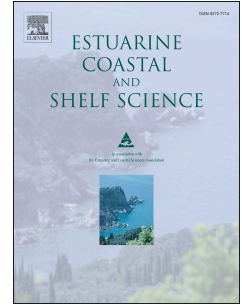


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Assessment of larval connectivity in a sandy beach mole crab through a coupled bio-oceanographic model

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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.

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

3

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

19

20 **KEY WORDS:** mole crab, larval connectivity, sandy beach, individual-based
21 model

22

23 **RUNNING PAGE HEAD:** mole crab larval connectivity

24

1. INTRODUCTION

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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 & Sponaugle 2009). Factors such as larval behavior (Woodson & 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 & 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 & McLachlan 2005, Fanini et al. 2020). Particularly, the species development strategy may affect the distribution patterns. In this context, sandy beach

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

13 The Uruguayan coast extends for nearly 400 km from the inner and brackish
14 Río de la Plata (RdIP) estuary to the marine Southwestern Atlantic Ocean
15 shores (Lercari & Defeo 2015). Crustaceans constitute a conspicuous
16 component of Uruguayan sandy beaches. Among them, the mole crab *Emerita*
17 *brasiliensis* is an intertidal filter feeder found in reflective and dissipative
18 beaches of the Atlantic coast of South America, from Venezuela to Uruguay
19 (Defeo & Cardoso 2002, Celentano et al. 2010). The mole crab presents a
20 complex life cycle, with a planktonic larval phase that develops in the nearshore
21 during 2 to 3 months and an adult benthic phase (Otegui & Soares-Gomes
22 2007). The precise distribution of *E. brasiliensis* larvae in the water column is
23 not known; however, larvae for the congeneric *Emerita analoga* in Chile are
24 found in the upper 15 m of the water column (Veas et al. 2013). The relatively

1 long larval phase could imply a high dispersal potential, and larvae transport by
2 the coastal circulation could be an important factor in determining its local and
3 latitudinal distribution (Sorte et al. 2001). It is known that first and last larval
4 stages of *E. brasiliensis* are concentrated near the coast. Veloso and Valentin
5 (1993) proposed that larval stages would stay close to the coast, being kept in
6 circulation cells until reaching the megalopa stage. This has been reported as a
7 common pattern in *Emerita* species (Efford 1970). The length of reproductive
8 and recruitment seasons of *E. brasiliensis* in Uruguay presents interannual
9 variability, both being longer in warm years (Celentano & Defeo 2016).
10 Particularly, during La Niña events, the coast of Uruguay is characterized by a
11 stronger influence of warm oceanic tropical waters that promote the abundance
12 and individual growth of this species (Celentano & Defeo 2016).

13 Coupled bio-oceanographic models are useful tools for assessing connectivity
14 patterns in marine species. Notably, individual based models (IBM) allow
15 observing different regions of population isolation as a function of larval
16 dispersal (Cowen et al. 2007). In this paper, larval connectivity patterns of *E.*
17 *brasiliensis* in the coast of Uruguay were assessed through a coupled bio-
18 oceanographic model in order to: 1) evaluate the interannual variability of larval
19 connectivity and its possible relation with ocean circulation; and 2) determine
20 the effects of the length of reproductive period in the connectivity of *E.*
21 *brasiliensis*.

22

23

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

1 outflow events (Piola et al. 2005). La Niña years, which are associated with
2 relatively low continental discharges, may still induce expanded northeastward
3 coastal plumes in response to anomalously strong southwesterly winds.

4

5 **2.2. Hydrodynamic and biophysical model**

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

11 The physical model used for this study is detailed in Matano et al. (2014). For
12 the sake of completeness, a summary of the model configuration is detailed.
13 The model grid, which covers the coast of Uruguay, extends from 66°W to 44°W
14 and from 44°S to 25°S with a 1/24° spatial resolution (~3.8 km) and 40 terrain-
15 following vertical levels, with enhanced resolution at the surface. The bottom
16 topography was derived from the ETOPO1 (1' resolution) (Amante & Eakins
17 2009), which was smoothed to minimize the pressure gradient errors associated
18 with terrain following coordinates (Mellor et al. 1994). The model includes a
19 daily discharge of the RdIP, a constant discharge of 2000 m³ s⁻¹ from the
20 Patos/Mirim lagoons and five tidal harmonics (M₂, S₂, N₂, K₁, and O₁). At the
21 surface, the model is forced by the QuikSCAT (the period 2000-2007) and
22 ASCAT (period 2008-2012) daily wind stress and by climatological heat and
23 freshwater fluxes from the COADS data set.

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

13

14 **2.3. Biological model: sites and timing of larval release**

15 Mole crabs are typical burrowing forms found on exposed sandy beaches
16 (McLachlan & Defeo 2018). A macroscale study of *E. brasiliensis* shows a clear
17 shift from continuous reproduction in subtropical sandy beaches to
18 discontinuous reproduction in temperate sandy beaches (Defeo & Cardoso
19 2002). *E. brasiliensis* larvae hatch as zoea from eggs carried by adult females
20 (Delgado & Defeo 2006), which in temperate beaches of the coast of Uruguay
21 are mainly observed from November to April (Celentano & Defeo 2016).
22 Therefore, for modeling purposes, and to evaluate temporal variations in larval
23 connectivity, larvae were released in spawning events in three different months:

1 November as the start of the reproductive season, January an intermediate
2 month in the reproductive season and April as the last possible date for larval
3 hatching.

