

Large-scale connectivity of the sandy beach clam *Mesodesma mactroides* along the Atlantic coast of South America, and climate change implications

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ARTICLE INFO

Keywords:

Yellow clam
Larval connectivity
Individual-based model
Salinity-dependent larval mortality
Temperature-dependent larval mortality
Warming hotspot

ABSTRACT

The yellow clam *Mesodesma mactroides* is a cool-water species that typifies sandy beaches of the Southwestern Atlantic Ocean (SAO), which embraces one of the strongest ocean warming hotspots. The region is influenced by the Rio de la Plata (RdIP), which represents a zoogeographic barrier that restricts its larval exchange. We investigated yellow clam larval connectivity patterns using an individual based model (IBM). The IBM combined outputs from a 3D hydrodynamic model with a clam submodel that considered salinity- and temperature-dependent mortality for the planktonic larvae. Connectivity across the RdIP estuary occurred only for larvae released in spring during a strong La Niña event. Mortality due to freshwater precluded larval transport across the RdIP, whereas larval mortality induced by warmer waters reduced connectivity, leading to self-recruitment in most areas. Warming acceleration in this hotspot could further restrict larval connectivity between populations in the SAO, with conservation implications for this threatened species.

1. Introduction

Knowledge on larval dispersal and demographic connectivity is crucial for understanding the dynamics and the persistence of spatially-structured stocks of marine invertebrate species that have a complex life cycle with a planktonic larval stage (Hastings and Botsford 2006). It is also essential to identify local populations that may constantly restock themselves over time and, at the same time, may contribute to the persistence of the metapopulation at a regional scale through larval exchange (Burgess et al., 2014; Lett et al., 2015). The pattern of larval transport, whether promoting self-recruitment or high connectivity among local populations, is fundamentally important for species that live in patchy habitats like intertidal zones (Robins et al., 2013; McLachlan and Defeo 2018).

Restrictions to larval dispersal in the ocean include present (Perrin et al., 2004; Banks et al., 2007) and past patterns of oceanic circulation

and physical barriers (Taylor and Hellberg 2006; Waters 2008). Freshwater plumes are important physical barriers that restrict larval dispersal (Teske et al., 2008). For example, the Amazon-Orinoco outflow inhibits gene flow of marine organisms between the Caribbean and northeast Brazil (Lessios et al., 2003). The Rio de la Plata (RdIP) estuary (Fig. 1), the widest estuary in the world, also influences circulation patterns of coastal marine waters in the Atlantic coast of South America and is a biogeographic barrier for many taxa exhibiting a marine planktonic larval dispersal (Bisbal 1995; Luppi et al., 2003; Ituarte et al., 2012).

The yellow clam *Mesodesma mactroides* (Reeve, 1854) is an intertidal bivalve that dominates the macrofauna community biomass on dissipative sandy beaches along the Atlantic coast of South America (Fiori and Defeo 2006). The genus *Mesodesma* has an Antarctic origin and is associated with cold water systems (Von Ihering, 1907). The species is distributed from São Paulo State, Brazil (24°S) to the south of Buenos Aires Province, Argentina (41°S), along hundreds of kilometers

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<https://doi.org/10.1016/j.marenvres.2022.105591>

Received 9 August 2021; Received in revised form 16 February 2022; Accepted 27 February 2022

