



Assessment of larval connectivity in a sandy beach mole crab through a coupled bio-oceanographic model

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ABSTRACT

The biophysical mechanisms influencing larval distribution and their impacts on the metapopulation dynamics of sandy beaches, particularly the connectivity patterns associated with larval dispersal, are poorly understood. Here, we identify larval connectivity patterns of the mole crab *Emerita brasiliensis* in the coast of Uruguay. A biophysical individual based model (IBM) of larval transport was coupled to a regional high-resolution physical model to estimate the monthly and interannual variation of larval connectivity, as well as the impact of the length of the reproductive period on it. Larval connectivity showed marked interannual variations, which were mainly related to interannual changes in seasonal winds and associated ocean circulation patterns, particularly during La Niña years. The southernmost area where *E. brasiliensis* occurs only received larvae from the nearest release area in November and January spawning events during a strong La Niña year, characterized by intense northeasterly winds. The Uruguayan coast constitutes the leading (poleward) edge of the distribution of *E. brasiliensis*, where climate change effects are projected to intensify. Extrapolation of these results to a climate change scenario with stronger La Niña events, suggest that larval transport to southernmost beaches will become more probable.

1. Introduction

Connectivity, defined as the exchange of individuals among marine populations, is a central research topic in marine ecology. For most benthic species with complex life cycles, this exchange occurs primarily during the pelagic larval stage (Cowen and Sponaugle, 2009). Factors such as larval behavior (Woodson and McManus, 2007) and environmental conditions (e.g., winds, ocean currents) are the main contributors to larval retention and/or self-recruitment (Wing et al., 1998; Diehl et al., 2007). Ocean fronts, for example, generate circulation patterns that restrict larval exchange leading to higher genetic differentiation over relatively small spatial scales (White et al., 2010). In addition to physical conditions, the dispersal capacity of larvae also depends on the

planktonic larval duration (PLD), which affects the ecology and evolution of benthic marine populations through their effects on dispersal distance, the spread of sibling larvae, the level of larval mortality, and population connectivity (Burgess and Marshall, 2011). Larval recruitment variability in the coastal ocean depends on the interaction between a series of physical forcing factors, including winds (e.g. Roughgarden et al., 1988; Wing et al., 1998; Roegner et al., 2007; Morgan et al., 2009, 2011) and currents (Queiroga et al., 2005, 2006).

Physical and biological factors are main driving forces of community and population patterns in macrofauna inhabiting sandy beach ecosystems (Defeo and McLachlan, 2005; Fanini et al., 2020). Particularly, the species development strategy may affect the distribution patterns. In this context, sandy beach species have two development strategies

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(McLachlan and Defeo, 2018): (1) internal fertilization, direct development, sometimes with parental care, and low fecundity (e.g., whelks, peracarids); and (2) external fertilization, high fecundity and planktonic larvae (e.g., clams). In the latter, the planktonic larval stage is the main dispersal phase that has a pivotal role in connectivity (Cowen and Sponaugle, 2009). The larvae of many intertidal species develop in the nearshore and must cross the surf zone to complete their onshore migration to benthic adult habitats (Shanks et al., 2015; Brown et al., 2019). However, connectivity patterns between sandy beaches related to larval dispersal are still to be explored, and mechanisms that influence the larval distribution and its consequences in the metapopulation dynamics are poorly understood (McLachlan and Defeo, 2018).

The Uruguayan coast extends for nearly 400 km from the inner and brackish Río de la Plata (RdIP) estuary to the marine Southwestern Atlantic Ocean shores (Lercari and Defeo, 2015). Crustaceans constitute a conspicuous component of Uruguayan sandy beaches. Among them, the mole crab *Emerita brasiliensis* is an intertidal filter feeder found in reflective and dissipative beaches of the Atlantic coast of South America, from Venezuela to Uruguay (Defeo and Cardoso, 2002; Celentano et al., 2010). The mole crab presents a complex life cycle, with a planktonic larval phase that develops in the nearshore during 2–3 months and an adult benthic phase (Otegui and Soares-Gomes, 2007). The precise distribution of *E. brasiliensis* larvae in the water column is not known; however, larvae for the congeneric *Emerita analoga* in Chile are found in the upper 15 m of the water column (Veas et al., 2013). The relatively long larval phase could imply a high dispersal potential, and larvae transport by the coastal circulation could be an important factor in determining its local and latitudinal distribution (Sorte et al., 2001). It is known that first and last larval stages of *E. brasiliensis* are concentrated near the coast. Veloso and Valentin (1993) proposed that larval stages would stay close to the coast, being kept in circulation cells until reaching the megalopa stage. This has been reported as a common pattern in *Emerita* species (Efford, 1970). The length of reproductive and recruitment seasons of *E. brasiliensis* in Uruguay presents interannual variability, both being longer in warm years (Celentano and Defeo, 2016). Particularly, during La Niña events, the coast of Uruguay is characterized by a stronger influence of warm oceanic tropical waters that promote the abundance and individual growth of this species (Celentano and Defeo, 2016).

Coupled bio-oceanographic models are useful tools for assessing connectivity patterns in marine species. Notably, individual based models (IBM) allow observing different regions of population isolation

as a function of larval dispersal (Cowen et al., 2007). In this paper, larval connectivity patterns of *E. brasiliensis* in the coast of Uruguay were assessed through a coupled bio-oceanographic model in order to: 1) evaluate the interannual variability of larval connectivity and its possible relation with ocean circulation; and 2) determine the effects of the length of reproductive period in the connectivity of *E. brasiliensis*.

2. Materials and methods

2.1. Regional oceanography

In the study area, the RdIP flows into the Southwestern Atlantic Ocean generating an estuarine system of about 35,000 km², with 5–15 m water depth (Guerrero et al., 1997). Seasonal patterns are observed in climatic and oceanographic features, with fall-winter being characterized by a balance between onshore and offshore winds and a maximum in the continental drainage, generating a NNE drift of the estuarine waters along the Uruguayan coast (Guerrero et al., 1997). Regional winds undergo large seasonal variations (Palma et al., 2004): during austral spring-summer, north-northeasterly winds are dominant and a minimum runoff is observed, resulting in southwestward advection of low-salinity waters (Guerrero et al., 1997). Consequently, in spring-summer shelf waters penetrate the estuary up to Punta del Este in Uruguay, near José Ignacio (Fig. 1) (Guerrero et al., 1997).