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

14

15 **2.4. Transport duration and recruitment success**

16

17 The larval development of *E. brasiliensis* varies between two and three months
18 depending on water temperature (Veloso & Valentin 1993, Otegui & Soares-
19 Gomes 2007). Laboratory experiments indicate that the duration of *E.*
20 *brasiliensis* larval stage correlates positively with water temperature (mean PLD
21 is 49 days at 24 to 26 °C and 90 days at 18-20°, Otegui & Soares -Gomes
22 2007). Hence, four different PLDs of 50, 60, 80 and 90 days (from hatching to
23 megalopa) were used in the IBM to deal with water temperature variability in the
24 coastal ocean during different release months. The IBM did not model larval

1 growth as a function of temperature, but used drift of particles with a constant
2 weight for the PLD scenarios defined above.

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

20 To determine the interannual variability of larval connectivity, larval transport
21 experiments using the model’s current fields during the 2000–2012 period were
22 run. A total of 12 years x 3 months of release x 1 depth x 4 PLD x 3 replicates
23 were evaluated. For each case, 500,000 particles were released from randomly
24 assigned coordinates within the different release areas, defined as a 10 km x 10

1 km region around each beach. The number of particles was assigned as a
2 trade-off between computational constraints and actual larval density estimates
3 in the region (Velooso & Valentin 1993).

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

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

1 Finally, interannual variability in wind and ocean surface currents were
2 evaluated for years among which larval connectivity patterns showed
3 conspicuous contrasts. Monthly data of surface wind were obtained from ERA-
4 Interim reanalysis ([https://www.ecmwf.int/en/forecasts/datasets/archive-
5 datasets/reanalysis-datasets/era-interim](https://www.ecmwf.int/en/forecasts/datasets/archive-datasets/reanalysis-datasets/era-interim)), which have a spatial resolution of
6 0.4° (Berrisford et al. 2011). Seasonal mean wind patterns were also calculated.
7 Mean seasonal surface current maps were constructed using the
8 hydrodynamical model velocities.

9

10

3. RESULTS

11

12 **3.1. Larval connectivity: interaction effects between interannual 13 variability and months of spawning events**

14 The highest connectivity probabilities were observed for November and January
15 spawning events (50 and 60 days PLD), in both cases for self-recruitment in
16 recruitment area or beach 5 (Fig. 2 a, b, c and d). In these spawning events, the
17 main connectivity pattern was southwestward, with highest probabilities of larval
18 transport being observed from release area 5 to recruitment areas 3 and 4 (Fig.
19 2, Fig. 3b) and from release area 4 to recruitment area 3. However, for release
20 area 4 self-recruitment was higher than larval transport to recruitment area 3. In
21 addition, there was interaction of spawning month with interannual variability:
22 during November spawning release area 5 also supplied larvae to recruitment
23 area 2 in 2000 and 2008, with low probabilities (Fig. 3a).

1 During April larval release, only longer PLDs are biologically significant
2 (because water temperature is typically lower) and hence self-recruitment was
3 not as important as in November and January (Fig. 2). In addition, the direction
4 of larval transport was towards the north-east (e.g. opposite to the main
5 direction observed in November and January spawning events). The larval
6 transport direction reverse during April was consistent with changes in surface
7 ocean circulation, which was northeastwards in fall. The highest probabilities of
8 larval transport were observed from release area 4 to recruitment area 5 when
9 considering 80 and 90 days PLD, and from release area 2 to recruitment areas
10 3 and 5 (Fig. 2 e and f). The larval transport from release area 3 was very low
11 because of the low number of ovigerous females in this area. The probability of
12 larval transport from release area 4 to recruitment area 5 was one order of
13 magnitude higher than transport from release area 3 to recruitment area 5 (Fig.
14 3c). Regardless of the month of larval release, there was no larval transport
15 from release area 1 to the other recruitment areas, because the number of
16 ovigerous females in this area was zero and therefore defined as a sink. The
17 larvae that reached recruitment area 1 came from release area 2 only (Fig. 2).

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

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 5-6 m s⁻¹ in 2000). 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

1 surface currents (Fig. 7) and the alongshore current in the study area
2 (Supplementary video) showed that southwestward surface currents in 2008 (La
3 Niña year) explained the connectivity pattern observed from area 2 towards
4 recruitment area 1. On the other hand, in summer and spring 2011 (also strong
5 La Niña event), mean surface currents in the coast of Uruguay were offshore
6 (Fig. 7), thus preventing larval transport from area 2 towards recruitment area 1.

7 During the April larval release, larval transport was northeastward, and only in
8 2006 and 2012 there was positive larval transport from release area 2 to
9 recruitment areas 4 and 5 (Fig. 3c). In 2006, southerly winds in fall and south-
10 westerly in winter, and in La Niña 2012 strong westerly winds in fall (Fig. 5) led
11 to surface currents stronger (Fig. 7) than the mean seasonal pattern (Fig. 6) and
12 the coastal surface current was northeastward (Fig. S3, Supplementary
13 Material), which may have promoted larval transport between area 2 to
14 recruitment areas 4 and 5. There was no clear pattern of larval connectivity
15 during El Niño years.

16

17

4. DISCUSSION

18 The coupled bio-oceanographic model developed here was a useful tool to
19 assess: (1) the interannual variability in larval connectivity of the mole crab
20 *Emerita brasiliensis* between sandy beaches; and (2) the effect of the length of
21 the reproductive period on larval connectivity. In addition, variability in larval
22 connectivity was observed depending on the month of the larval release or
23 spawning event. During November and January, typical months for *E.*

1 *brasiliensis* larval dispersal, the main larval transport was southwestward. In
2 contrast, larvae released in April drifted northeastward. During winter,
3 southwesterly winds create geostrophic currents that advect the freshwater of
4 the RdIP northeastward (Palma et al. 2008, Matano et al. 2014). These patterns
5 reverse in summer, when northeasterly winds advect relatively salty waters from
6 the Brazilian shelf southward (Matano et al. 2014).

