.P., Armstrong, D.A., 2009. Green crab larval retention in Willapa Bay, Washington. An intensive Lagrangian modeling approach. Estuaries Coasts 32, 893–905.

Bárcena, J.F., Garcia, A., Gómez, A.G., Alvarez, C., Juanes, J.A., Revilla, J.A., 2012a. Spatial and temporal flushing time approach in estuaries influenced by river and tide. An application in Suances Estuary (Northern Spain). Estuarine, Coastal and Shelf Science 112, 40-51.

Bárcena, J.F., García, A., García, J., Álvarez, C. , Revilla, J.A., 2012b. Surface analysis of free surface and velocity to changes in river flow and tidal amplitude on a shallow mesotidal estuary: An application in Suances Estuary (Nothern Spain). Journal of Hidrology 14, 301-318.

Bas C., Luppi T., Spivak E., Schejter L., 2009. Larval dispersion of the estuarine crab *Neohelice granulata* in coastal marine waters of the Southwest Atlantic. Estuarine, Coastal and Shelf Science 83, 569-576.

Bidegain, G., 2013. Ecological dynamics of a native and an introduced clam species: Implications for conservation and fisheries management. PhD thesis. University of Cantabria. 306 pp.

Bidegain,G., Juanes, J.A., 2013. Does expansion of Manila clam *Ruditapes philippinarum* cause competitive displacement of the European native clam *Ruditapes decussatus*? Journal of Experimental Marine Biology and Ecology 445. 44-52.

Borsa, P., Millet, B., 1992. Recruitment of the calm *Ruditapes decussatus* Estuarine, Coastal and Shelf Science, 35: 289-300.

Botsford, L., Hastings, A., Gaines, S.D., 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters 4, 144–150.

Cannas, A., 2010. Population dynamics of *Ruditapes decussatus* (L.) and settlement of *Ruditapes philippinarum* (Adams & Reeve) in Sardinia, Italy. PhD Thesis. University of Cagliari.

Carriker, M. R., 1961. Interrelation of functional morphology, behaviour, and autecology in early stages of the bivalve *Mercenaria rnercenaria*. J. Elisha Mitchell scient Soc. 77, 168-241.

Chessa, L.A., Paesanti, F., Pais, A., Scardi, M., Serra, S., Vitale, L., 2005. Perspective for development of low impact aquaculture in western Mediterranean lagoon: the case of the carpet clam *Tapes decussatus*. Aquacult. Int. 13, 147-155.

Chícharo, L. & M. A. Chícharo (2000). Short-term fluctuations in bivalve larvae compared with some environmental factors in a coastal lagoon (South Portugal). Scientia marina 64 (4), 1-8.

Chícharo, L., Chícharo, M.A., 2001a. Effects of environmental conditions on planktonic abundances, benthic recruitment and growth rates of the bivalve mollusc *Ruditapes decussates* in a Portuguese coastal lagoon. Fish Res 53, 235–250.

Chícharo, L., Chícharo, M.A., 2001b. A Juvenile Recruitment Prediction Model for *Ruditapes decussatus* (L.) (Bivalvia: Mollusca). Fisheries Research, 53 (3), 219-233

Chung, E.-Y., Hur, S.B., Hur, Y.-B., Lee, J.S., 2001. Gonadal maturation and artificial spawning of the Manila clam *Ruditapes philippinarum* (Bivalvia: Veneridae), in Komso Bay, Korea. J. Fish. Sci. Tech. 4, 208-218.

Dippner, J.W., 2004. Mathematical modelling of the transport of pollution in water, in Mathematical Models, edited by J. A. Filar and J. B. Krawczyk in Encyclopedia of Life Support Systems (EOLSS), Developed under the Auspices of the UNESCO, Eolss Publishers, Oxford,UK, [http://www.eolss.net].

Edwards, K. P., Hare, J.A., Werner, F.E., Seim, H., 2007. Using 2-dimensional dispersal kernels to identify the dominant influences on larval dispersal on continental shelves. Mar. Ecol. Prog. Ser. 352, 77–87.

Epifanio, C. E., Masse, A.K., Garvine, R.W., 1989. Transport of blue crab larvae by surface currents off Delaware Bay, USA. Mar. Ecol. Progr. Ser. 54, 35-41.

Forward, R.B., 1987. Larval release in decapod crustaceans: an overview. Bull Mar Sci 41, 65-176.

Gaines, S.D., Bertness, M., 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology 74, 2430-2435.

Galván, C., Juanes, J.A., Puente, A., 2010. Ecological classification of European transitional waters in the North-East Atlantic eco-region. Estuarine, coastal and shelf science 87 (3), 442-450.

García, A., Juanes, J.A., Álvarez, C., Revilla, J.A., Medina, R., 2010a. Assesment of the response of a shallow macrotidal estuary to changes in hydrological and wastewater inputs through numerical modelling. Ecological Modelling 221, 1194-1208.

García, A., Sámano, M.L., Juanes, J.A., Medina, R., Revilla, J.A., Álvarez, C., 2010b. Assessment of the effects of a port expansion on algae appearance in a costal bay through mathematical modelling. Application to San Lorenzo Bay (North Spain). Ecological Modelling 221, 1413–1426.

Gove D, Paula J., 2000. Rhythmicity of larval release in three species of intertidal brachyuran crabs (Crustacea: Brachyura) from Inhaca Island (Mozambique). Mar Biol 136, 685-691.

Herbert, R. J. H., Willis, J., Jones, E., Ross, K., Hübner, R., Humphreys, J., Jensen, A., Baugh, J., 2012. Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam, *Ruditapes philippinarum*, in the UK. Journal of Biogeography 39, 585-599.

Hinata, H., Tomisu, K., 2005. Numerical simulation on advective process of planktonic larvae of the clam Ruditapes philippinarum in Tokyo Bay. Bulletin Fisheries Research Agency, Supplement 3, 59–66.

Hinata, H., Furukawa, K., 2006. Ecological network linked by the planktonic larvae of the clam *Ruditapes philippinarum* in Tokyo Bay, in: E. Wolanski (Ed), The environment in Asia Pacific Harbours, Netherlands, pp. 35-45.

Hinckley, S., Hermann, A.J., Mier, K.L., Megrey, B.A., 2001. Importance of spawning location and timing to successful transport to nursery areas: a simulation study of Gulf of Alaska walleye pollock. ICES J Mar Sci 58, 1042–1052.

Hinrichsen, H.-H., Kraus, G., Böttcher, U., Köster, F., 2009. Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas. ICES Journal of Marine Science: Journal du Conseil 66(1), 101-108.

Hirzel, A., 2001. When GIS comes to life. Linking landscape- and population ecology for large population management modelling: the case of Ibex (*Capra ibex*) in Switzerland. PhD thesis. Inst Ecol, Lab Conserv Biol. Univ Lausanne, Switzerland

Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: how to compute habitatsuitability maps without absence data? Ecology 83, 2027– 2036.

Hsieh, C-h., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., Sugihara, G., 2006. Fishing elevates variability in the abundance of exploited species. Nature 443, 859–862.

Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155, 269–301

Hunter, J.R., 1987. The application of Lagrangian particle-tracking techniques to modelling of dispertion in the sea. In: Noye, J. (Ed.), Numerical Modelling: Application to Marine Systems. Elsevier, Amsterdam, pp. 257–269.

Incze, L. S., Naimie, C.E., 2000. Modeling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. Fisheries Oceanography 9, 99-113.

Ishii, R., Sekiguchi, H., Nakahara, Y. & Jinnai, Y., 2001. Larval recruitment of the manila clam *Ruditapes philippinarum* in Ariake Sound, southern Japan. Fisheries Science 67, 579– 591.

Ishii, R., Sekiguchi, H. & Jinnai, Y., 2005. Vertical distributions of larvae of the clam *Ruditapes philippinarum* and the striped horse mussel *Musculista senhousia* in eastern Ariake Bay, southern Japan. Journal of Oceanography 61, 973–978.

Jones, P.J.S., 2006. Collective action problems posed by no-take zones. Marine Policy 30, 143-156.

Juanes, J.A., Bidegain, G., Echavarri-Erasun ,B., Puente, A., García, A., García, A., Bárcena, J.F., Álvarez, C., García-Castillo, G., 2012. Differential distribution pattern of native *Ruditapes decus*satus and introduced *Ruditapes philippinarum* clam populations in the Bay of Santander (Gulf of Biscay). Considerations for fisheries management, Ocean and Coastal Management 69, 316-326.

Kim, C.-K., Park, K. and Powers, S. P., 2012. Establishing Restoration Strategy of Eastern Oyster via a Coupled Biophysical Transport Model. Restoration Ecology. doi: 10.1111/j.1526-100X.2012.00897.x

Koutitas C., 1988. Mathematical models in Coastal Engineering. Pentech Press Limited, London,UK.

Kowalik, Z., Murty, T., 1993. Numerical modeling of ocean dynamics. World Scientific Publishing. Singapore, 481 pp.

Kuroda, N., 2005. Larval transportation and settlement mechanism to tidal flat in Japanese littleneck clam *Ruditapes philippinarum*. Bulletin Fisheries Research Agency, Supplement 3, S67–S77.

Laing I., Child A.R., 1996. Comparative tolerance of small juvenile palourdes (*Tapes decussatus* L.) and Manila clams (*Tapes philippinarum* Adams & Reeve) to low temperature. Journal of Experimental Marine Biology and Ecology 195, 267 – 285.

Largier, J. L., 2003. Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13 (1), S71–S89.

Lefebvre, A., Ellien, C., Davoult, D., Thiebaut, E., Salomon, J.C., 2003. Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/ diffusion model. Estuar. Coast. Shelf Sci. 57, 421–433.

Leis, J.M., 2006. Are larvae of demersal fishes plankton or nekton? Adv Mar Biol 51, 59–141.

Levitan, D.R., 1995. The ecology of fertilization in free-spawning invertebrates, In L. McEdward (Ed), Ecology of marine invertebrate larvae. CRC Press. p. 123–156.

López, I., Álvarez, C., Gil, J.L., García, A., Bárcena, J.F., Revilla, J.A., 2013. A method for the source apportionment in bathing waters through the modelling of wastewater discharges: Development of an indicator and application to an urban beach in Santander (Northern Spain). Ecological Indicators 24, 334-343.

Mann, R., 1986. *Arctica islandica* (Linne) larvae: active depth regulators or passive particles. Am Mal. Union Spec. Ed. 3, 51-57.