El Niño Southern Oscillation (ENSO) events have a strong influence in the region, especially on wind patterns and precipitation (Barreiro, 2010). Some El Niño years are associated with northeasterly winds, others with southwesterly winds and others have no well-defined wind direction. La Niña events are characterized by below average RdIP discharges and northeasterly winds (Matano et al., 2014). On a regional scale, the seasonal variability of the RdIP plume appears to be controlled by the variability of the alongshore wind stress. However, at interannual time scales the effects of anomalies of alongshore wind and precipitation over southeast South America act to compensate each other, preventing large northeastward river plume extensions associated with large outflow events (Piola et al., 2005). La Niña years, which are associated with relatively low continental discharges, may still induce expanded northeastward coastal plumes in response to anomalously strong southwesterly winds.

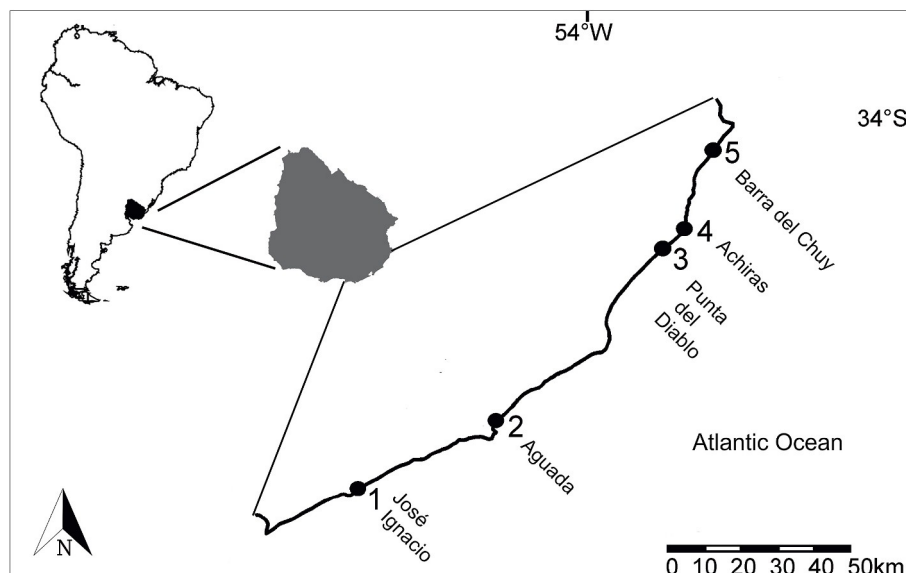


Fig. 1. South Atlantic Ocean with the coast of Uruguay and the geographical location of sandy beaches selected as release/recruitment areas for *E. brasiliensis*.

2.2. Hydrodynamic and biophysical model

E. brasiliensis larval connectivity (i.e., the exchange of individuals among areas along the coast of Uruguay) was assessed through a spatially explicit IBM of larval transport coupled to hydrodynamic model outputs of a 3-D interannual configuration of an implementation of the Regional Oceanic Modeling System (ROMS) at nearly 3.8 km resolution for the period 2000–2012.

The physical model used for this study is detailed in Matano et al. (2014). For the sake of completeness, a summary of the model configuration is detailed. The model grid, which covers the coast of Uruguay, extends from 66°W to 44°W and from 44°S to 25°S with a 1/24° spatial resolution (~3.8 km) and 40 terrain-following vertical levels, with enhanced resolution at the surface. The bottom topography was derived from the ETOPO1 (1° resolution) (Amante and Eakins, 2009), which was smoothed to minimize the pressure gradient errors associated with terrain following coordinates (Mellor et al., 1994). The model includes a daily discharge of the RdIP, a constant discharge of 2,000 m³ s⁻¹ from the Patos/Mirim lagoons and five tidal harmonics (M₂, S₂, N₂, K₁, and O₁). At the surface, the model is forced by the QuikSCAT (the period 2000–2007) and ASCAT (period 2008–2012) daily wind stress and by climatological heat and freshwater fluxes from the COADS data set.

For the initial condition and lateral open boundaries, the model uses the solution of an ocean model experiment using a 1/12° resolution grid of the Southwest Atlantic nested into a 1/4° resolution grid of the southern hemisphere. The latter experiment and its performance are described in Combes and Matano (2014). The model resolution is adequate to study larval dispersal along a relatively homogeneous sandy shoreline with straight isobaths, as is the case of the study area. This circulation model reproduces very well ocean currents (Fig. S1 and S2) and has already been used in dispersal studies (Franco et al., 2018). The IBM was executed in the Ichthyop code (Lett et al., 2008), and connectivity between areas adjacent to sandy beaches was computed for larvae that successfully reached a recruitment area, according to the criteria and scenarios described below.

2.3. Biological model: sites and timing of larval release

Mole crabs are typical burrowing forms found on exposed sandy beaches (McLachlan and Defeo, 2018). A macroscale study of *E. brasiliensis* shows a clear shift from continuous reproduction in subtropical sandy beaches to discontinuous reproduction in temperate sandy beaches (Defeo and Cardoso, 2002). *E. brasiliensis* larvae hatch as zoea from eggs carried by adult females (Delgado and Defeo, 2006), which in temperate beaches of the coast of Uruguay are mainly observed from November to April (Celentano and Defeo, 2016). Therefore, for modeling purposes, and to evaluate temporal variations in larval connectivity, larvae were released in spawning events in three different months: November as the start of the reproductive season, January an intermediate month in the reproductive season and April as the last possible date for larval hatching.

Five areas adjacent to sandy beaches (spawning and recruitment zones where larvae are released in the model) were defined as starting point for individual larval transport following the morphology of the coast of Uruguay (Fig. 1). From south-west to north-east, larvae recruitment areas were adjacent to the oceanic sand beaches Jose Ignacio (1), Aguada (2), Punta del Diablo (3), Achiras (4) and Barra del Chuy (5). Areas 2 to 5 were designed as release and recruitment areas; area 1 does not exhibit ovigerous females (Celentano and Defeo, 2006), and therefore it can be defined as a sink area. This categorization of sink/source areas for *E. brasiliensis* is based on population analysis detailed in Celentano and Defeo (2006) and Celentano et al. (2010).

2.4. Transport duration and recruitment success

The larval development of *E. brasiliensis* varies between two and

three months depending on water temperature (Veloso and Valentin, 1993; Otegui and Soares-Gomes, 2007). Laboratory experiments indicate that the duration of *E. brasiliensis* larval stage correlates positively with water temperature (mean PLD is 49 days at 24–26 °C and 90 days at 18–20 °C, Otegui and Soares-Gomes, 2007). Hence, four different PLDs of 50, 60, 80 and 90 days (from hatching to megalopa) were used in the IBM to deal with water temperature variability in the coastal ocean during different release months. The IBM did not model larval growth as a function of temperature, but used drift of particles with a constant weight for the PLD scenarios defined above.