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

1 Niña events were reflected in larval connectivity patterns, but no clear patterns
2 of larval connectivity emerged during El Niño years.

3 Wind effects on coastal currents have been proposed as a key explanatory
4 factor of recruitment variability for *Emerita analoga* off the coast of southern
5 California (Wooldridge et al. 2016). Empirical data provided by Sorte et al.
6 (2001) showed that *E. analoga* populations in Oregon occurred sporadically and
7 appeared to be restocked by larvae drifting northward from California, and that
8 increased northward transport occurred in winter during El Niño events, which
9 are characterized by anomalously strong southerly winds (Peterson et al. 2002).
10 Diehl et al. (2007) also found that wind stress, and its influence on upwelling
11 and relaxation, can significantly affect *E. analoga* recruitment magnitude and
12 variation along the central California coastline. In Uruguay, northeasterly winds
13 are responsible for generating upwelling events between Punta del Este (33 km
14 West from Jose Ignacio, area 1 in Fig. 1) and Cabo Polonio (46 km west from
15 area 3 in Fig. 1) (Framiñan et al. 1999, Pimenta et al. 2008, Trinchin et al.
16 2019). Additionally, more upwelling events are observed during La Niña years
17 compared to El Niño (Trinchin et al. 2019).

18 The length of the reproductive period also affected larval connectivity. During La
19 Niña years, when ovigerous females may release larvae until April (Celentano &
20 Defeo 2016), the direction of larval transport was opposite to that observed in
21 November or January release events. In a climate change scenario, an
22 increasing frequency of extreme La Niña events is anticipated (Cai et al. 2015),
23 and thus larval connectivity from areas 2 and 4 to area 5 is expected to occur
24 more frequently in April. Celentano & Defeo (2016) also found that La Niña

1 events positively influenced adult abundance and growth of *E. brasiliensis* in
2 area 5 (Barra del Chuy beach). Moreover, reproductive and recruitment periods
3 were more extended and recruitment was higher during La Niña warm years
4 compared to neutral years. Present results showed that larval transport to area
5 5 occurs in April, when self-recruitment is not as important as in November and
6 January.

7 The Uruguayan coast constitutes the leading (southernmost or poleward) edge
8 of *E. brasiliensis* distribution (Celentano & Defeo 2016). It has been
9 hypothesized that climate change effects will intensify at the edge of species'
10 ranges (Poloczanska et al. 2013). Present results suggest that the
11 southernmost beach where *E. brasiliensis* occurs (area 1) only received larvae
12 from area 2 in November and January spawning during La Niña year 2008,
13 characterized by strong northeasterly winds and strong southwestward surface
14 currents. In this context, during strong La Niña years the seeding of larvae to
15 this southernmost site would be promoted in austral spring and summer from
16 release area 2. Thus, the transport of particles to the southernmost edge of *E.*
17 *brasiliensis* distribution requires the simultaneous occurrence of two processes:
18 i) larvae spawned in November and January under strong La Niña events in the
19 release area 2; and ii) strong northeasterly winds and southwestward surface
20 currents during spring and summer. This pattern resembles a spasmodic
21 recruitment pattern that characterizes sink populations located at the edge of
22 the distribution range of a metapopulation (Caddy & Defeo 2003).

23 Other strong La Niña years during the time series analyzed were in 2000 and
24 2011 (Fig. S4, Supplementary Material). In 2000, ROMS outputs started in April

1 (austral fall), and thus transport during the previous summer could not be
2 assessed. For the 2011 strong La Niña event, the lack of connectivity from
3 release area 2 to recruitment area 1 could be attributed to the simultaneous
4 occurrence of estuarine and oceanic upwelling events in the coast of Uruguay
5 (Trinchin et al. 2019). Along the coast of Uruguay, most upwelling events occur
6 under low RdIP discharge conditions (Pimenta et al. 2008, Simionato et al.
7 2010, Trinchin et al. 2019). In summer, 2008 the discharge anomaly was not as
8 low as observed in 2011 and may have limited or prevented upwelling (see
9 Trinchin et al. 2019). Thus, in summer 2008 the relatively strong northeasterly
10 winds along the coast combined with moderate RdIP discharge, reinforced
11 larval connectivity between areas 2 and 1. Larvae are highly susceptible to
12 offshore transport, thereby limiting recruitment in upwelling regions (Morgan &
13 Fisher 2010). Hence, larval transport to recruitment area 1 is feasible during
14 strong La Niña years, with the exception of those when upwelling events occur.

15 Few studies accounted for the impact of climate change on connectivity
16 patterns (Ayata et al. 2010, Lett et al. 2010, Andrello et al. 2015, LaCroix et al.
17 2018). Ocean warming implies that organisms need to accommodate to
18 increasing temperatures by shifting their biogeographical range poleward,
19 tracking the migration of isotherms (Poloczanska et al. 2013). Additionally,
20 changes in ocean circulation also influence the distribution of marine species by
21 affecting dispersal patterns (Ling 2008). For the study area, Ortega et al. (2016)
22 found that the position of the warm water front depicted by the 20°C isotherm, a
23 proxy of tropical waters, showed a long-term poleward shift at a rate of ca. 9 km
24 yr⁻¹. Thus, larvae seeding in the southernmost beach of the mole crab

1 distribution during strong La Niña years would favor larval recruitment, also
2 promoted by higher salinities and temperatures during these events.
3 Extrapolated to a climate change scenario with stronger La Niña events, these
4 results suggest that the likelihood of larval transport to recruitment area 1 will
5 increase and would help seeding this beach, which may be demographically
6 important, since very low mole crab abundance has been observed and no
7 ovigerous females are found in this area, therefore acting as a sink population
8 (Celentano & Defeo 2006). Hence, protecting and managing beach area 2 as a
9 main source of larvae for the southernmost area of distribution would be critical
10 for *E. brasiliensis* conservation, which is a significant result in a context of
11 metapopulation dynamics studies in sandy beaches (Harris et al. 2014, Fanini
12 et al. 2020).