Matias, D., Joaquim, S., Leitao, A., Massapina, C., 2009. Effect of geographic origin, temperature and timing of broodstock collection on conditioning, spawning success and larval viability of *Ruditapes decussates* (Linne, 1758). Aquacult. Int., 17, 257-271.

Metaxas, A., Saunders, M., 2009. Quantifying the “bio”- components in biophysical models of larval transport in marine benthic invertebrates: Advances and pitfalls. Biological Bulletin 216, 257–272.

Minchinton, T.E., Scheibling, R.S., 1991. The influence of larval supply and settlement on the population structure of barnacles. Ecology 72, 1867–1879.

Miyake, Y., Kimura, S., Kawamura, T., Horii, T., Kurogi, H., Kitagawa, T., 2009. Simulating larval dispersal processes for abalone using a coupled particle-tracking and hydrodynamic model: implications for refugium design. Mar Ecol Prog Ser 387:205-222

Morgan, S. G., 1995. Life and death in the plankton: larval mortality and adaptation, in: Ecology of Marine Invertebrate Larvae, L. R. McEdward, ed. CRC Press, Boca Raton, FL, pp. 279–321.

Myers, R. A., 1997. Comment and reanalysis: paradigms for recruitment studies. Can. J. Fish. Aquat. Sci., 54: 978–981.

North, E.W., Schlag, Z., Hood, R.R., Zhong, L., Li, M., Gross, T., 2006. Modeling dispersal of *Crassostrea ariakensis* oyster larvae in Chesapeake Bay. Maryland Department of Natural Resources, 55 p.

North, E.W., Schlag, Z., Hood, R.R., Li, M., Zhong, L., Gross,T., Kennedy, V. S., 2008. Vertical swimming behaviour influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Mar. Ecol. Prog. Ser. 359, 99-115.

North, E.W., Gallego, A., Petitgas, P., 2009. Manual of recommended practices for modelling physical–biological interactions during fish early life. ICES Cooperative Research Report No. 295, International Council for the Exploration of the Sea (ICES), Copenhagen.

Ojea, J., Martínez, D., Novoa, S., Cerviño-Otero, A., 2005. Ciclo gametogénico de una población de almeja japonesa *Ruditapes philipinarum* (Adams & Reeve, 1850) en la ría de Camariñas (noroeste de España) y relación con la composición bioquímica mayoritaria. Boletín. Instituto Español de Oceanografía 21(1-4), 337-442.

Park, K.L., Choi, K.S., 2004. Application of enzyme-linked immunosorbent assay for studying of reproduction in the Manila clam *Ruditapes philippinarum (*Mollusca: Bivalvia): I. Quantifying eggs. Aquaculture 241 (1–4), 667-687.

Pérez-Camacho A. 1980. Biología de *Venerupis pullastra* (Montagu 1803) y *Venerupis decussata* (Linne 1767) (Mollusca, Bivalvia), con especial referencia a los factores determinantes de la producción. Bol. Inst. Esp. Oceanogr. 281, 44–74.

Perianez, R., 2004. A particle-tracking model for simulating pollutant dispersion in the Strait of Gibraltar. Marine Pollution Bulletin 49 (7–8), 613–623.

Perianez, R., Elliott, A.J., 2002. A particle tracking method for simulation the dispersion of non-conservative radionuclides in coastal waters. Journal of Environmental Radioactivity 58 (1),13–33.

Peterson, C.H., 2002. Recruitment overfishing in a bivalve mollusc fishery: hard clams (*Mercenaria mercenaria*) in North Carolina. Canadian Journal of Fisheries and Aquatic Science 59, 96-104

Pineda, J., Hare, J.A., Sponaugle, S., 2007. Larval dispersal and transport in the coastal ocean and consequences for population connectivity. Oceanography 20, 22–39.

Proctor, R., Elliott, A.J., Flather, R.A., 1994. Forecast and hindcast simulations of the Braer oil spill. Marine Pollution Bulletin 28 (4), 219–229.

Puente, A., Juanes, J.A., García-Castrillo, G., Ávarez, C., Revilla, J.A., Gil, J.L., 2002. Baseline study of soft bottom benthic assemblages in the bay of Santander (Gulf of Biscay). Hydrobiologia 475/476, 141–149.

Rigal, F., Viard, F., Ayata, S.D., Comtet, T., 2010. Does larval supply explain the low proliferation of the invasive gastropod Crepidula fornicata in a tidal estuary? Biological Invasions 12 , 3171-3186.

Rodriguez, S.R., Ojeda, F.P., Inestrosa, N.C., 1993. Settlement of benthic marine invertebrates. Mar. Ecol. Prog. Ser. 97, 193–207.

Rodriguez-Moscoso, E., Pazo, J.P., Garcia, A., Cortés, F.F., 1992. Reproductive cycle of Manila clam, *Ruditapes philippinarum* (Adams & Reeve 1850) in Ria of Vigo (NW Spain). Scientia Marina 56(1), 61-67.

Rodríguez-Moscoso, E., Arnaiz, R., 1998. Gametogenesis and energy storage in a population of the grooved carpet-shell clam, *Tapes decussatus* (Linné, 1787), in northwest Spain. Aquaculturem 162(1-2), 125-139.

Roegner, G. C., 2000. Transport of larval molluscs through a shallow estuary. Journal of Plankton Research 22, 1779-1800

Roegner, G. C., Armstrong, D., Shanks, A., 2007. Wind and tidal influences on crab recruitment to an Oregon estuary. Marine Ecology Progress Series 35, 177-188.

Roughan, M., Macdonald, H.S., Baird., M.E., Glasby, T.M., 2011. Modelling coastal connectivity in a Western Boundary Current: seasonal and inter- annual variability. Deep-Sea Res. Part II 58, 628–644.

Roughgarden, J., Gaines, S., Possingham, H.P., 1988. Recruitment dynamics in complex life cycles. Science 241, 1460–1466.

Savina, M., Lacroix, G., Ruddick, K., 2010. Modelling the transport of common sole larvae in the southern North Sea: Influence of hydrodynamics and larval vertical movements. J Mar Syst 81, 86−98.

Siegel, D.A., Kinlan, B.P., Gaylord, B., Gaines, S.D., 2003. Lagrangian descriptions of marine larval dispersion. Marine Ecology Progress Series 260, 83-96.

Solidoro, C., Pastres, R., Melaku-Canu, D., Pellizzato, M., Rossi, R., 2000. Modelling the growth of *Tapes philippinarum* in Northern adriatic lagoons. Mar. Ecol. Prog. Ser. 199, 137-148.

Spencer, B.E., Edwards, D.B., Millican, P.F., 1991. Cultivation of Manila clam. Lab. Leafl., MAFF Direct. Fish. Res., Lowestoft, 29 pp.

Stephens, S.A., Broekhuizen, N., Macdiarmid, A.B., Lundquist, C.J., McLeodand, L., Haskew, R., 2006. Modelling transport of larval New Zealand abalone (*Haliotis iris*) along an open coast. Marine Freshwater Research 57, 519-532.

Suzuki, T., Ichikawa, T., Momoi, M., 2002. The Approach to Predict Sources of Pelagic Bivalve Larvae Supplied to Tidal Flat Areas by Receptor Mode Model: A Modeling Study Conducted in Mikawa Bay. Bulletin of the Japanese Society of Fisheries Oceanography 2, 88-101

Tamburri, M.N, Finelli, C.M, Wethey, D.S., Zimmer-Faust, R.K., 1996. Chemical induction of larval settlement behavior in flow. Biol Bull 191, 367–373

Thompson, C.M., 2011. Species-specific patterns in bivalve larval supply to a coastal embayment. Massachusetts Institute of Technology and Woods Hole Oceanographic Institute. PhD Thesis.

Tremblay, M.J., Loder, J.W., Werner, F.E., Naimie, C.E., Page, F.H., Sinclair M.M., 1994. Drift of sea scallop larvae *Placopecten magellanicus* on Georges Bank: a model study of the roles of mean advection, larval behavior and larval origin. Deep-Sea Res. Part II 47, 7–49.

Turner, E.J., Zimmer-Faust, R.K., Palmer, M.A., Luckenbach, M., Pentchef, N.D., 1994. Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water soluble chemical cue. Limnol Oceanogr 39, 1579–1593.

Urrutia, M.B., Ibarrola, I., Iglesias, J.I.P., Navarro, E., 1999. Energetics of growth and reproduction in a high-tidal population of the clam *Ruditapes decussatus* from Urdaibai Estuary (Basque Country, N. Spain). Journal of Sea Research 42(1), 35-48.

Vela, J.M., Moreno, O., 2005. Perfil bio-ecológico de la almeja fina (*Tapes decussatus* Linneo, 1758), Acuicultura, Pesca y Marisqueo en el Golfo de Cádiz. Junta de Andalucía, pp. 641-662.

Verdier-Bonnet, C., Carlotti, F., Rey, C., Bhaud, M., 1997. A model of larval dispersal coupling wind-driven currents and vertical larval behaviour: application to the recruitment of the annelid *Owenia fusiformis* in Banyuls Bay, France. Mar Ecol Prog Ser 160, 217–231.

Vincenzi, S., Caramori, G., Rossi, R., Leo, G.A.D., 2006. A GIS-based habitat suitability model for commercial yield estimation of *Tapes philippinarum* in a Mediterranean coastal lagoon (Sacca di Goro, Italy). Ecological Modelling 193, (1-2), 90-104.

Yap, W.G., 1977. Population biology of the Japanese little-neck clam, Tapes philippinarum, in Kaneohe Bay, Oahu, Hawaiian Islands. Pac Sci 31(3), 223-244.

Ye, Y., 2000. Is recruitment related to spawning stock in penaeid shrimp fisheries – ICES Journal of Marine Science 57, 1103–1109.

Young-Baek, H., Jean-Hee, B., Sung-Bum, H., 2005. Comparison of Development and Larval Growth of Four Venerid Clams. Journal of the World Aquaculture Society 36(2), 179-187.

Zhang, G., Yan, X., 2006. A new three-phase culture method for Manila clam, *Ruditapes philippinarum*, farming in northern China. Aquaculture 258, 452-461.

Zeng, C., Naylor, E., 1996. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab Carcinus maenas: implications for ebb tide offshore dispersal. Marine Ecology Progress Series 132, 71– 82.