0141-1136/© 20XX

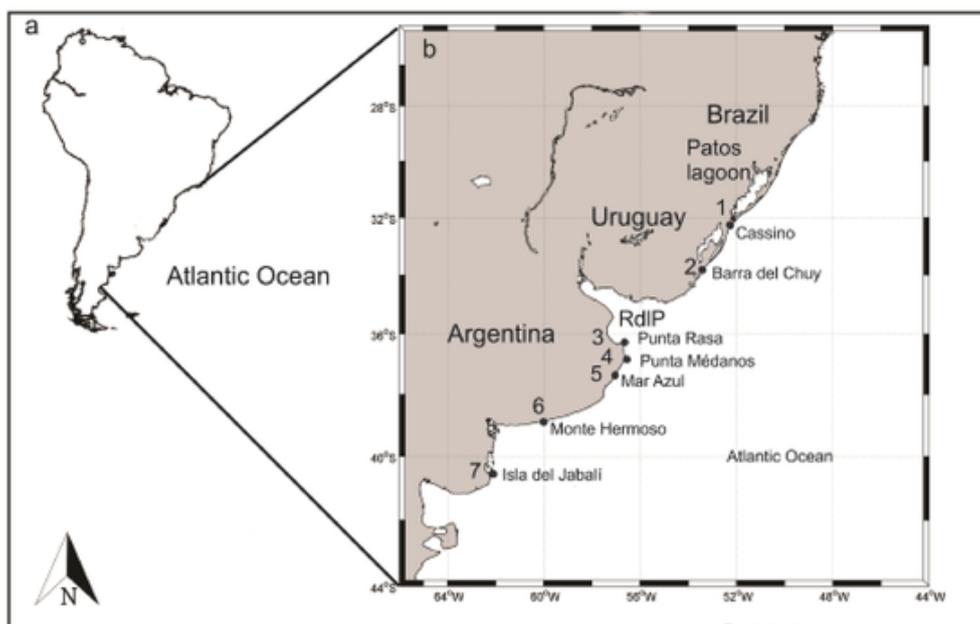


Fig. 1. Geographic range of the yellow clam *M. mactroides* along sandy beaches of South America (a), highlighting the seven sites analyzed in this study (ROMS domain, b). These beaches are sequentially numbered in the poleward direction from 1 to 7 and were defined as release areas from where virtual particles were released in the IBM. The RdIP estuary and the Patos Lagoon, freshwater sources included in the ROMS simulations, are indicated.

of sandy beaches in Brazil, Uruguay and Argentina (Fig. 1, see also McLachlan et al., 1996). The distribution of the yellow clam is interrupted by the RdIP estuary, mainly because of salinity variations (Fiori and Cazzaniga 1999).

The population features of *M. mactroides* vary markedly within its latitudinal distribution range (Fiori and Defeo 2006). The southernmost edge of *M. mactroides*, located at Isla del Jabali in Argentina (Fig. 1), tends to exhibit null recruitment (Fiori and Defeo 2006), suggesting a spasmodic recruitment pattern that characterizes sink populations situated at the edge of the distribution range of a metapopulation (Caddy and Defeo 2003). Thus, larval dispersal could affect yellow clam abundance and distribution among subpopulations and the overall persistence of the whole metapopulation (Defeo 1996).

Variations in habitat quality are critical for the yellow clam, which is considered as a high substrate specific species, inhabiting only fine to medium grain sizes (Defeo et al., 1992). *M. mactroides* is also sensitive to salinity variations (Saucó et al., 2013) and can be considered as a moderately euryhaline species, tolerating salinities from 15 to 35 (Carvalho et al., 2015). Reduced salinities near freshwater streams or rivers have been reported as unfavorable environments for the species (Olivier et al., 1971; Defeo and de Alava 1995; Marins and Levy 2000). Decreased recruitment in Uruguayan beaches has been recorded close to freshwater discharges (Defeo and de Alava 1995).

The Southwestern Atlantic Ocean (SAO) includes one of the largest and most intense warming hotspots in the global ocean (South Brazil-Uruguay marine hotspot), where the rate of increase in sea surface temperature (SST) doubled average global warming (Hobday and Pecl 2014; Belkin 2016). The systematic increase in SST observed in the SAO during the past 25 years is affecting the demography and population dynamics of the yellow clam (Ortega et al., 2016; Gianelli et al., 2021). Since the mid-1990s, this cool-water clam has experienced mass mortalities throughout its biogeographic range (Fiori and Cazzaniga 1999; Fiori et al., 2004; Ortega et al., 2016; Vázquez et al., 2016). These mass mortalities occurred first in 1993 in southern Brazil, and followed the progressive southward displacement of isotherms, reaching Argentina in 2002 (Ortega et al., 2016). The species suffered a drastic decline in abundance throughout its geographic range (Ortega et al., 2012, 2016),

and could be considered as a threatened species, perhaps with a status of “critically endangered” (*sensu* IUCN 1994).

Variable circulation patterns, including numerous mesoscale features (e.g. river plumes, fronts), could impose constraints to larval transport and connectivity (Gilg and Hilbish 2003; Ayata et al., 2010). In this context, the RdIP estuary constitutes a biogeographic barrier for many taxa exhibiting a marine planktonic larval dispersal, including the yellow clam. This takes utmost importance for this metapopulation, whose distribution and abundance appear to be modulated by recruitment pulses driven by environmental factors (Lima et al., 2000; Ortega et al., 2012; Defeo et al., 2013). These recruitment pulses could be affected by changes in connectivity.

This work assesses large-scale larval connectivity patterns of the yellow clam *M. mactroides* along its entire geographic range, using an individual based model (IBM). The biological model also incorporates the effects of salinity and water temperature on larval connectivity by including, respectively, salinity- and temperature-dependent larval mortality.