13 In summary, the results suggest the influence of the regional circulation
14 (simulated by the ROMS implementation) on larval connectivity patterns in *E.*
15 *brasiliensis*. Interannual variability in connectivity patterns was closely
16 associated with mean wind patterns during La Niña years, and also by an
17 interaction between years and length of the spawning period. Larval supply to
18 the southernmost recruitment area only came from the closest release area
19 during a strong La Niña event, when wind anomalies were strong enough to
20 support this process. In a climate change scenario with stronger La Niña
21 events, larval transport to the southernmost beach becomes more probable and
22 may favor seeding larvae to this beach.

23

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9

10

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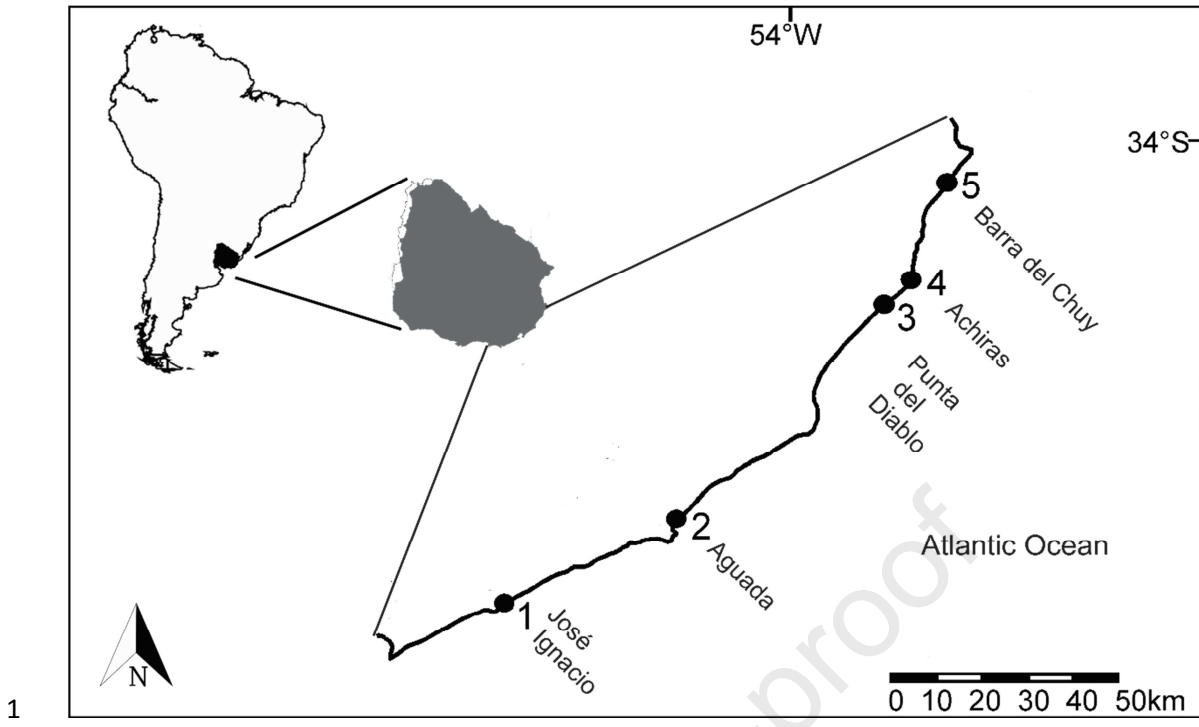
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2 Fig. 1. South Atlantic Ocean with the coast of Uruguay and the geographical
3 location of sandy beaches selected as release/recruitment areas for *E.*
4 *brasiliensis*.