Figure footnotes

Figure 1 - Study area for the model: Bay of Santander estuary and adjacent waters located in the northern coast of Spain (Gulf of Biscay). Bathymetry (m) data of the modeled area are presented. Tidal-river annual mean currents (ms^{-1}) (a, b, c) and wind currents (d, e, f) for Spring, Summer and Autumn scenarios,

Figure 2 – Habitat suitability (HS) maps obtained from Bidegain et al. ((2013) for *R. decussatus* (a) and *R. philippinarum* (b) in the Bay of Santander, classified into 4 HS index

(HSI) classes using GIS techniques: unsuitable (HSI <25), barely suitable (25≤ HSI >50), moderately suitable (50≤ HSI ≤75), highly suitable (HSI >75). Spawning zones for *R. decussatus* (c) and *R. philippinarum* (d) considered in the simulations, delimited by areas with habitat suitability index values greater than 75 (i.e. highly suitable areas). Density of adult clams (>20 mm) found by Bidegain et al. (2012) in each zone following the methodology of Juanes et al. (2012) is presented in brackets. A different color is given to each spawning ground which also represents the larvae coming from each of them in Figure 6.

Figure 3 – Observed (white quadrates) and predicted recruitment (individuals/m^2) obtained with the LARVAHS model (black circles), the NO BEHAVIOR model (gray triangles) and the NO HS model (black crosses) are presented. Results are presented for Spring, Summer and Autumn season scenarios, for *R. decussatus* (A, B) and *R. philippinarum* (C, D) in Elechas and Raos sites respectively. Error bars for observed data represent the standard error.

Figure 4 – *R. decussatus* larval dynamics regarding vertical behavior are represented in time sequential figures: (A) Day 1 (B) Day 5, (C) Day 15 and (D) Day 18. In right subfigures of each sequential figures points and lines represent the particle-tracking of two randomly selected larvae.

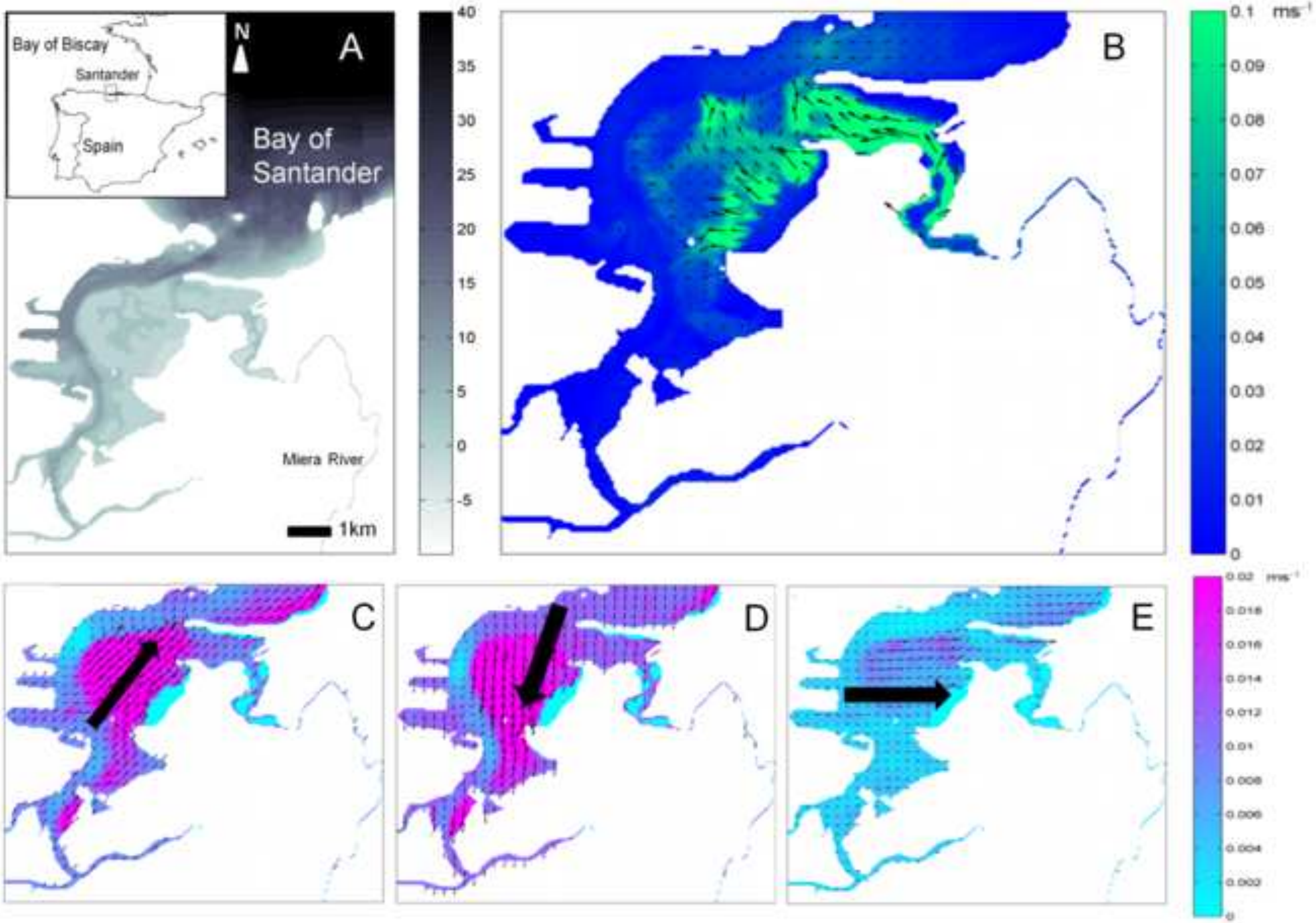
Figure 5 – Spatial representation of predicted recruitment for *R. decussatus* in Spring (a), Summer (b) and Autumn (c) scenarios and for *R. philippinarum* in the same scenarios respectively (d, e, f). Rectangles represent spawning zones and dots represent larvae recruited coming from their respective same color spawning zone. Colors used are identical to those given in Figure 2.

Figure 6 – Connectivity matrices adapted from Savina et al. (2010) for the 3 seasonal scenarios (Spring, Summer and Autumn) and 2 tidal scenarios (neap and spring tides) simulated for *R. decussatus* (A) and *R. philippinarum* (B). The colors indicate the percentage of the total larvae recruited in a given nursery ground (x-axis) coming from each spawning ground (y-axis).

Figure 7 –Success in recruitment of each spawning ground in terms of final recruitment within the whole Bay, presented by means of predicted final recruitment (%) in different seasonal scenarios (Spring, Summer and Autumn) for (a) *R. decussatus* and (b) *R. philippinarum*. The error bars represent the ± SE of the mean recruitment of neap and spring tide scenarios.

Figure 8 – Predicted recruitment density in nursery grounds (Habitat suitability index, HSI>75), calculated as the sum of recruitment of larvae coming from all spawning grounds at different seasons and tidal scenarios and divided by the total area of the nursery ground.

Figure 1 color



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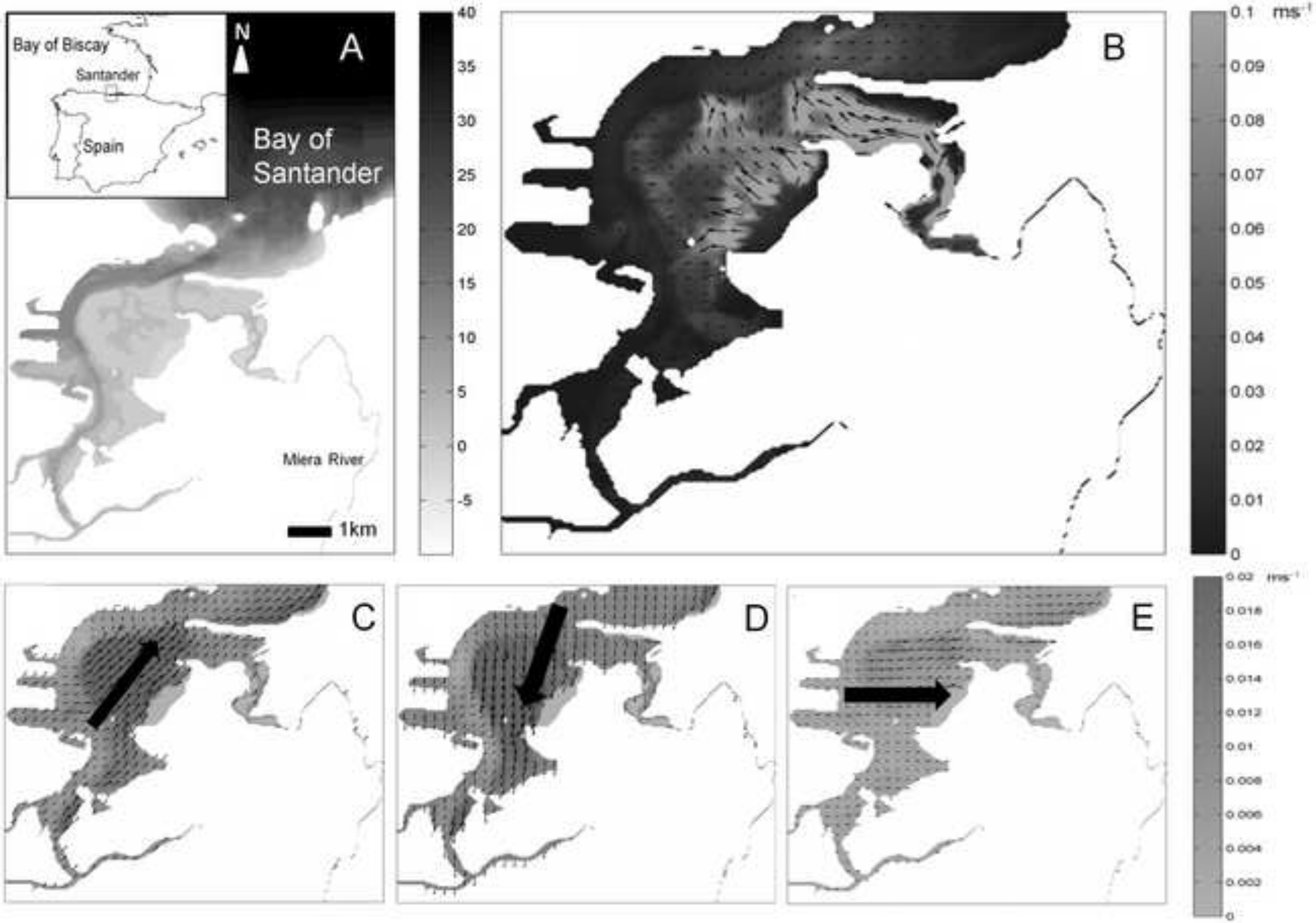