Along the coast of Uruguay, mole crab recruitment to the benthic population mainly occurs between February and May, but it can eventually extend until June (Celentano and Defeo, 2016). Though there is no information on larval behavior, larvae of the congeneric *E. analoga* are weak swimmers, unable to stem water currents (Johnson, 1939), and they present no diel vertical migration behavior (Yannicelli et al., 2006). Consequently, a passive horizontal transport procedure was implemented for *E. brasiliensis*, using a forward Euler method with a time step of 0.75 h. The current velocities, temperature and salinity fields from ROMS simulations were interpolated in time to feed the IBM time step (Lett et al., 2008). Simulations consisted in tracking the locations and properties of the water where each individual simulated larva is located at each time step. A time step of 0.75 h was chosen in order to provide details on larval position in time (Meerhoff et al., 2018). A successful larva reached (or was found within) a “recruitment area” at the end of its PLD. Recruitment areas coincided with spawning areas (release areas), except for area 1 which was only a recruitment area. Since megalopa are good swimmers, further horizontal transport towards the intertidal was not considered.

To determine the interannual variability of larval connectivity, larval transport experiments using the model's current fields during the 2000–2012 period were run. A total of 12 years × 3 months of release × 1 depth × 4 PLD × 3 replicates were evaluated. For each case, 500,000 particles were released from randomly assigned coordinates within the different release areas, defined as a 10 km × 10 km region around each beach. The number of particles was assigned as a trade-off between computational constraints and actual larval density estimates in the region (Veloso and Valentin, 1993).

Since the release coordinates of each individual are assigned randomly in the model (Lett et al., 2008), the number of larvae released differed among areas in the same simulation, as well as among simulations for the same area. To estimate connectivity from one area to another as the probability of a larva to reach successfully a recruitment area from a release area, the number of successful larvae was divided by the number of larvae released in each area at the given simulation. Relevant larval success probabilities were obtained from each simulation run.

In order to evaluate differences between simulations and to assess the relative importance of spawning month, PLD and spawning year on larval connectivity, the magnitude of effects of variance sources was estimated using analysis of variance (ANOVA) following Corell et al. (2012) and White et al. (2013). The variance components were calculated according to Underwood (1996) and a nested analysis ANOVA was used, with year and PLD as main factors, and month nested in year. Additionally, the effect of *E. brasiliensis* fecundity on connectivity was estimated using the abundance of ovigerous females in the spawning areas obtained from Uruguayan sandy beaches sampled bimonthly during 22 months (Celentano and Defeo, 2006). To this end, values of each column representing release areas in the connectivity matrix were multiplied by abundance to adjust connectivity values, following Garavelli et al. (2016).

Finally, interannual variability in wind and ocean surface currents were evaluated for years among which larval connectivity patterns showed conspicuous contrasts. Monthly data of surface wind were obtained from ERA-Interim reanalysis (<https://www.ecmwf.int/en/forecasts/datasets/archive-datasets/reanalysis-datasets/era-interim>),

which have a spatial resolution of 0.4° (Berrisford et al., 2011). Seasonal mean wind patterns were also calculated. Mean seasonal surface current maps were constructed using the hydrodynamical model velocities.

3. Results

3.1. Larval connectivity: interaction effects between interannual variability and months of spawning events

The highest connectivity probabilities were observed for November and January spawning events (50 and 60 days PLD), in both cases for self-recruitment in recruitment area or beach 5 (Fig. 2a–d). In these spawning events, the main connectivity pattern was southwestward, with highest probabilities of larval transport being observed from release area 5 to recruitment areas 3 and 4 (Figs. 2 and 3b) and from release area 4 to recruitment area 3. However, for release area 4 self-recruitment was higher than larval transport to recruitment area 3. In addition, there was interaction of spawning month with interannual variability: during November spawning release area 5 also supplied larvae to recruitment area 2 in 2000 and 2008, with low probabilities (Fig. 3a).

During April larval release, only longer PLDs are biologically significant (because water temperature is typically lower) and hence self-recruitment was not as important as in November and January

(Fig. 2). In addition, the direction of larval transport was towards the north-east (e.g. opposite to the main direction observed in November and January spawning events). The larval transport direction reverse during April was consistent with changes in surface ocean circulation, which was northeastwards in fall. The highest probabilities of larval transport were observed from release area 4 to recruitment area 5 when considering 80 and 90 days PLD, and from release area 2 to recruitment areas 3 and 5 (Fig. 2 e and f). The larval transport from release area 3 was very low because of the low number of ovigerous females in this area. The probability of larval transport from release area 4 to recruitment area 5 was one order of magnitude higher than transport from release area 3 to recruitment area 5 (Fig. 3c). Regardless of the month of larval release, there was no larval transport from release area 1 to the other recruitment areas, because the number of ovigerous females in this area was zero and therefore defined as a sink. The larvae that reached recruitment area 1 came from release area 2 only (Fig. 2).

The most important source of variation for larval connectivity was the interaction between year, month of larval release and PLD (Fig. 4). However, for larvae released from area 2 that reached recruitment area 1, the only critical sources of variance were the year and the interaction between year and month of larval release, with all PLDs showing the same pattern. In 2008, the highest connectivity probability was observed in January (Fig. 3a), while for larvae released in November there was high connectivity in 2005 and 2008 (Fig. 3b).