5

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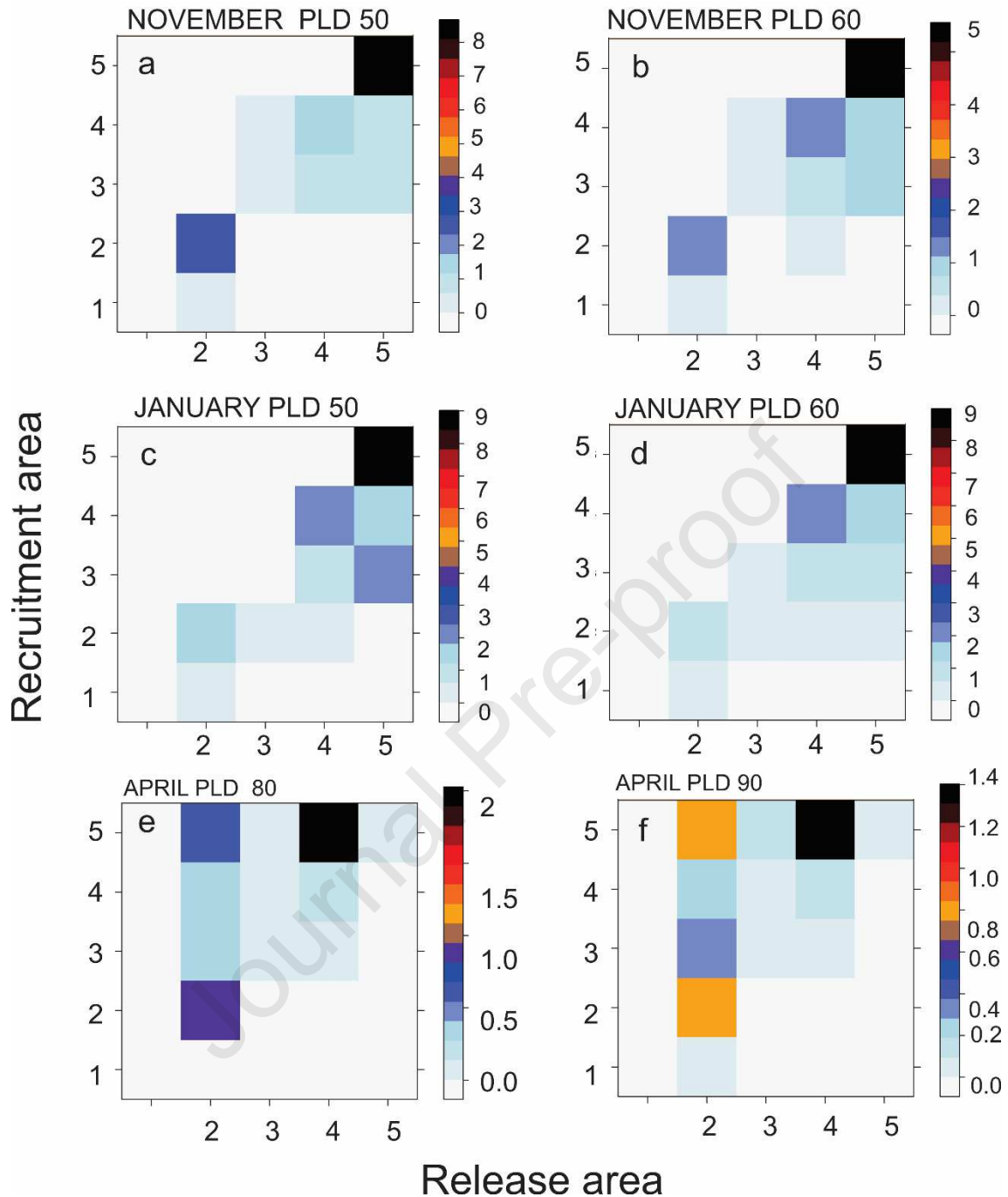
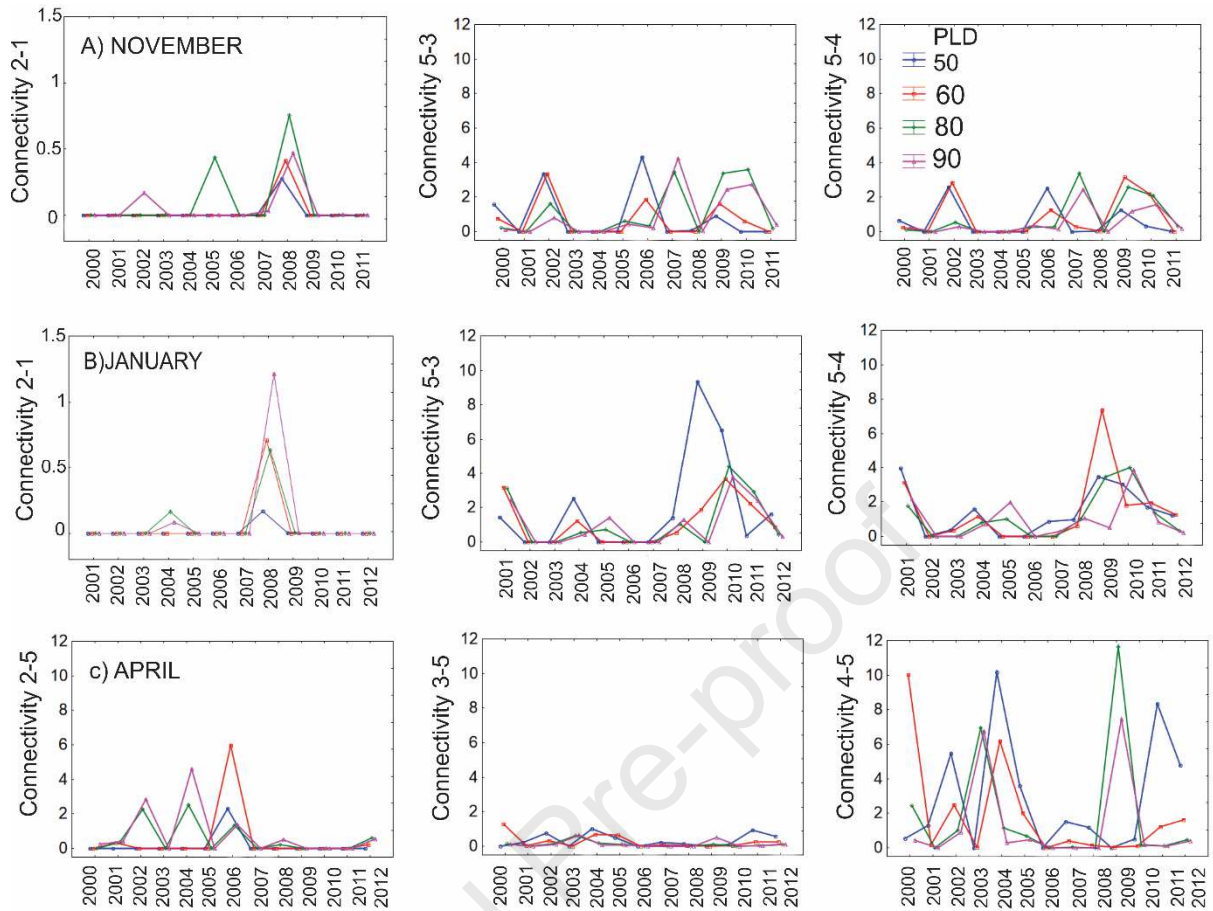