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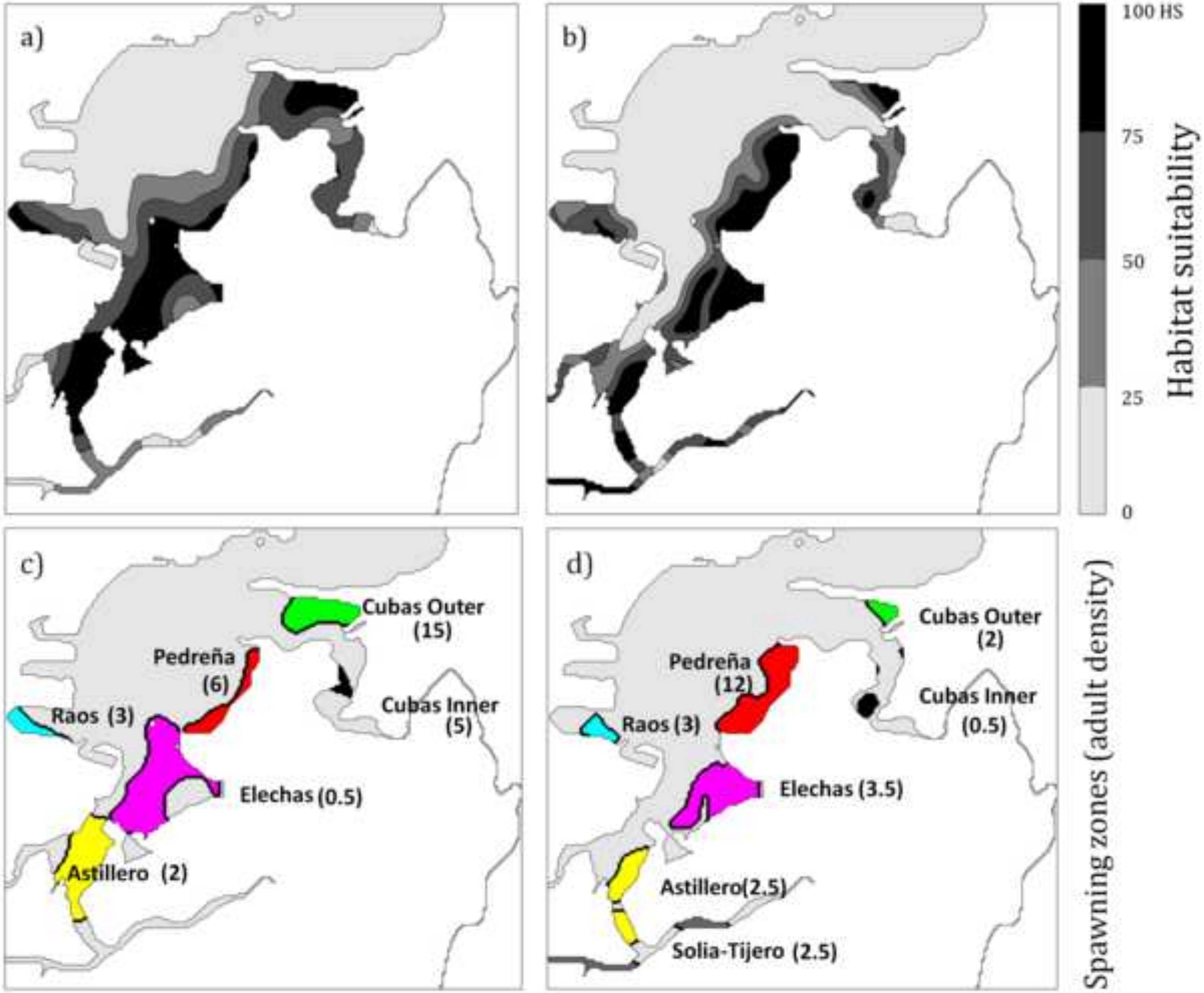

Figure2 black white

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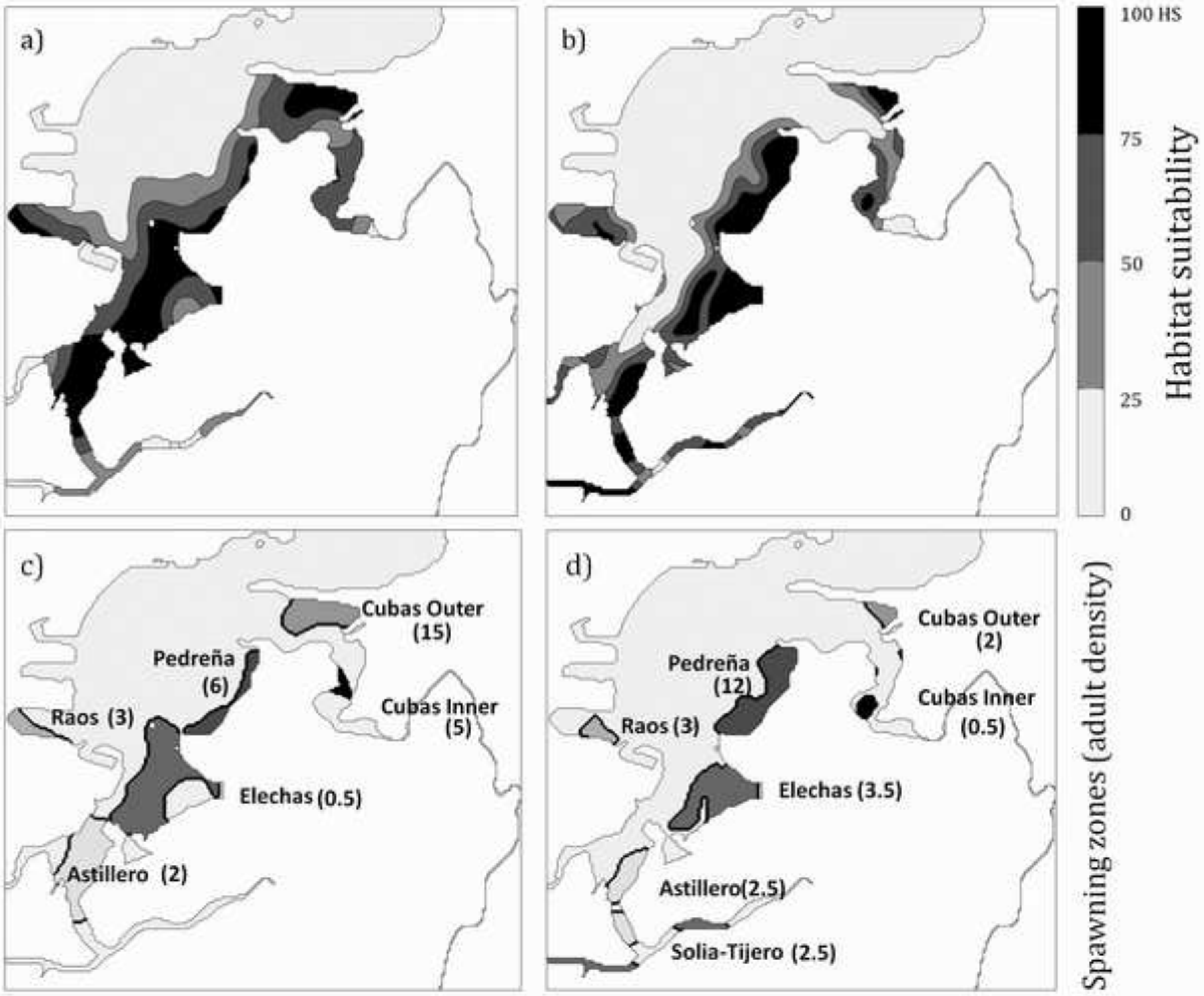

Figure 3

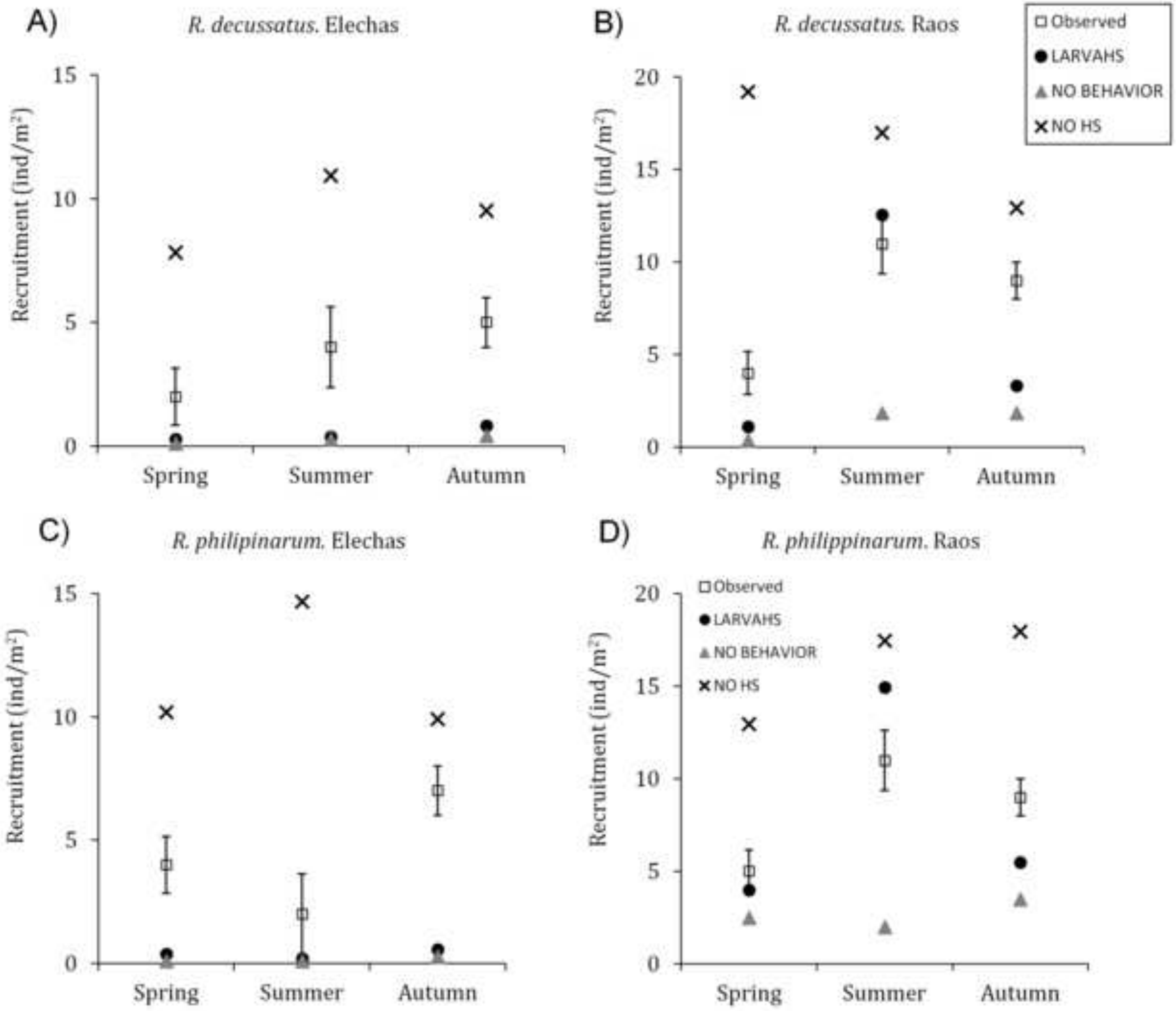
A)
R. decussatus. Elechas
Recruitment (ind/m²)
0
5
10
15
Spring
Summer
Autumn
B)
R. decussatus. Raos
Recruitment (ind/m²)
0
5
10
15
20
Spring
Summer
Autumn
□ Observed
● LARVAHS
▲ NO BEHAVIOR
× NO HS
C)
R. philipinarum. Elechas
Recruitment (ind/m²)
0
5
10
15
Spring
Summer
Autumn
D)
R. philippinarum. Raos
Recruitment (ind/m²)
0
5
10
15
20
□ Observed
● LARVAHS
▲ NO BEHAVIOR
× NO HS
Spring
Summer
Autumn