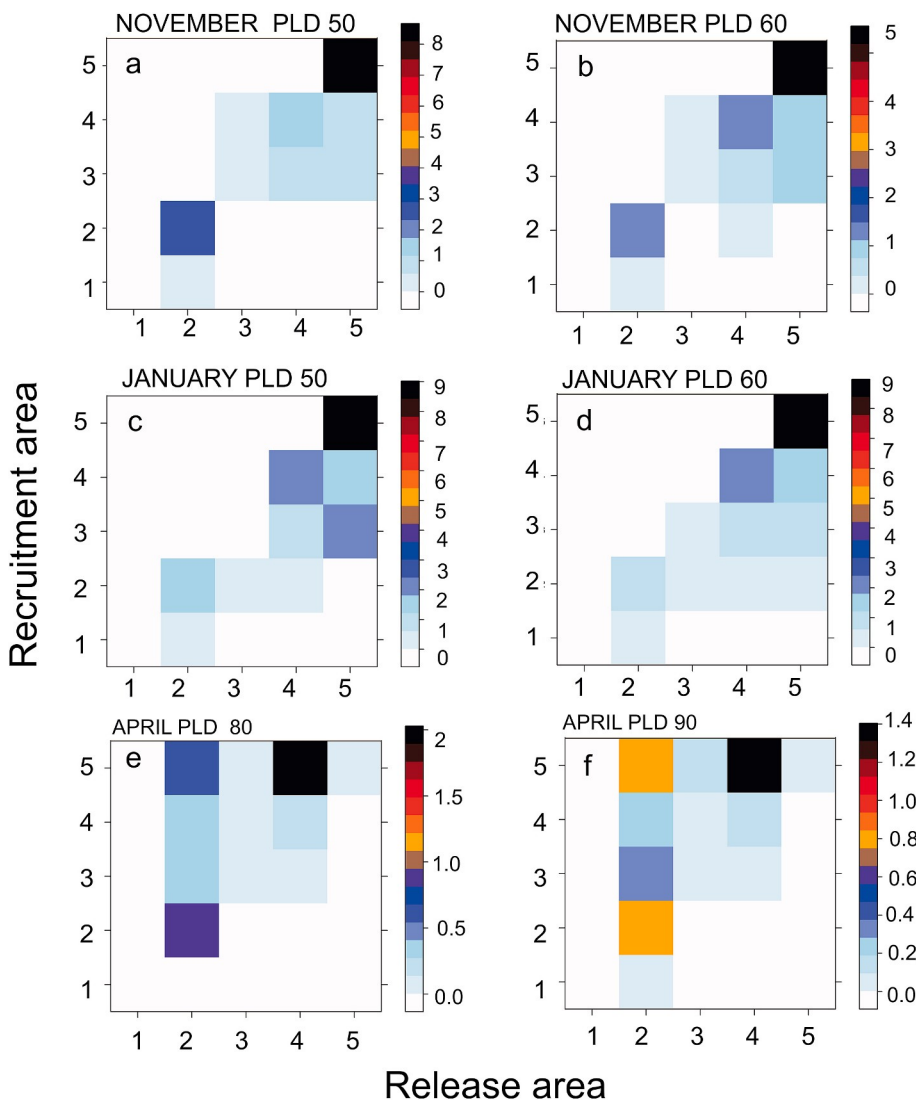


Fig. 2. Mean connectivity matrices for three different months of larval release and four planktonic larval duration (PLD in days). Twelve years of simulations and three replicates were averaged, and connectivity (here expressed as proportions in different color scales) was corrected by ovigerous female abundance in the release areas. Areas are numbered following Fig. 1. Only biologically significant PLD for the corresponding months are presented from all the results modelled. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

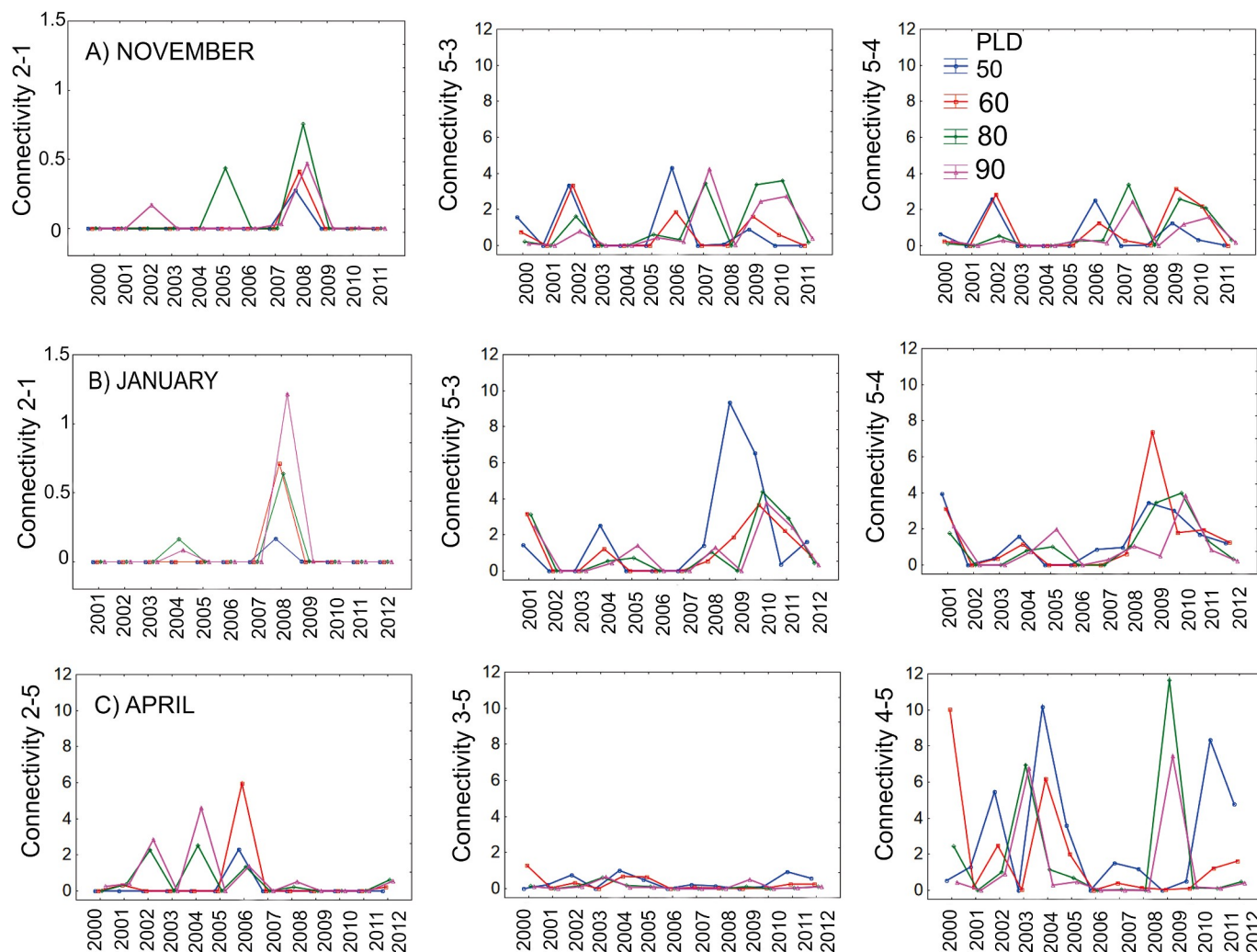


Fig. 3. *E. brasiliensis* connectivity between sandy beach recruitment areas for the period 2000–2012, corrected by female fecundity for larvae released in November (a), January (b) and April (c) and four planktonic larval duration (PLD, 50: blue, 60: red, 80: green, and 90 days: purple). Areas are numbered following Fig. 1. ROMS outputs started on April 2000 and therefore time series of summer connectivity started in 2001. Connectivity is presented from release area number # towards recruitment area # (e.g., Connectivity 2–5 means connectivity from release area 2 towards recruitment area 5. Note that connectivity towards area 1 is one order of magnitude minor than others). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Larval connectivity, wind patterns and ocean surface currents

Interannual changes in seasonal wind patterns were observed during La Niña events. In La Niña event 2000 (Fig. 5), an increase in northeasterly winds was observed during summer (maximum values of $5\text{--}6\text{ m s}^{-1}$). In La Niña 2008, easterly-northeasterly winds were also high during summer (4.5 m s^{-1} , Fig. 5), and in spring 2008 northeasterly winds were higher than in neutral years (maximum values of 6 m s^{-1}).