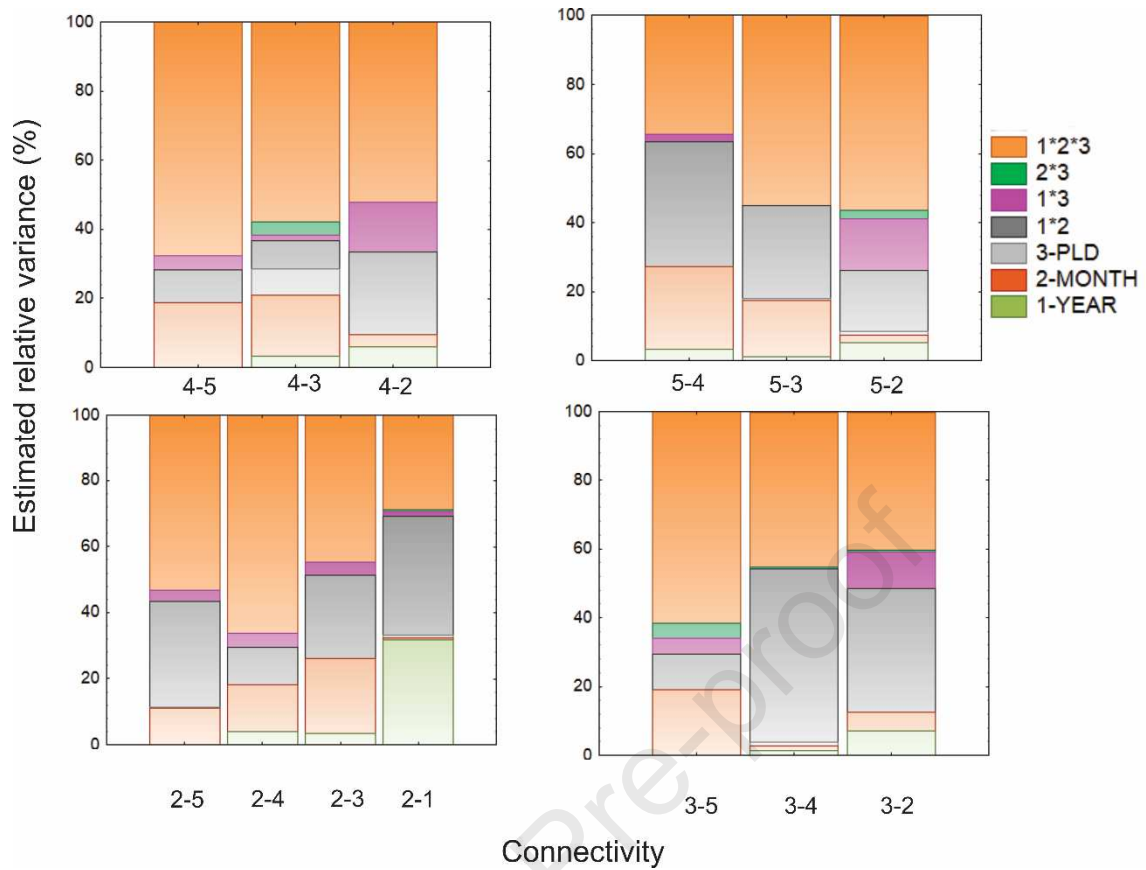
Fig. 2. Mean connectivity matrices for three different months of larval release and four planktonic larval duration (PLD in days). Twelve years of simulations and three replicates were averaged, and connectivity (here expressed as proportions in different color scales) was corrected by ovigerous female 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.