Figure 4 color
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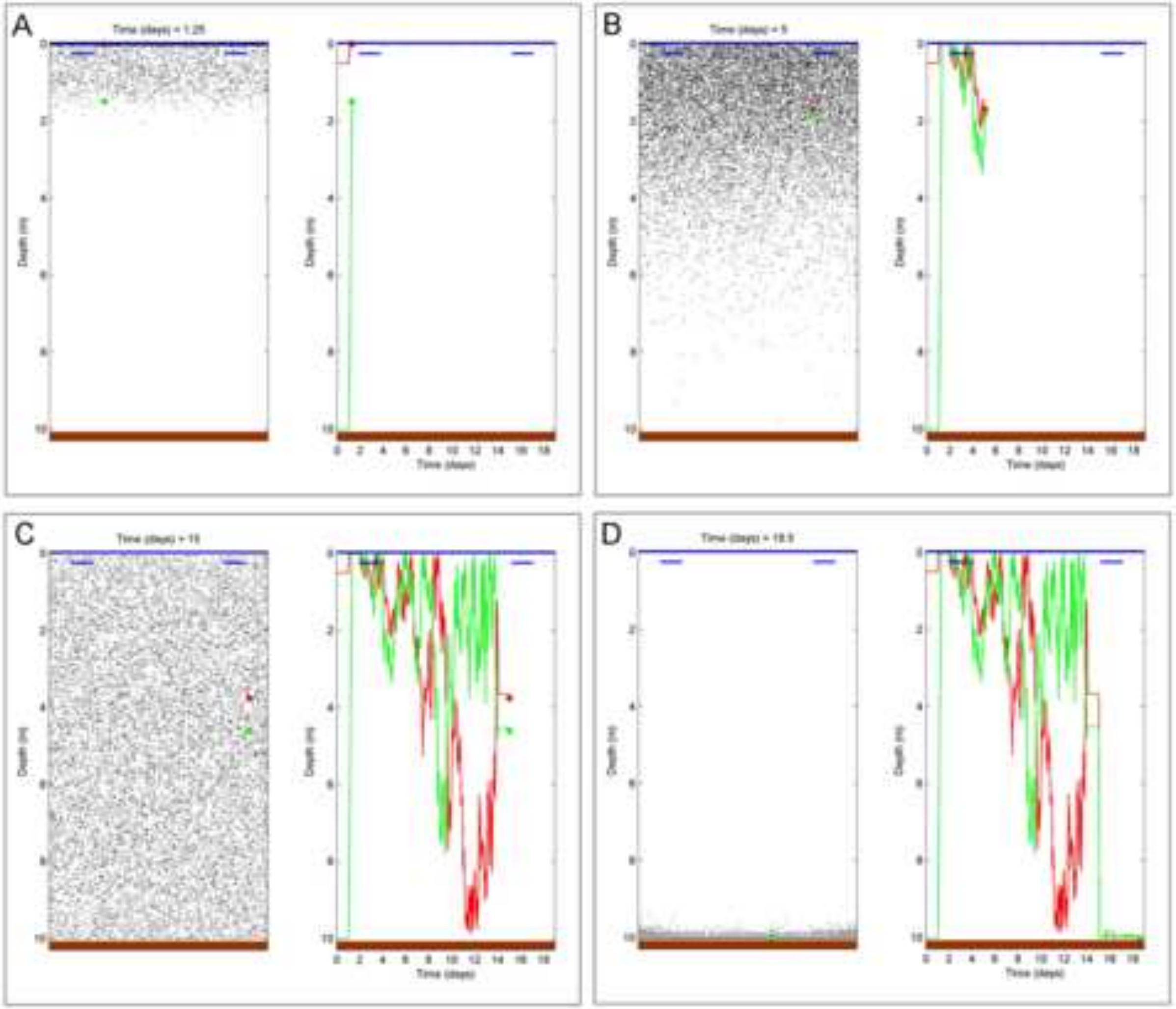

Figure 4 black white

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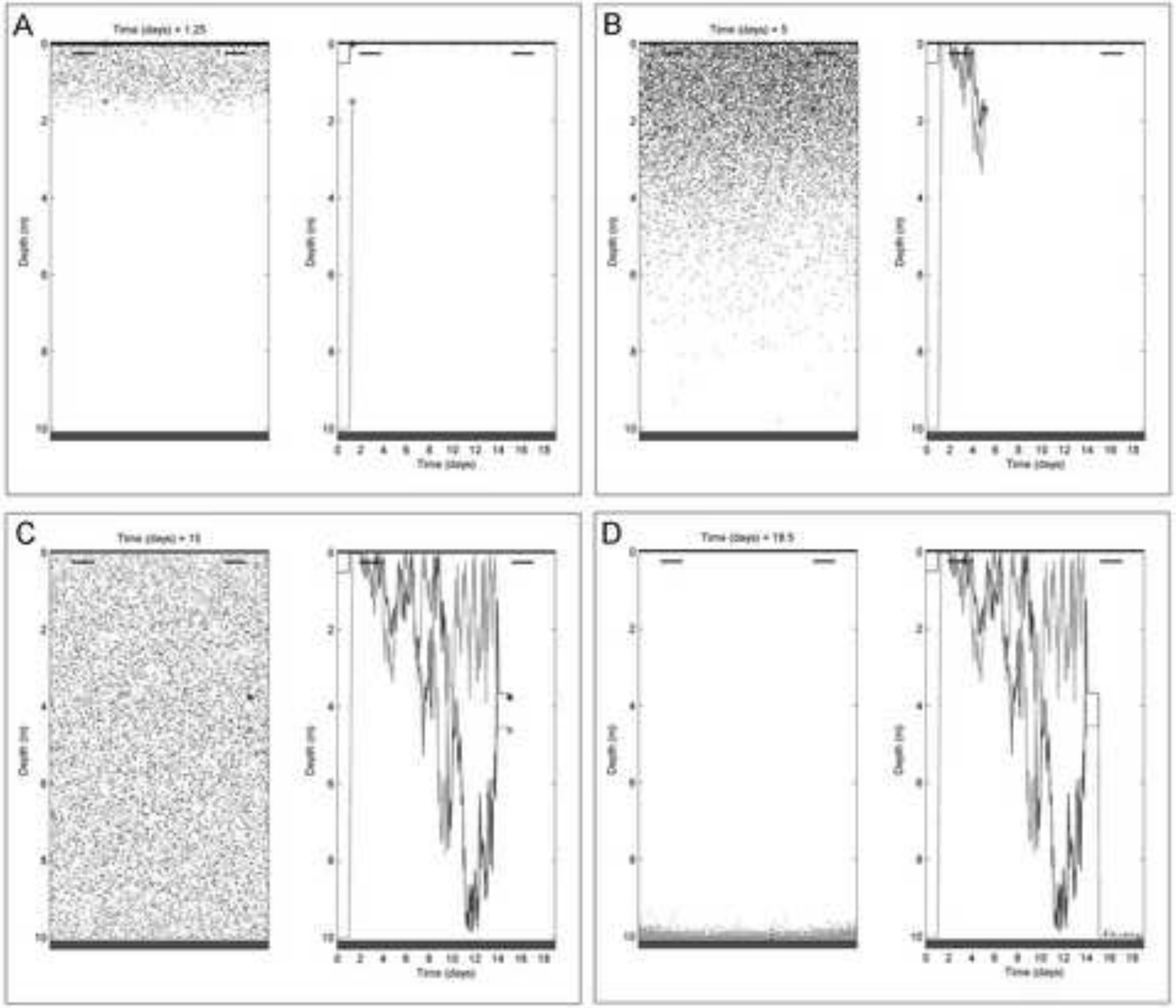