2. Materials and methods

2.1. Study area oceanography

The study area comprises the continental shelf of the southern Brazil, Uruguay, and Argentina (Fig. 1). The shelf is relatively narrow at its northern end and widens progressively to the south, where it reaches a maximum width of about 850 km in Argentina (Acha et al., 2018). The region is characterized by a complex oceanography with high seasonal variations modulated by the confluence of two water masses with different characteristics (Matano et al., 2010; Piola et al., 2018). The SAO southern shelf is mainly occupied by a relatively cold and fresh type of northward flowing subantarctic waters, the Subantarctic Shelf Water. The northern shelf is occupied by southward flowing Subtropical Shelf Water (STSW). STSW is composed by modified Tropical Water (TW) is diluted by continental runoff from the coast of southern Brazil (Piola et al., 2000). TW is part of the southward flowing Brazil Current along the shelf break, and it is the warmest shallow water in the region (Campos et al., 1995). SSTs in the SAO (southern Brazil, Uruguay and

northern shelf of Argentina) have not only experienced a warming trend but also a consistent poleward shift (ca. 9 km y⁻¹, Ortega et al., 2016) of the warm water front (represented by the 20 °C isotherm) separating the warm and salty waters of the northern region from the cold and fresher waters of the south.

The RdIP freshwater discharge—the second largest in the southern hemisphere—strongly influences coastal waters (Guerrero et al., 1997). Its estuary is an extensive and shallow coastal plain located at 35°S. Circulation within this estuary is not only controlled by the continental runoff but also by tidal and wind forcing (Dogliotti et al., 2016). The RdIP shows a weak seasonality of its discharge (Guerrero et al., 1997) but important interannual variations, with large runoff fluctuations primarily associated with El Niño Southern Oscillation (ENSO) (Piola et al., 2005; Acha et al., 2012; Jorge-Romero et al., 2021). The two main tributaries of the RdIP—the Parana and Uruguay rivers (García and Mechoso 2005)—show similarly strong interannual oscillations of their transports, which are also in phase with ENSO events (Pasquini and Depetris 2007). Transports increase during warm (El Niño) events and decrease during cold (La Niña) events (Dogliotti et al., 2016). During some El Niño years, high RdIP discharges are correlated with anomalous northeasterly winds, which preclude the plume's natural tendency to extend farther downstream (Piola et al., 2005). However, the impact of these variations on the RdIP plume characteristics remains uncertain (Matano et al., 2014).

2.2. Hydrodynamic model

Larval connectivity of the yellow clam was assessed with a spatially explicit IBM of larval transport coupled to the output of a 3-D, high-resolution (~3.8 km) hydrodynamic model. 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 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). This model is described in detail in Matano et al. (2014), and includes daily discharges of the RdIP, a constant discharge from the Patos Lagoon (set to 2000 m³/s) and five tidal components (M2, S2, N2, K1, and O1 harmonics). This model has been validated against in-situ and satellite observations (e.g. Combes and Matano 2014; Matano et al., 2014). Circulation fields produced by the model have been used to identify the main routes of detrainment of Subantarctic shelf waters from the Patagonian shelf (Franco et al., 2018) and to assess the larval connectivity of the mole crab *Emerita brasiliensis* in the coast of Uruguay (Meerhoff et al., 2020). The IBM was ran using the Ichthyop code (Lett et al., 2008), and connectivity between areas 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

Observations show significant geographic variations in the recruitment characteristics of *M. mactroides*: Brazilian populations have an extended or quasi-continuous recruitment season, whereas Uruguayan and Argentinean populations have seasonal recruitment that became almost negligible at the southernmost edge of the range (41°S) (Fiori and Defeo 2006). Two spawning periods are observed for Uruguayan (Masello 1987) and Argentine populations (Olivier et al., 1971): the first from October to December (austral spring) and the second from February to April (late austral summer). Based on these observations, we simulated two larval release events: one in November and another in February, with both release events being set on the 1st, 4th and 7th days of these months along the 12-year time series, in order to assess variability at a weekly scale.

Annual recruitment patterns during summer–autumn indicate a 3-month planktonic phase in Argentina (Hermann et al., 2009). Larval development seems to be shorter in Uruguayan and Brazilian beaches (Defeo 1996). Recent laboratory experiments report a complete larval development in 27 days at a mean water temperature of 20 °C (Santos et al., 2020). Consequently, different planktonic larval duration (PLD) periods were used in the simulations (30, 60 and 90 days), with 5-day variability in each case. Hence, 9 different PLDs were used (25, 30 and 35; 55, 60 and 65; and 80, 85 and 90 PLDs) to assess larval connectivity. *M. mactroides* larvae were considered as passive particles distributed within the surface layer, as assumed for modeling connectivity patterns in the congeneric *Mesodesma donacium* in Chile (Olivares 2005). Thus, a passive horizontal transport procedure was implemented for *M. mactroides*, 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).