1

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

11



1

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

9

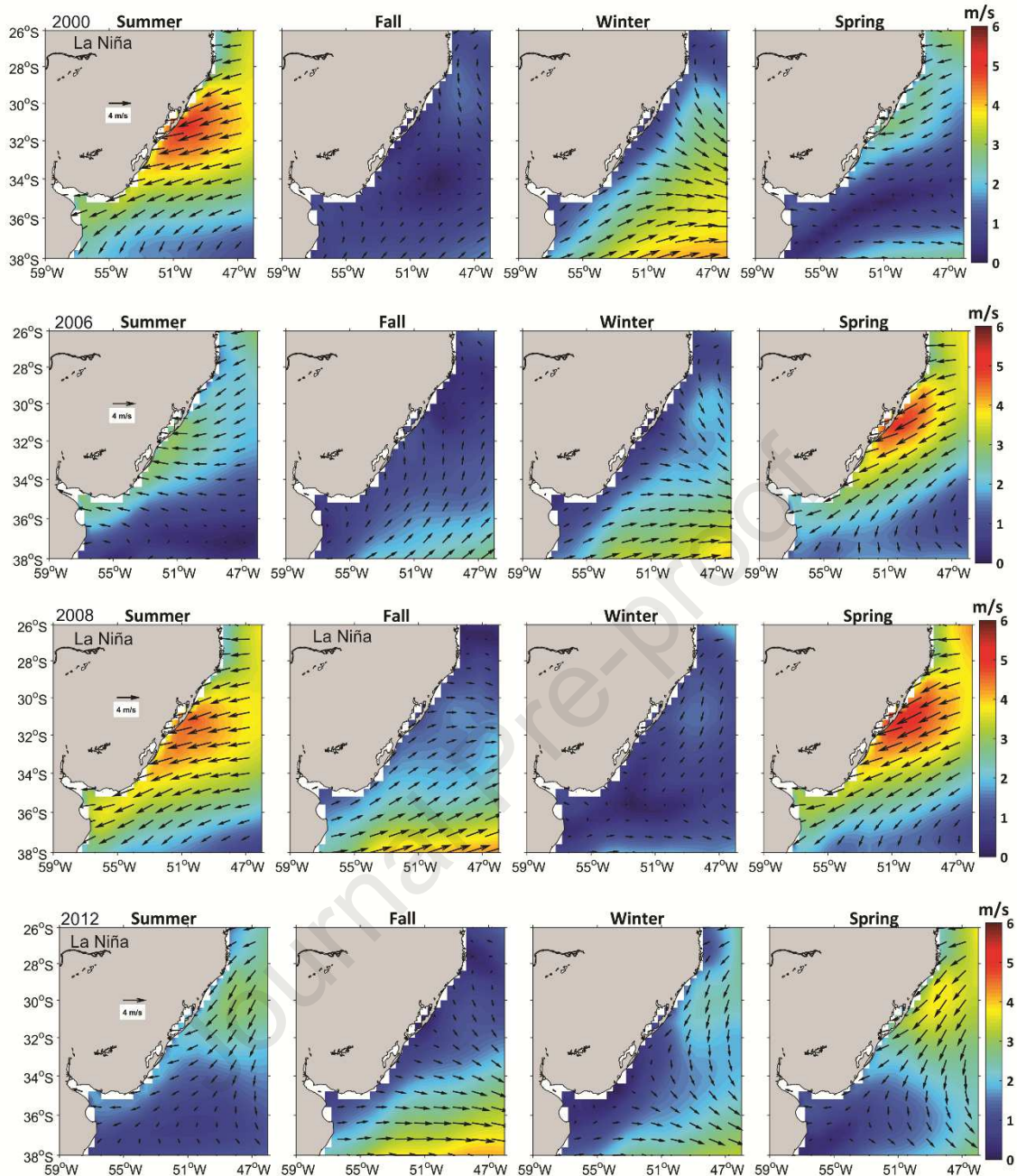
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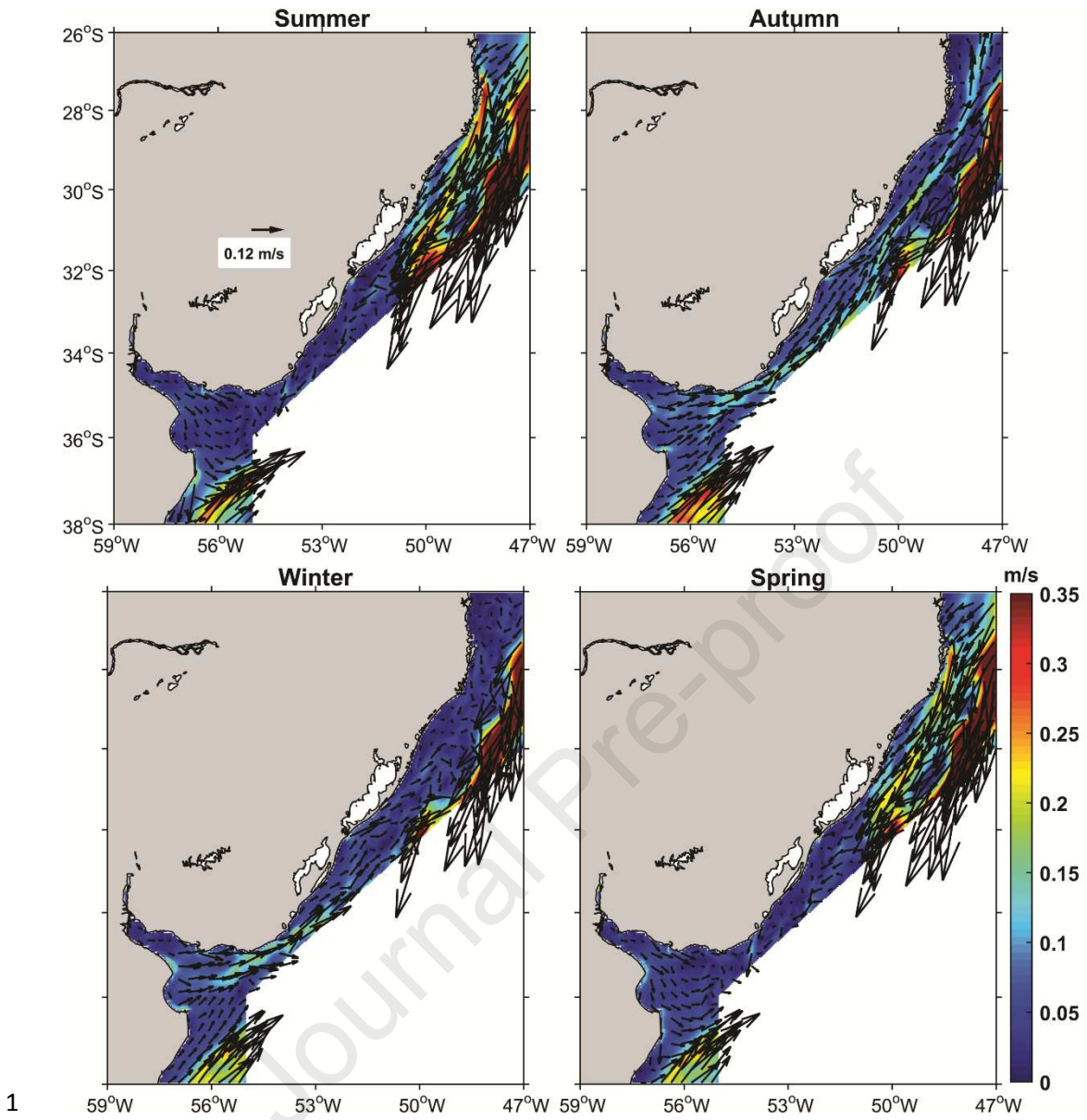
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2 Fig. 5. Seasonal mean wind velocity (from ERA_Interim) for the study area and
 3 selected years among which larval connectivity patterns showed conspicuous
 4 contrasts. Arrows indicate mean wind magnitude and direction and background
 5 colors the wind intensity (see color scale at right). La Niña seasons are marked
 6 in the map based on the Oceanic Niño Index (ONI index,
 7 [https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5](https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php)
 8 .php) from NOAA.