Figure 5 color

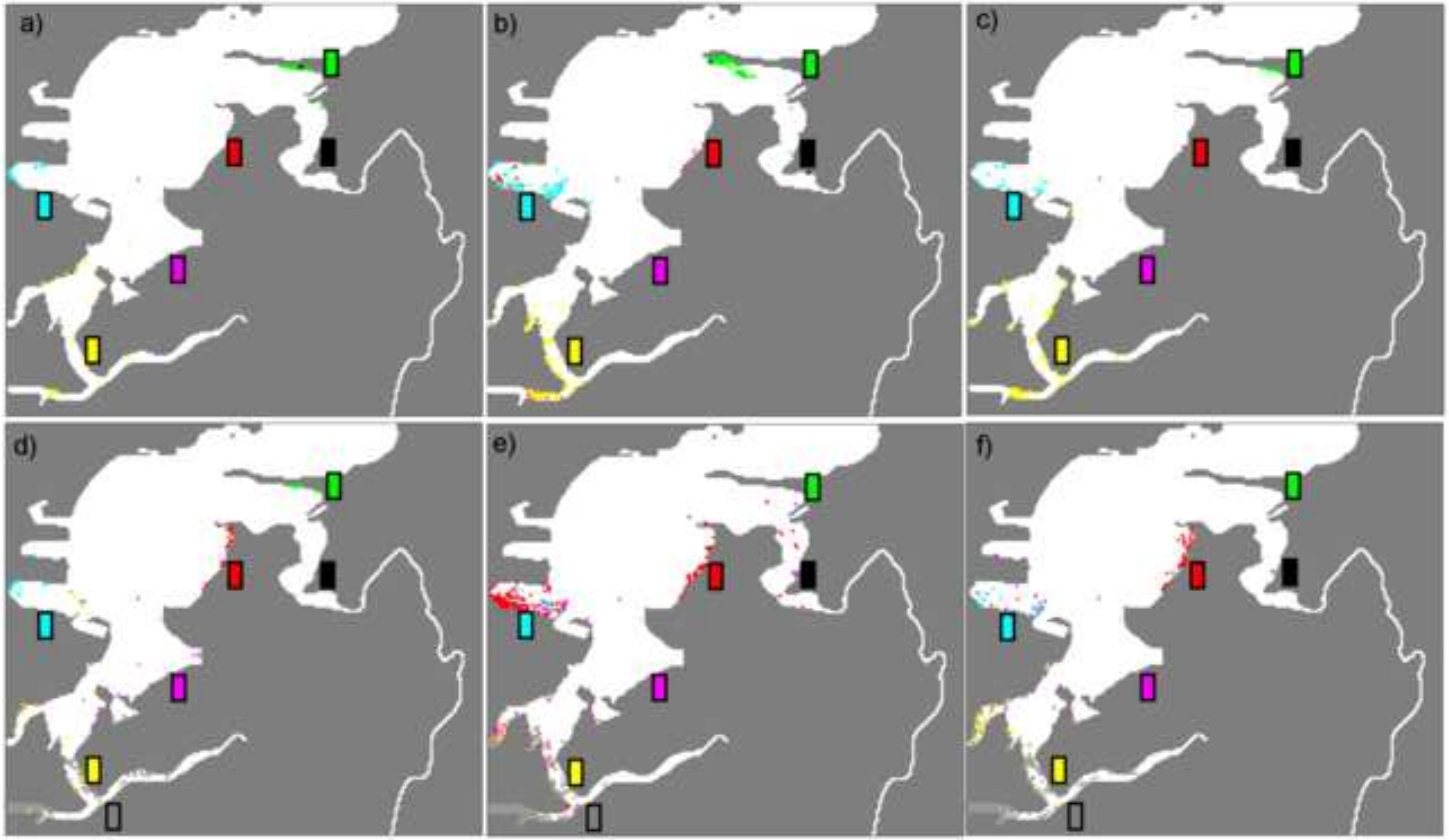

Figure 5 black white

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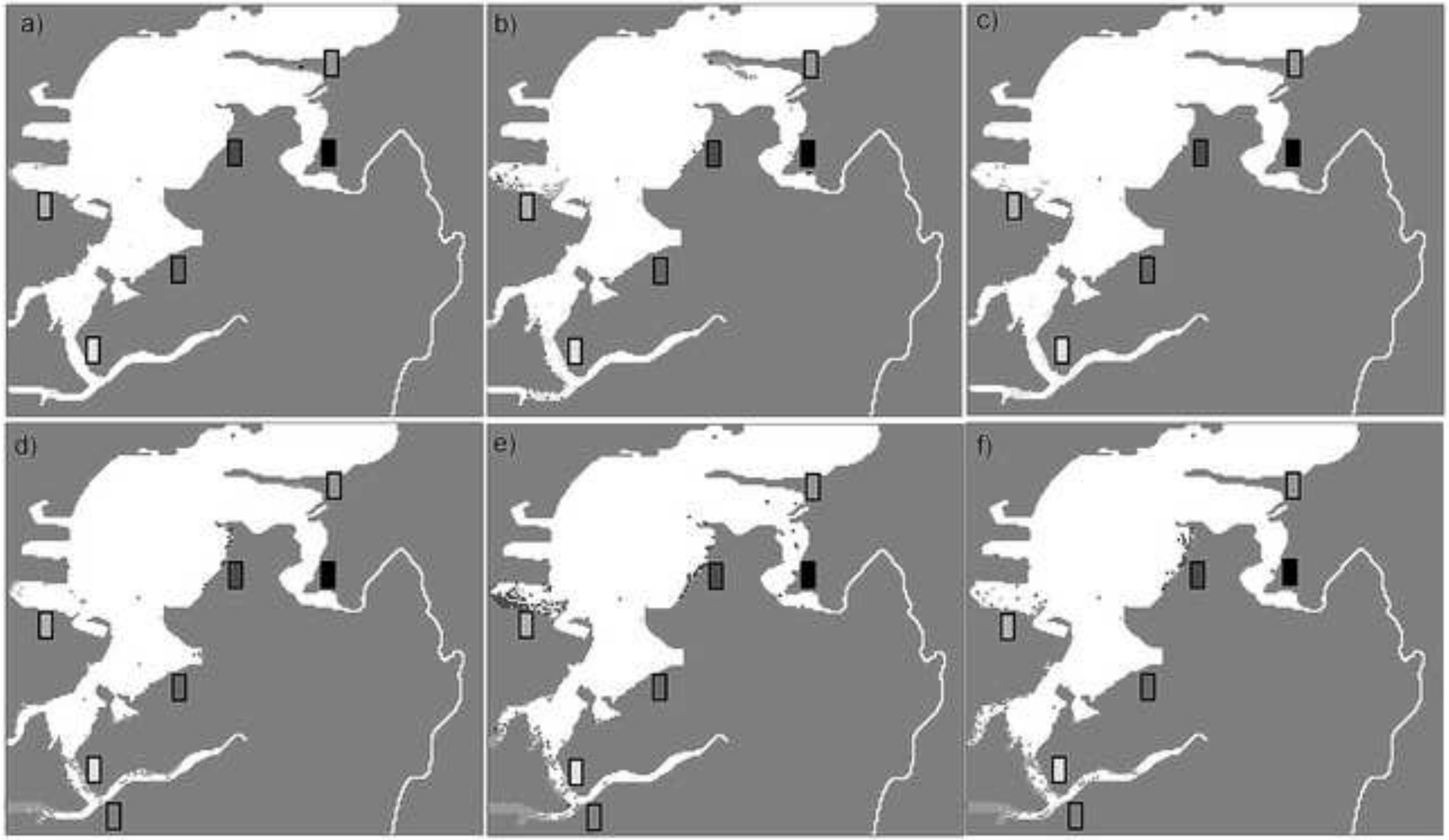