Seven areas adjacent to sandy beaches (release zones where larvae are released in the model) were selected as starting points for individual larval transport following the morphology of the coast in Argentina, Uruguay and Brazil (Fig. 1). From northeast to southwest, larvae release and recruitment areas were adjacent to the oceanic sandy beaches Cassino (1) in Brazil, Barra del Chuy (2) in Uruguay, and Punta Rasa (3), Punta Médanos (4), Monte Hermoso (5), Mar Azul (6) and Isla del Jabalí (7) in Argentina (Fig. 1). Areas 1 and 2 are located to the northeast of the RdIP, while areas 3, to 7 are located southwest of the estuary.

To study the interannual variability in larval connectivity between selected areas, larval transport experiments were run using the velocity fields of the hydrodynamic model during the 2000–2012 period. We evaluated 12 (years) x 2 (months of release) x 1 (depth) x 9 PLD x 3 (replicates). This analysis was conducted twice: (1) with replicates obtained from larval release during the same day of the month; and (2) from replicates obtained during larval releases the 1st, 4th and 7th of February and November in order to assess weekly scale variability. For each case, 250,000 particles were released from randomly assigned coordinates within the different release sites (release sites were defined as boxes outside the points in Fig. 1). To assess the relative importance of spawning day, and month, PLD, and year on connectivity, the magnitude of effects of variance sources were estimated following Corell et al. (2012) and White et al. (2013), using analysis of variance (factorial ANOVA), with day, month, year and PLD as main factors (Zar 1999; Krzywinski et al., 2014).

Salinity is an important limiting factor of yellow clam distribution and mortality (Saucó et al., 2013), and therefore, the IBM was modified to consider larval mortality due to low salinities. Laboratory experiments show 100% mortality for yellow clam adults at a salinity of 4 (Saucó et al., 2013), while others showed similar mortality for adults and juveniles at 6.5 and 5.7 salinity values (Carvalho et al., 2015). Thus, 100% larval mortality was assumed at salinities <7 in the IBM. An ancillary set of sensitivity simulations was conducted using the same timing, release areas, PLD and passive movement, and included a salinity-dependent larval mortality factor.

Our area of study is one of the most intense warming hotspots of the global ocean, and variations in SST may affect the biology of the yellow clam (Ortega et al., 2016; Silva Santos et al., 2016). Laboratory experiments show changes in yellow clam larval development that affects its survival at water temperature up to 24.5 °C (Santos et al., 2020). Thus, we conducted another set of simulations that account for larval mortality at water temperatures >24.5 °C. Assessment of larval mortality sensitivity to temperature and salinity variations allow estimating the combined effects of these variables on larval survival and connectivity patterns.

Interannual variability in RdIP outflow and ocean surface currents was also evaluated during years of conspicuous contrasts in larval con-

nectivity patterns. Monthly data of river discharge were obtained from Instituto Nacional del Agua, Argentina (<https://www.ina.gov.ar>), and mean seasonal surface current maps were constructed using the hydrodynamic model velocities. Finally, seasonal mean wind patterns were also calculated. We used monthly data of surface wind from ERA-Interim reanalysis (<https://www.ecmwf.int/en/forecasts/datasets/archive-datasets/reanalysis-datasets/era-interim>), with a spatial resolution of 0.4° (Berrisford et al., 2011).

3. Results

3.1. Connectivity patterns

Larval connectivity was observed from release area 1 to area 2, and among the areas 3, 4, 5 and 6 (Fig. 2). There was also larval transport from release area 2 to recruitment area 4 (Fig. 3B, Supplementary material S1). There was no larval transport towards area 7 at the southern limit of *M. mactroides* distribution (Fig. 3, Supplementary material S2).

The most important source of variation for larval connectivity in the yellow clam was the interaction between year, month of larval release and PLD (Fig. 2A). The weekly scale variability (among different days of larval release) was negligible in all the patterns analyzed (Fig. 2B). The interaction of the factor day with the other factors explained an important percentage of the variance in some cases (e.g., connectivity from release area 4 towards recruitment area 3, Fig. 2B). The larval transport across the RdIP estuary occurred only for larvae released in November 2010 for 85 and 90 days PLD (Fig. 3, Supplementary material S1D). The sensitive analysis showed that the main patterns of larval connectivity were maintained, despite the day of the month larvae were released (mean connectivity matrices from larvae released the same day: Fig. 3, and from larvae released different days the same month, Supplementary material S2).