The mean seasonal pattern of surface currents showed that in summer, weak southwestward surface currents were apparent along the coast, and a similar pattern was observed during spring. In fall, northeastward coastal surface currents occurred (Fig. 6). In spring 2000 and 2008, surface currents were stronger (Fig. 7) than the mean seasonal pattern (Fig. 6).

Changes in larval connectivity patterns during different months of spawning events followed wind and surface current patterns. For example, for larvae released in November, larval connectivity from release area 5 to recruitment area 2 was observed only in 2000 and 2008 (Fig. 3). Both years were characterized by La Niña events: 2008 with anomalously strong easterly northeasterly winds during spring, and 2000 with mild northeasterly winds in spring (Fig. 5). In addition, larvae that reached recruitment area 1 came only from release area 2, with very

low probabilities only in November and January 2008 (Fig. 3), characterized by a La Niña event with stronger northeasterly winds in summer and spring than other years (Fig. 5) and stronger southwestward surface currents in the coast of Uruguay (Fig. 7). The seasonal surface currents (Fig. 7) and the alongshore current in the study area (Supplementary video) showed that southwestward surface currents in 2008 (La Niña year) explained the connectivity pattern observed from area 2 towards recruitment area 1. On the other hand, in summer and spring 2011 (also strong La Niña event), mean surface currents in the coast of Uruguay were offshore (Fig. 7), thus preventing larval transport from area 2 towards recruitment area 1.

During the April larval release, larval transport was northeastward, and only in 2006 and 2012 there was positive larval transport from release area 2 to recruitment areas 4 and 5 (Fig. 3c). In 2006, southerly winds in fall and south-westerly in winter, and in La Niña 2012 strong westerly winds in fall (Fig. 5) led to surface currents stronger (Fig. 7) than the mean seasonal pattern (Fig. 6) and the coastal surface current was northeastward (Fig. S3, Supplementary Material), which may have promoted larval transport between area 2 to recruitment areas 4 and 5.

There was no clear pattern of larval connectivity during El Niño years.

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.ecss.2020.107035>

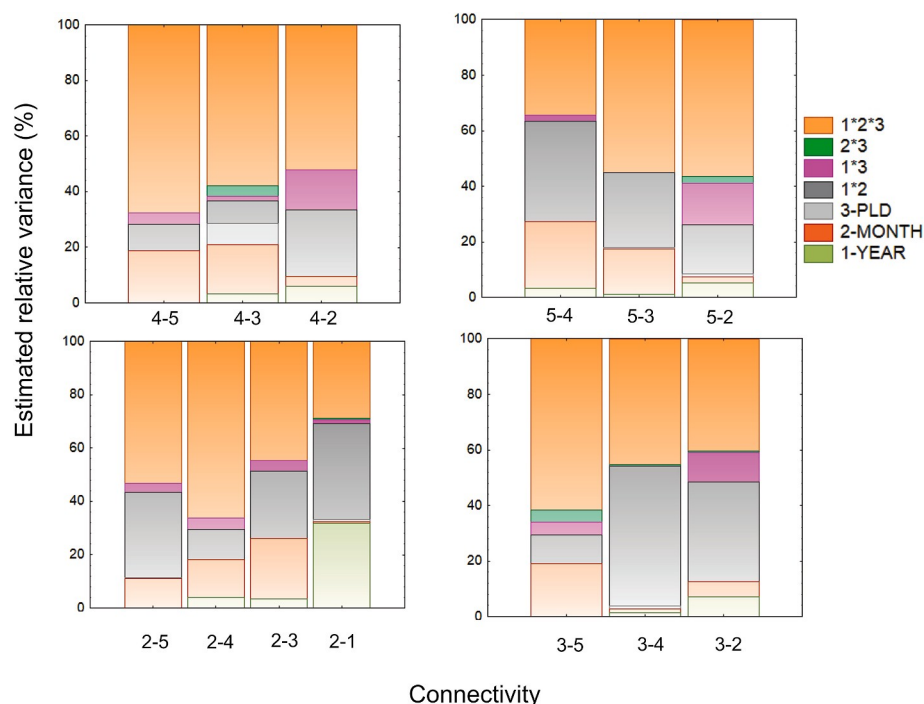


Fig. 4. Relative variance components (%) for *E. brasiliensis* larval connectivity in the coast of Uruguay, corrected by the abundance of ovigerous females per spawning area and calculated considering the factors year, month of larval release and planktonic larval duration (PLD). Year (1), month of larval release (2), and planktonic larval duration (PLD, 3) were used as components of the variance, and the interactions between factors are presented (i.e. 1 × 2: interaction of the factors year and month of larval release). Areas are numbered following Fig. 1.

4. Discussion

The coupled bio-oceanographic model developed here was a useful tool to assess: (1) the interannual variability in larval connectivity of the mole crab *Emerita brasiliensis* between sandy beaches; and (2) the effect of the length of the reproductive period on larval connectivity. In addition, variability in larval connectivity was observed depending on the month of the larval release or spawning event. During November and January, typical months for *E. brasiliensis* larval dispersal, the main larval transport was southwestward. In contrast, larvae released in April drifted northeastward. During winter, southwesterly winds create geostrophic currents that advect the freshwater of the RdIP northeastward (Palma et al., 2008; Matano et al., 2014). These patterns reverse in summer, when northeasterly winds advect relatively salty waters from the Brazilian shelf southward (Matano et al., 2014).