Figure 6 color

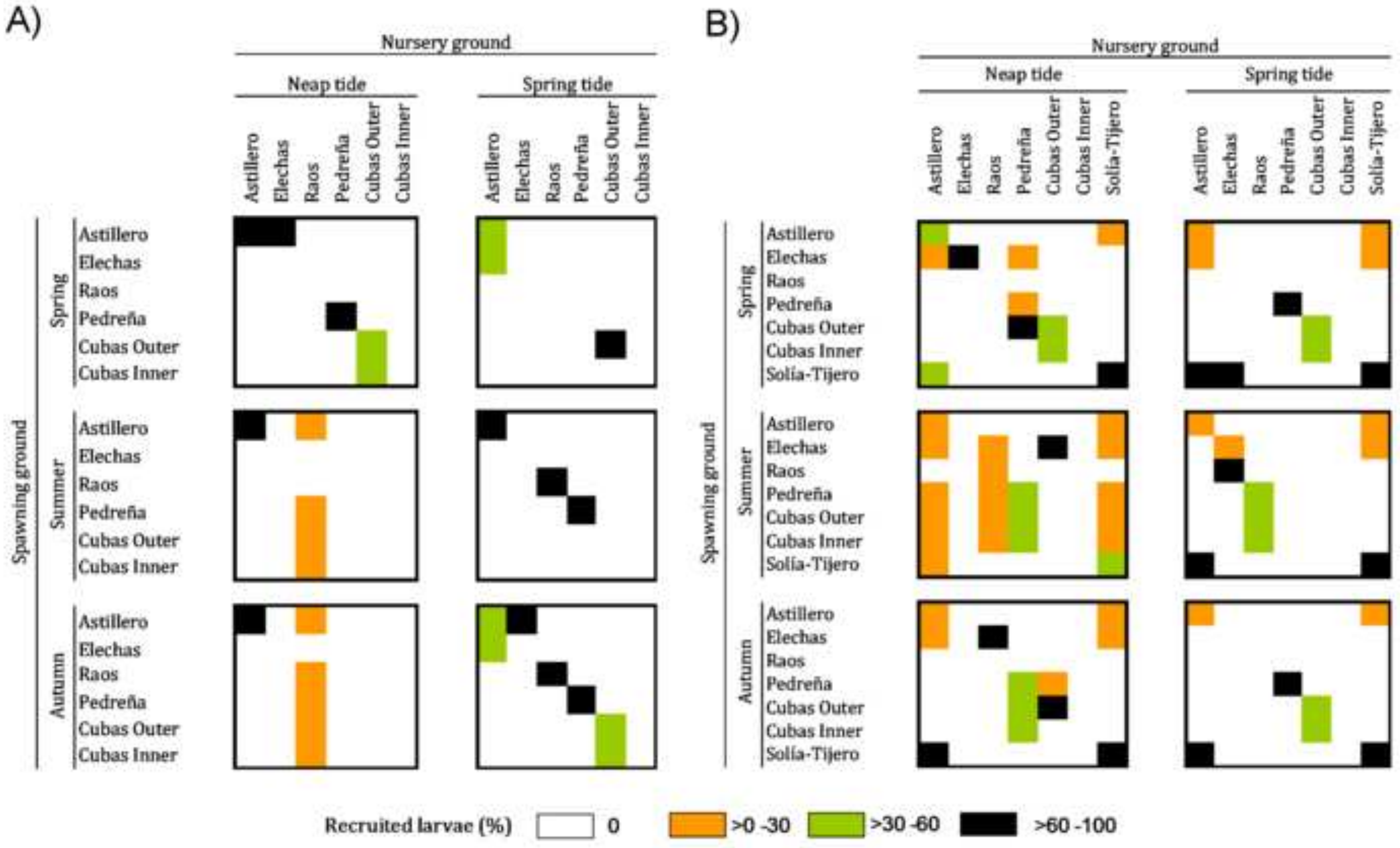

Figure 6 black white

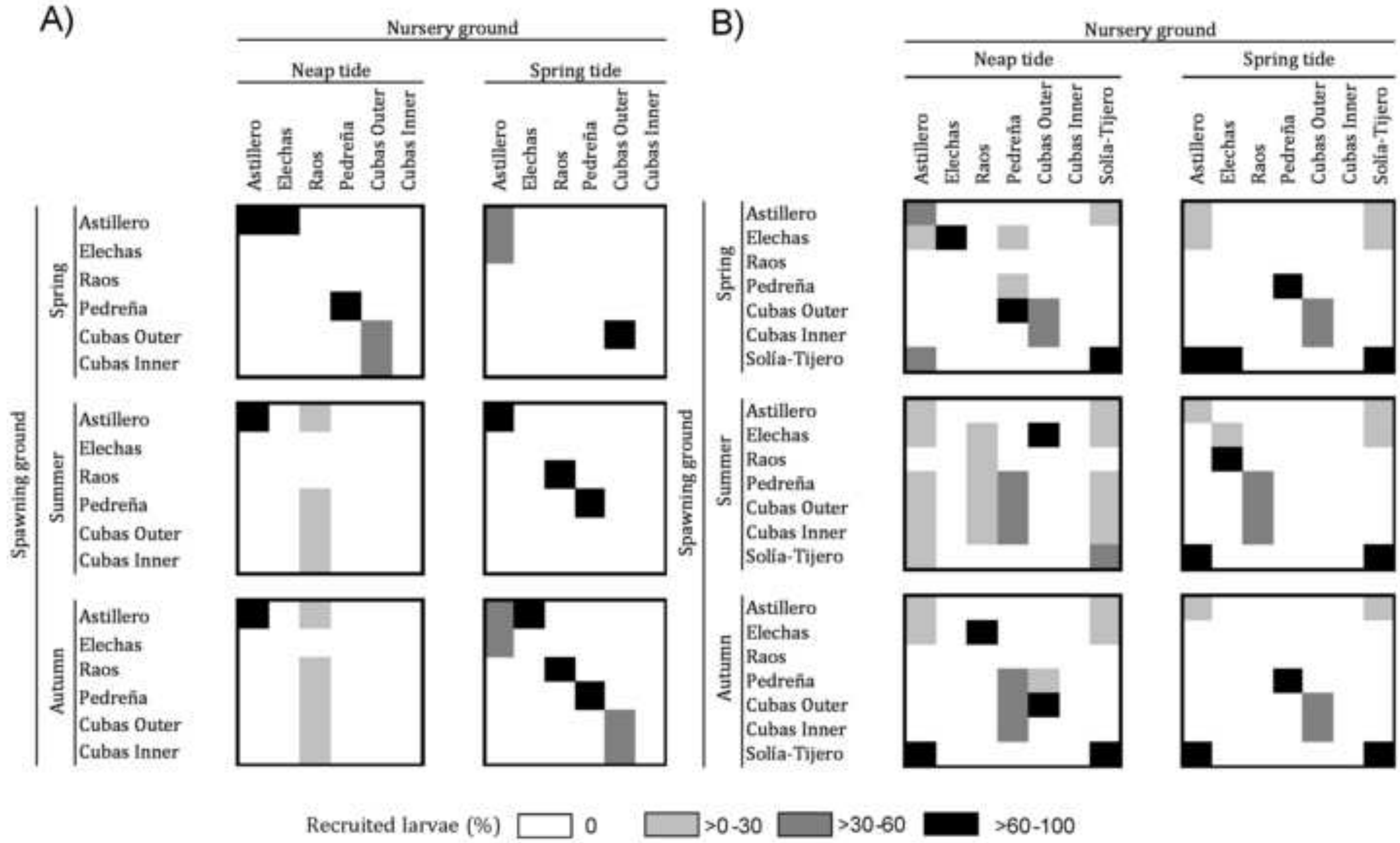

Figure 7

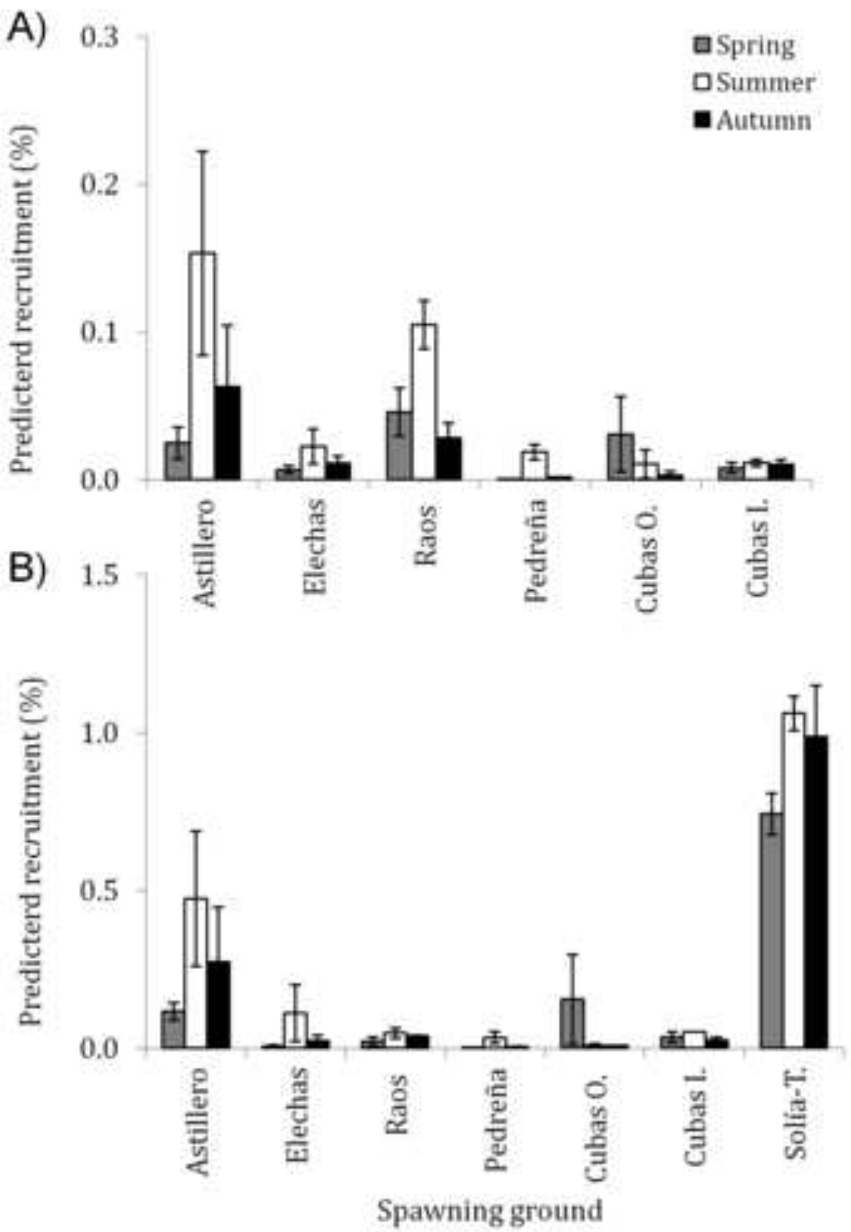
A)
B)
Predicterd recruitment (%)
0.0
0.1
0.2
0.3
0.5
1.0
1.5
▨ Spring
☐ Summer
■ Autumn
Astillero
Elechas
Raos
Pedreña
Cubas O.
Cubas I.
Solía-T.
Spawning ground

Figure 8

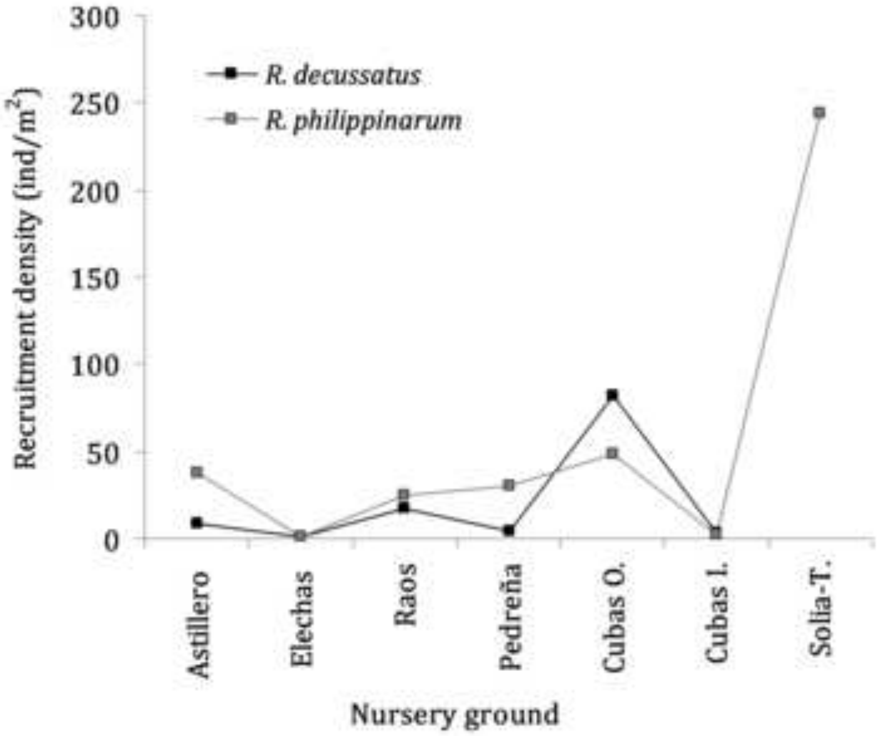
300
250
200
150
100
50
0
Recruitment density (ind/m^2)
R. decussatus
R. philippinarum
Astillero
Elechas
Raos
Pedreña
Cubas O.
Cubas I.
Solia-T.
Nursery ground

Table 1

Life cycle	**Life days** *R. decussatus*	**Life days** *R.philippinarum*	**Swimming capability**	**Direction and movement probability**	**Swimming speed** (mm/s)
Egg	0 – 1	0 – 1	No	0	0
Trocophore Larvae	1 – 2	1 – 2	Yes	90% chance of move up	0.5
D, Umbo Larvae	2 – 14	2 – 10	Yes	Probabilities that shift their distribution from the upper layer to the lower layer as they increase in age, from a 51% chance of move up in each time step to a 51.7% chance of swimming down (linear function of particle age).	0.5-3 (speed increases linearly with age)
Pediveliger Larvae	15 – 21	10 – 15	Yes	100% chance of move down and stay within a 1 m water column from sea-bottom. In this water column, 50% chance of move up and 50% chance of move down	3

Table 1- Summary of larval behavior for *R. decussatus* and *R. philippinarum*. It details, for egg and larval phases, the duration (life days) and the capability and the vertical swimming behavior, adapted from Suzuki et al. (2002), Kuroda (2005), Ishii et al. (2005) and North et al. (2006:2008).