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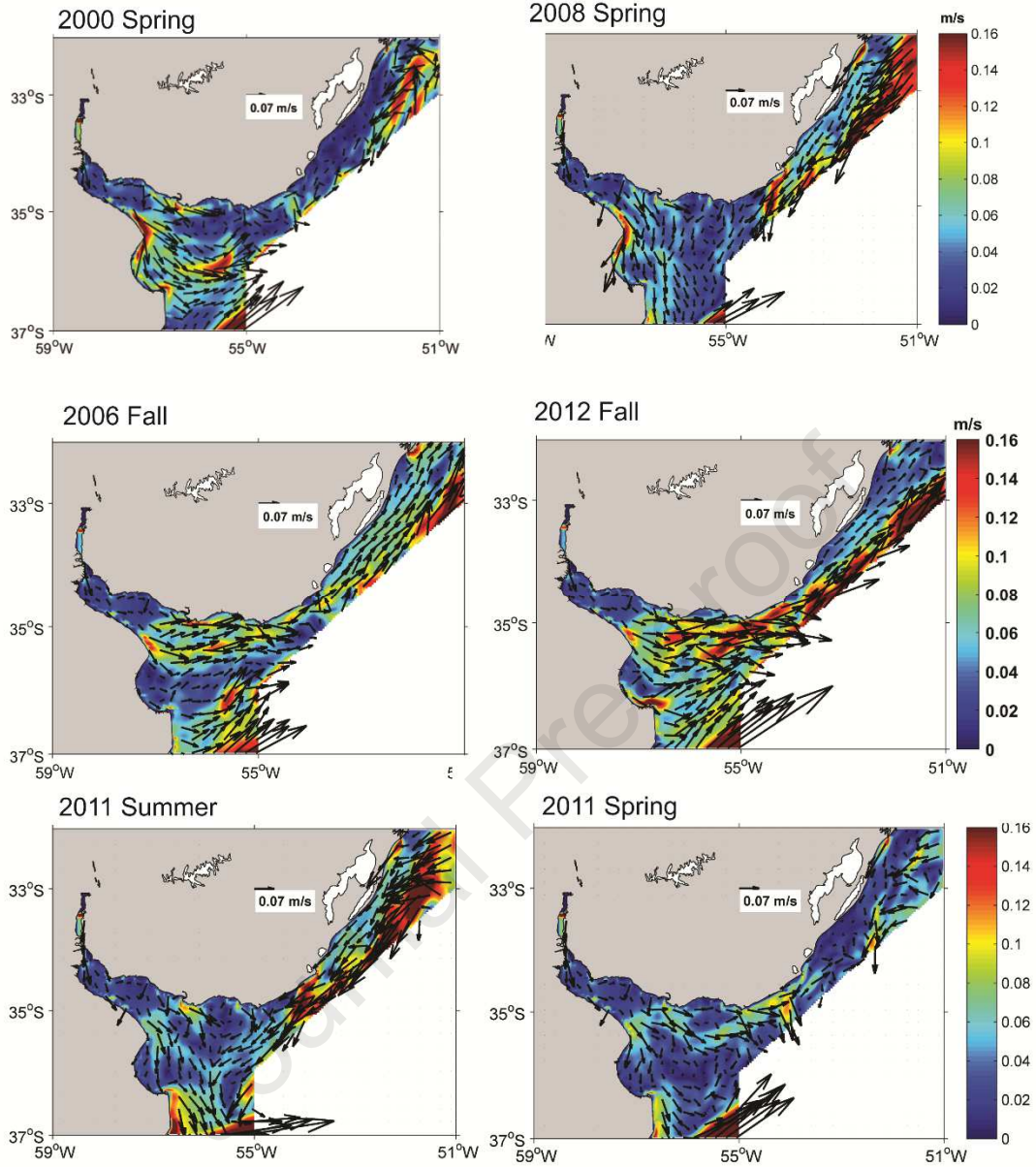
2 Fig. 6. Seasonal mean surface currents for the study area and period studied
 3 (from ROMS outputs). Arrows indicate mean current magnitude and direction.

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

Highlights

Emerita brasiliensis larval connectivity was studied through individual-based models

12-year ROMS outputs were used to address connectivity in the coast of Uruguay

Connectivity changed drastically during La Niña event with intense northeasterly winds

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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