Larval connectivity of *E. brasiliensis* in the Uruguayan coast was asymmetric and presented interannual variability related to changes in wind patterns and surface currents, particularly during strong La Niña years. The ENSO signal generates complex climatic configurations that modify precipitation and wind patterns in this region (Barreiro, 2010), which in turn impact on the shelf circulation and water mass characteristics (Piola et al., 2005). During the analyzed period, La Niña events were characterized by below average RdIP discharges and northeasterly winds (Matano et al., 2014). However, wind patterns during La Niña events depend on the period of analysis. For example, during the 1950–2001 period (Piola et al., 2005), La Niña events were characterized by a decrease of the RdIP discharge, but there was no definite pattern of wind direction. These two forcing factors, RdIP discharge and wind direction, prevent or significantly weaken the northeastward penetration of low salinity waters derived from the RdIP. On the other hand, El Niño events have poorly defined wind patterns in the area: some events appear to be associated with northeasterly winds, others with southwesterly winds and others have no well-defined wind direction (Matano et al., 2014). Hence, the effect of strong La Niña events were reflected in larval connectivity patterns, but no clear patterns of larval connectivity emerged during El Niño years.

Wind effects on coastal currents have been proposed as a key explanatory factor of recruitment variability for *Emerita analoga* off the

coast of southern California (Wooldridge et al., 2016). Empirical data provided by Sorte et al. (2001) showed that *E. analoga* populations in Oregon occurred sporadically and appeared to be restocked by larvae drifting northward from California, and that increased northward transport occurred in winter during El Niño events, which are characterized by anomalously strong southerly winds (Peterson et al., 2002). Diehl et al. (2007) also found that wind stress, and its influence on upwelling and relaxation, can significantly affect *E. analoga* recruitment magnitude and variation along the central California coastline. In Uruguay, northeasterly winds are responsible for generating upwelling events between Punta del Este (33 km West from Jose Ignacio, area 1 in Fig. 1) and Cabo Polonio (46 km west from area 3 in Fig. 1) (Framiñan et al., 1999; Pimenta et al., 2008; Trinchin et al., 2019). Additionally, more upwelling events are observed during La Niña years compared to El Niño (Trinchin et al., 2019).

The length of the reproductive period also affected larval connectivity. During La Niña years, when ovigerous females may release larvae until April (Celentano and Defeo, 2016), the direction of larval transport was opposite to that observed in November or January release events. In a climate change scenario, an increasing frequency of extreme La Niña events is anticipated (Cai et al., 2015), and thus larval connectivity from areas 2 and 4 to area 5 is expected to occur more frequently in April. Celentano and Defeo (2016) also found that La Niña events positively influenced adult abundance and growth of *E. brasiliensis* in area 5 (Barra del Chuy beach). Moreover, reproductive and recruitment periods were more extended and recruitment was higher during La Niña warm years compared to neutral years. Present results showed that larval transport to area 5 occurs in April, when self-recruitment is not as important as in November and January.

The Uruguayan coast constitutes the leading (southernmost or poleward) edge of *E. brasiliensis* distribution (Celentano and Defeo, 2016). It has been hypothesized that climate change effects will intensify at the edge of species' ranges (Poloczanska et al., 2013). Present results suggest that the southernmost beach where *E. brasiliensis* occurs (area 1) only received larvae from area 2 in November and January spawning during La Niña year 2008, characterized by strong northeasterly winds and strong southwestward surface currents. In this context, during strong La Niña years the seeding of larvae to this southernmost site

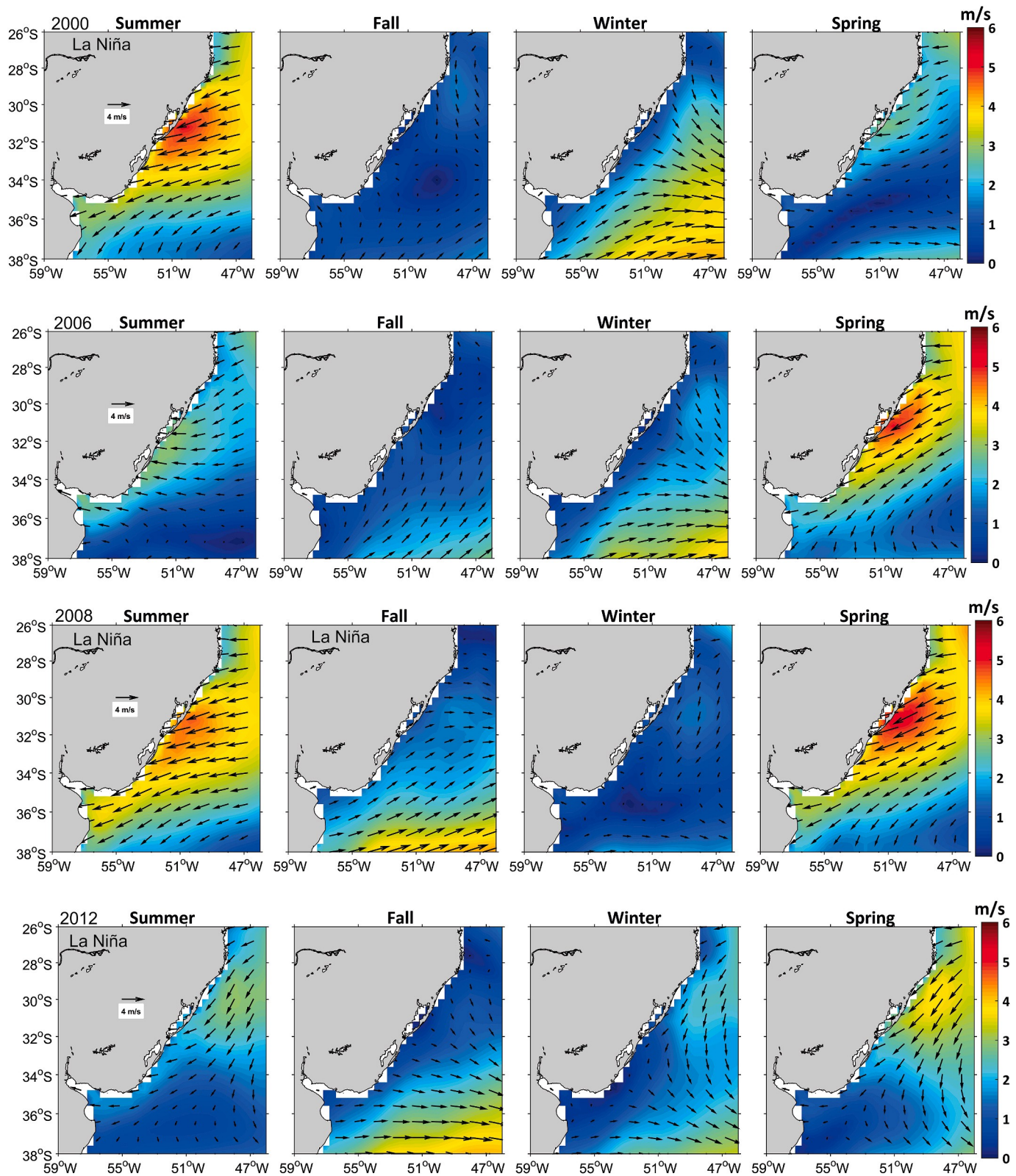


Fig. 5. Seasonal mean wind velocity (from ERA_Interim) for the study area and selected years among which larval connectivity patterns showed conspicuous contrasts. Arrows indicate mean wind magnitude and direction and background colors the wind intensity (see color scale at right). La Niña seasons are marked in the map based on the Oceanic Niño Index (ONI index, https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php) from NOAA. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