Table 2

Run	Season	Tide	Zone of release	Released (n)		Recruited LARVAHS (%)		Recruited NO BEHAVIOR (%)		Recruited NO HS (%)	
				R. dec.	*R.phil.*	*R. dec.*	*R.phil.*	*R.dec.*	*R. phil.*	*R. dec.*	*R. phil.*
1-37	Spring	Neap	Astillero	187922	127912	0.036	0.144	0.009	0.027	0.461	1.027
2-38	Spring	Neap	Elechas	75924	332893	0.009	0.011	0.001	0.002	0.282	0.639
3-39	Spring	Neap	Raos	67704	50127	0.062	0.036	0.019	0.000	0.690	0.804
4-40	Spring	Neap	Pedreña	164052	963480	0.001	0.003	0.001	0.002	0.215	0.460
5-41	Spring	Neap	Cubas O.	813750	26908	0.005	0.015	0.006	0.030	0.191	0.628
6-42	Spring	Neap	Cubas I.	44485	5724	0.004	0.017	0.001	0.001	0.234	0.384
43	Spring	Neap	Solía-T.	–	100812	–	0.808	–	0.410	–	1.587
7-44	Spring	Spring	Astillero	187922	127912	0.014	0.089	0.007	0.051	0.337	0.818
8-45	Spring	Spring	Elechas	75924	332893	0.004	0.002	0.001	0.001	0.203	0.353
9-46	Spring	Spring	Raos	67704	50127	0.030	0.006	0.008	0.000	0.439	0.722
10-47	Spring	Spring	Pedreña	164052	963480	0.001	0.004	0.001	0.002	0.115	0.242
11-48	Spring	Spring	Cubas O.	813750	26908	0.056	0.297	0.018	0.390	0.187	0.717
12-49	Spring	Spring	Cubas I.	44485	5724	0.011	0.052	0.009	0.035	0.200	0.524
50	Spring	Spring	Solía-T.	–	100812	–	0.676	–	0.290	–	1.514
13-51	Summer	Neap	Astillero	187922	127912	0.222	0.687	0.029	0.350	1.480	1.623
14-52	Summer	Neap	Elechas	75924	332893	0.034	0.200	0.026	0.230	0.994	1.225
15-53	Summer	Neap	Raos	67704	50127	0.089	0.064	0.021	0.074	1.219	1.319
16-54	Summer	Neap	Pedreña	164052	963480	0.024	0.051	0.021	0.220	0.914	0.909
17-55	Summer	Neap	Cubas O.	813750	26908	0.001	0.004	0.001	0.015	0.536	0.766
18-56	Summer	Neap	Cubas I.	44485	5724	0.009	0.052	0.013	0.080	0.722	0.908
57	Summer	Neap	Solía-T.	–	100812	–	1.115	–	0.360	–	1.718
19-58	Summer	Spring	Astillero	187922	127912	0.084	0.260	0.070	0.210	0.973	1.202
20-59	Summer	Spring	Elechas	75924	332893	0.011	0.021	0.022	0.097	0.898	0.920
21-60	Summer	Spring	Raos	67704	50127	0.121	0.032	0.038	0.068	1.393	1.231
22-61	Summer	Spring	Pedreña	164052	963480	0.013	0.016	0.020	0.070	0.934	0.890
23-62	Summer	Spring	Cubas O.	813750	26908	0.020	0.015	0.002	0.019	0.964	0.951
24-63	Summer	Spring	Cubas I.	44485	5724	0.013	0.052	0.002	0.052	0.951	0.978
64	Summer	Spring	Solía-T.	–	100812	–	1.006	–	0.090	–	1.746
25-65	Autumn	Neap	Astillero	187922	127912	0.104	0.447	0.013	0.260	0.934	1.256
26-66	Autumn	Neap	Elechas	75924	332893	0.016	0.041	0.007	0.290	0.352	0.589
27-67	Autumn	Neap	Raos	67704	50127	0.018	0.038	0.062	0.110	0.634	0.844
28-68	Autumn	Neap	Pedreña	164052	963480	0.002	0.004	0.001	0.016	0.308	0.643
29-69	Autumn	Neap	Cubas O.	813750	26908	0.000	0.007	0.001	0.001	0.392	0.699
30-70	Autumn	Neap	Cubas I.	44485	5724	0.013	0.035	0.009	0.068	0.378	0.681
71	Autumn	Neap	Solía-T.	–	100812	–	1.149	–	0.310	–	1.769
31-72	Autumn	Spring	Astillero	187922	127912	0.021	0.101	0.007	0.069	0.358	0.817
32-73	Autumn	Spring	Elechas	75924	332893	0.007	0.005	0.001	0.001	0.248	0.412
33-74	Autumn	Spring	Raos	67704	50127	0.038	0.040	0.010	0.002	0.809	0.790
34-75	Autumn	Spring	Pedreña	164052	963480	0.002	0.006	0.001	0.001	0.288	0.553
35-76	Autumn	Spring	Cubas O.	813750	26908	0.006	0.007	0.002	0.001	0.292	0.810
36-77	Autumn	Spring	Cubas I.	44485	5724	0.007	0.017	0.001	0.001	0.396	0.699
78	Autumn	Spring	Solía-T.	–	100812	–	0.824	–	0.190	–	1.722

Table 2 – Predicted recruitment scores (%) for simulated *R. decussatus* (*R. dec*) and *R. philippinarum* (*R. phil.*) eggs released (= released particles x 10^5) from each spawning zone (Astillero, Elechas, Raos, Pedreña, Cubas Outer, Cubas Inner, Solía-Tijero) in each seasonal (spring, summer and autumn) and tidal amplitude (spring or neap tides) scenario, for a total of 36 runs for *R. decussatus* (1-36, left digit in column 1) and 42 for *R. philippinarum* (37-78, right digit in column 1). Results computed by (1) LARVAHS model, (2) LARVAHS model with no

behavior submodel (NO BEHAVIOR) and LARVAHS model with no habitat suitability based recruitment submodel (NO HS) are presented.

Table 3

Species	Recruiment succes (%)			ANOVA test				
	LARVAHS	**NO BEHAVIOR**	**NO HS**	**df**	**SS**	**MS**	**F**	**p**
R. decussatus	0.03 ±0.01 **A**	0.01 ±0.002 **B**	0.58 ±0.06 **C**	2	75.8	37.9	122.3	***
R. philippinarum	0.20 ±0.05 **A**	0.11 ±0.02 **B**	0.93 ±0.06 **C**	2.0	70.0	35.0	37.7	***

Table 3 – Recruitment success (%, Mean ± SE) for *R. decussatus* (n= 36 simulations) and *R. philippinarum* (n=42) obtained using (i) the LARVAHS model, which incorporates larval behavior and habitat suitability based recruitment submodel, (ii) LARVAHS model with no behavior submodel (NO BEHAVIOR) and) (iii)LARVAHS model with no Habitat Suitability based recruitment submodel (NO HS). Results of the analysis of variance between recruitment obtained using different models are presented at right (*= p<0.05; **= p<0.001; ***= p <0.0001). Tukey HSD – test results are presented by letters (A, B, C) placed after each model mean. If any two means have at least one letter in common, they are not significantly different.

Table 4

	Recruitment succes (%)					
R. decussatus	*df*	*SS*	—	*MS*	*F*	*p*
Season	2	1.814	13.5	0.907	4.97	0.002 *
Tide	1	0.033	2.4	0.033	0.07	0.80
Spawning zone	5	8.381	62.2	1.680	9.19	0.001 *
Season x Tide	2	0.001	0.01	0.001	0.001	1.00
Season x Spawning zone	10	0.016	0.1	0.002	1.76	0.14
Tide x Spawning zone	5	2.927	21.7	0.585	2.70	0.04 *
Total		13.17				
R. philippinarum						
Season	2	2.140	8.0	1.068	3.90	0.04 *
Tide	1	0.258	0.9	0.258	0.37	0.55
Spawning zone	6	19.26	71.9	3.209	21.84	0.0001 ***
Season x Tide	2	0.061	0.2	0.181	0.17	0.89
Season x Spawning zone	12	3.190	11.9	0.262	1.78	0.12
Tide x Spawning zone	6	1.879	7.0	0.313	1.69	0.16
Total		26.78				

Table 4 – Multifactorial analysis of variance observed in recruitment. Three explanatory variables are considered: Tide amplitude (at which the runs start: neap or spring tide) and Season (at which the run executes; spring, summer and autumn were the seasons considered, governed by different predominating winds) which account for different hydrodynamic conditions and the Spawning zone from where the particles or eggs are released. Df: degrees of freedom, the sum of squares (SS) and the mean sum of square (MS) are estimates of the variance attributed to the explanatory variable. The ratio between SS and SST (total sum of squares) x 100 represents the contribution in percentage of the each factor to the overall variance. F is the statistic of the analysis of variance and the p-value corresponds to the probability that there is no difference in means between the different levels of the explanatory variable, and therefore significant effects can be deduced from $p < 0.05$ highlighted by an asterisks (*= $p<0.05$; **= $p<0.001$; ***= $p<0.0001$).

Video S1

Video S2