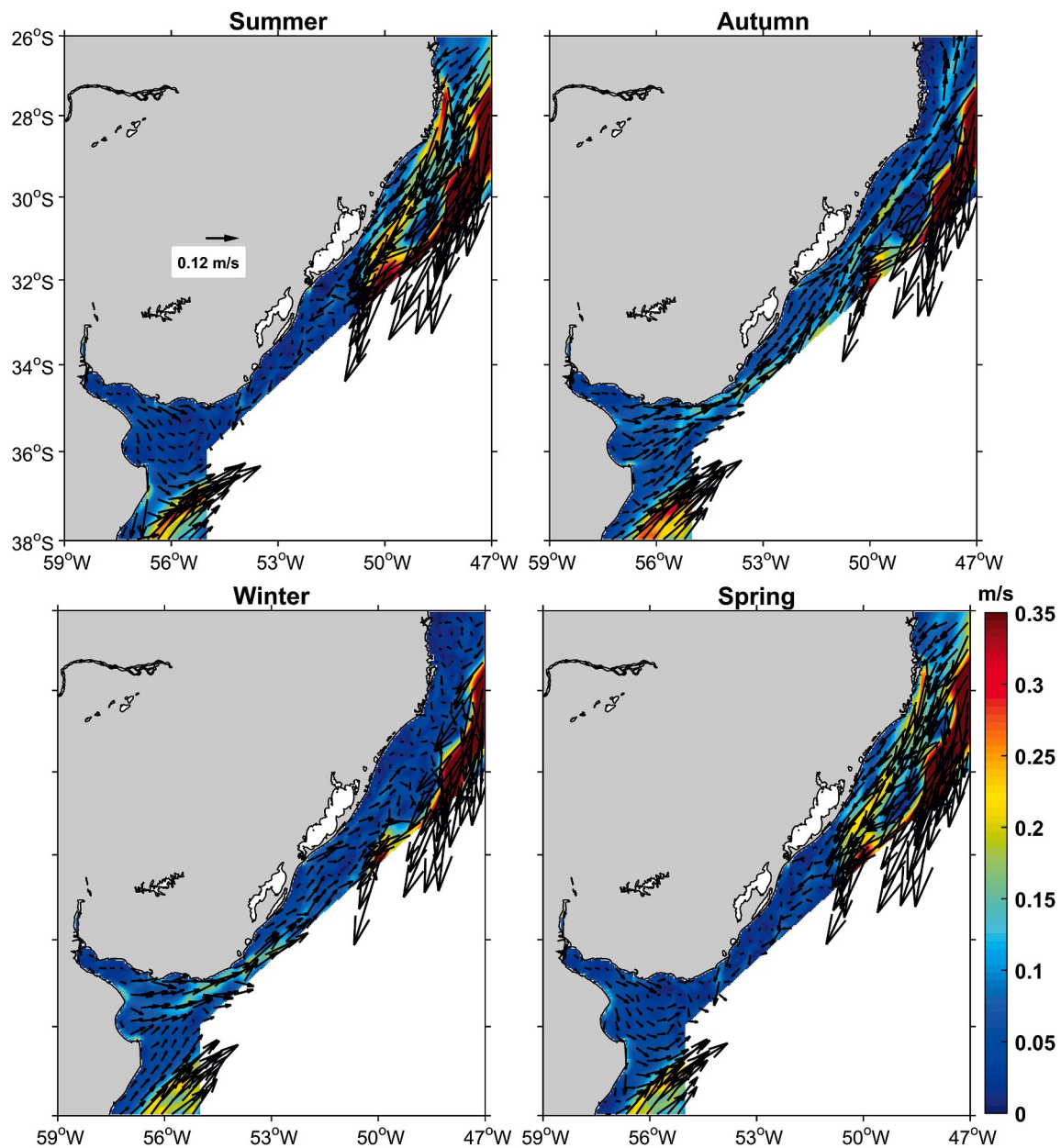


Fig. 6. Seasonal mean surface currents for the study area and period studied (from ROMS outputs). Arrows indicate mean current magnitude and direction.

would be promoted in austral spring and summer from release area 2. Thus, the transport of particles to the southernmost edge of *E. brasiliensis* distribution requires the simultaneous occurrence of two processes: i) larvae spawned in November and January under strong La Niña events in the release area 2; and ii) strong northeasterly winds and south-westward surface currents during spring and summer. This pattern resembles a spasmodic recruitment pattern that characterizes sink populations located at the edge of the distribution range of a metapopulation (Caddy and Defeo, 2003).

Other strong La Niña years during the time series analyzed were in 2000 and 2011 (Fig. S4, Supplementary Material). In 2000, ROMS outputs started in April (austral fall), and thus transport during the previous summer could not be assessed. For the 2011 strong La Niña event, the lack of connectivity from release area 2 to recruitment area 1 could be attributed to the simultaneous occurrence of estuarine and oceanic upwelling events in the coast of Uruguay (Trinchin et al., 2019). Along the coast of Uruguay, most upwelling events occur under low RdIP discharge conditions (Pimenta et al., 2008; Simionato et al., 2010;

Trinchin et al., 2019). In summer, 2008 the discharge anomaly was not as low as observed in 2011 and may have limited or prevented upwelling (see Trinchin et al., 2019). Thus, in summer 2008 the relatively strong northeasterly winds along the coast combined with moderate RdIP discharge, reinforced larval connectivity between areas 2 and 1. Larvae are highly susceptible to offshore transport, thereby limiting recruitment in upwelling regions (Morgan and Fisher, 2010). Hence, larval transport to recruitment area 1 is feasible during strong La Niña years, with the exception of those when upwelling events occur.

Few studies accounted for the impact of climate change on connectivity patterns (Ayata et al., 2010; Lett et al., 2010; Andreollo et al., 2015; Lacroix et al., 2018). Ocean warming implies that organisms need to accommodate to increasing temperatures by shifting their biogeographical range poleward, tracking the migration of isotherms (Poloczanska et al., 2013). Additionally, changes in ocean circulation also influence the distribution of marine species by affecting dispersal patterns (Ling, 2008). For the study area, Ortega et al. (2016) found that the position of the warm water front depicted by the 20 °C isotherm, a proxy

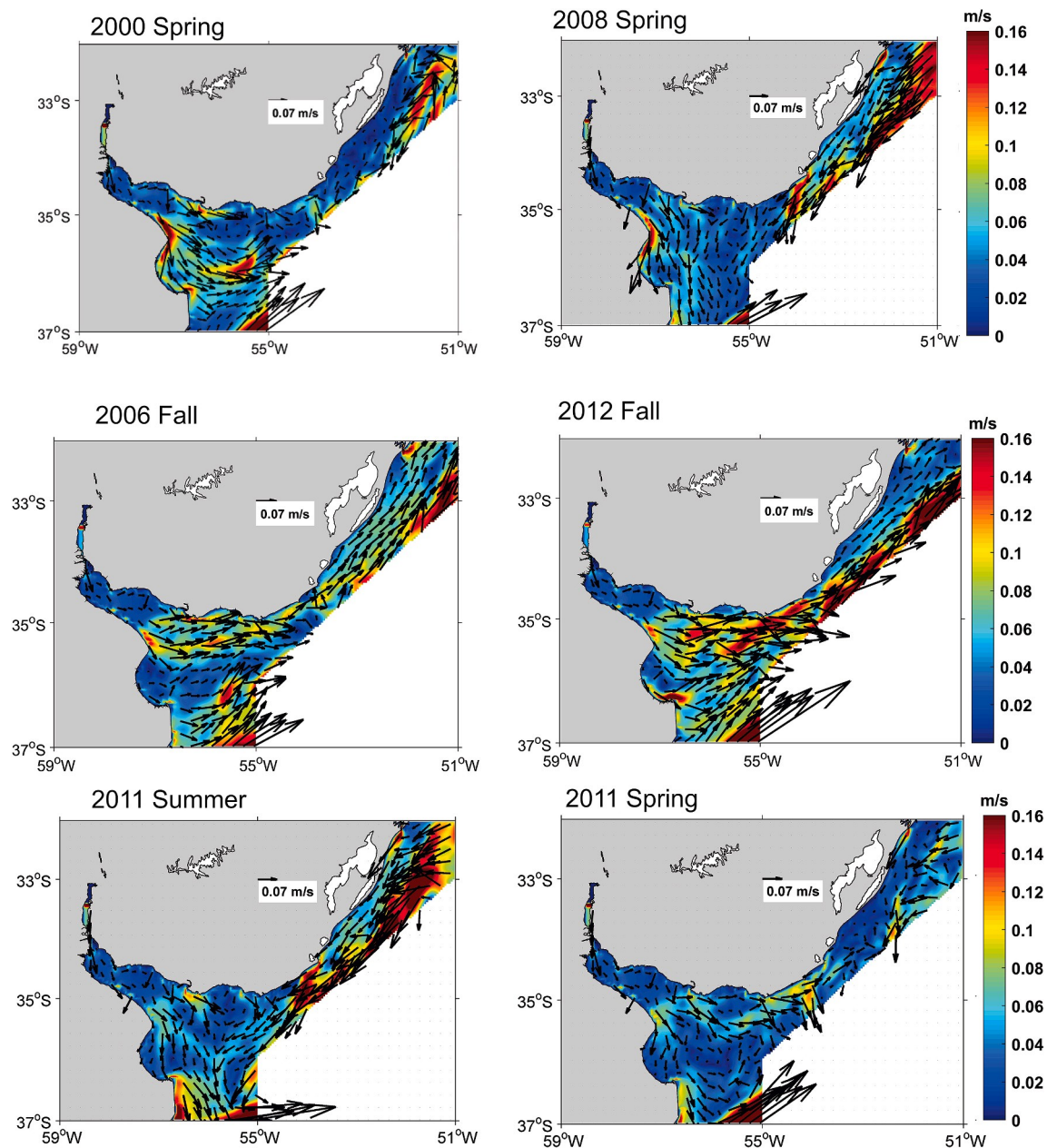


Fig. 7. Seasonal surface currents for selected years and seasons (from ROMS outputs) that showed conspicuous contrasts in larval connectivity patterns.

of tropical waters, showed a long-term poleward shift at a rate of ca. 9 km yr^{-1} . Thus, larvae seeding in the southernmost beach of the mole crab distribution during strong La Niña years would favor larval recruitment, also promoted by higher salinities and temperatures during these events. Extrapolated to a climate change scenario with stronger La Niña events, these results suggest that the likelihood of larval transport to recruitment area 1 will increase and would help seeding this beach, which may be demographically important, since very low mole crab abundance has been observed and no ovigerous females are found in this area, therefore acting as a sink population (Celentano and Defeo, 2006). Hence, protecting and managing beach area 2 as a main source of larvae for the southernmost area of distribution would be critical for *E. brasiliensis* conservation, which is a significant result in a context of metapopulation dynamics studies in sandy beaches (Harris et al., 2014; Fanini et al., 2020).

In summary, the results suggest the influence of the regional circulation (simulated by the ROMS implementation) on larval connectivity

patterns in *E. brasiliensis*. Interannual variability in connectivity patterns was closely associated with mean wind patterns during La Niña years, and also by an interaction between years and length of the spawning period. Larval supply to the southernmost recruitment area only came from the closest release area during a strong La Niña event, when wind anomalies were strong enough to support this process. In a climate change scenario with stronger La Niña events, larval transport to the southernmost beach becomes more probable and may favor seeding larvae to this beach.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.107035>.

Author statement

Meerhoff Erika: conceptualization, methodology, data analysis, writing- original draft preparation, reviewing and editing.
Defeo Omar: conceptualization, supervision, writing, reviewing and editing, funding acquisition.
Combes Vincent: ROMS implementation and validation, analysis of alongshore currents, writing, reviewing and editing.
Franco Barbara: writing, reviewing and editing.
Matano Ricardo: ROMS implementation and validation, writing, reviewing and editing.
Piola Alberto: writing, reviewing and editing.
Hernández-Vaca Freddy: wind data analysis, reviewing and editing.
Celentano Eleonora: Analysis of *Emerita* adult abundances, writing.

Source areas were identified

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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