3.2. February larval release

For larvae released in February, there was self-recruitment at most areas (diagonal of the connectivity matrices, Fig. 3A, Supplementary

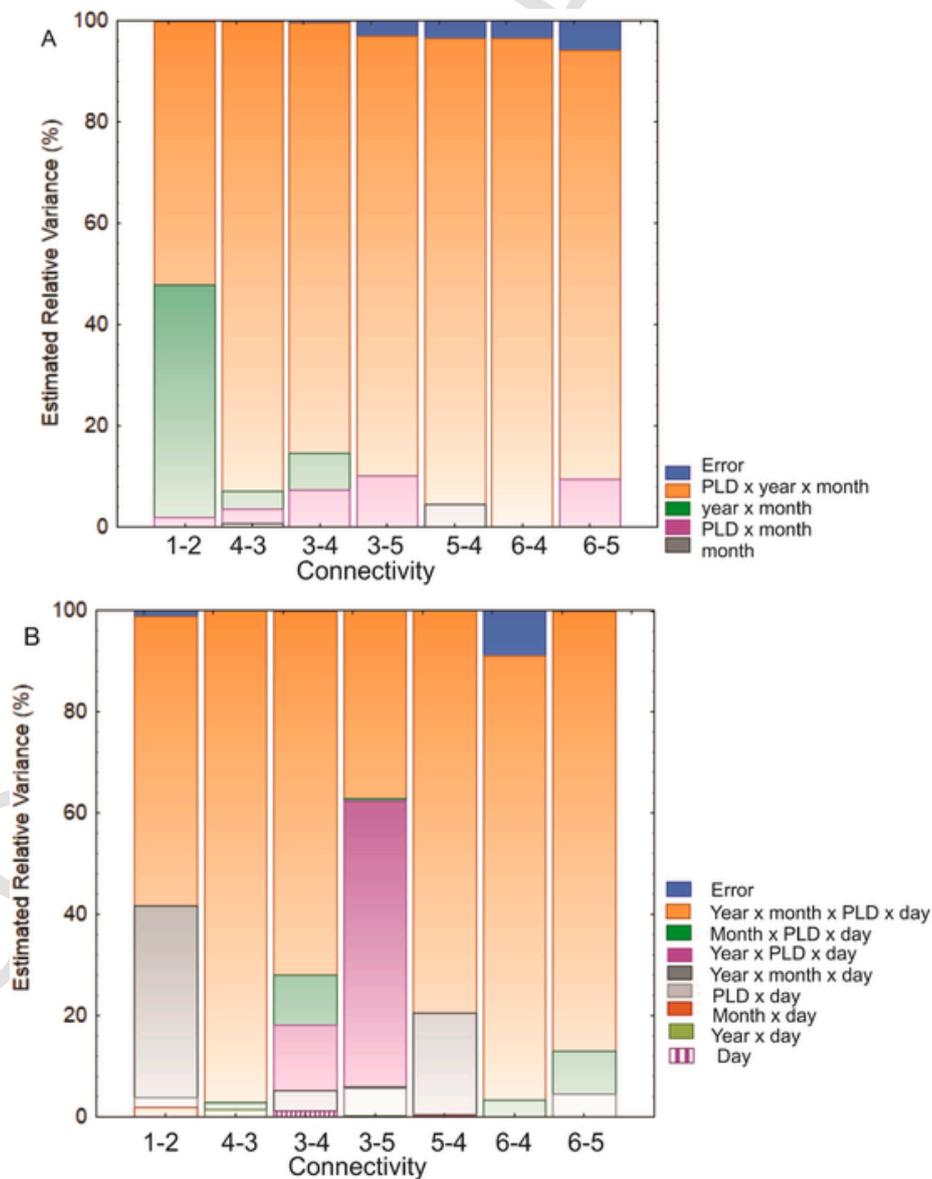


Fig. 2. Relative variance components (%) for *M. mactroides* larval connectivity along its geographic distribution range, using year, month of larval release, planktonic larval duration (PLD) and day as factors. Areas are numbered following Fig. 1. A) The replicates were simulated during the same day of larval release, B) different release events were simulated the 1st, 4th and 7th of February and November in order to access weekly scale variability.

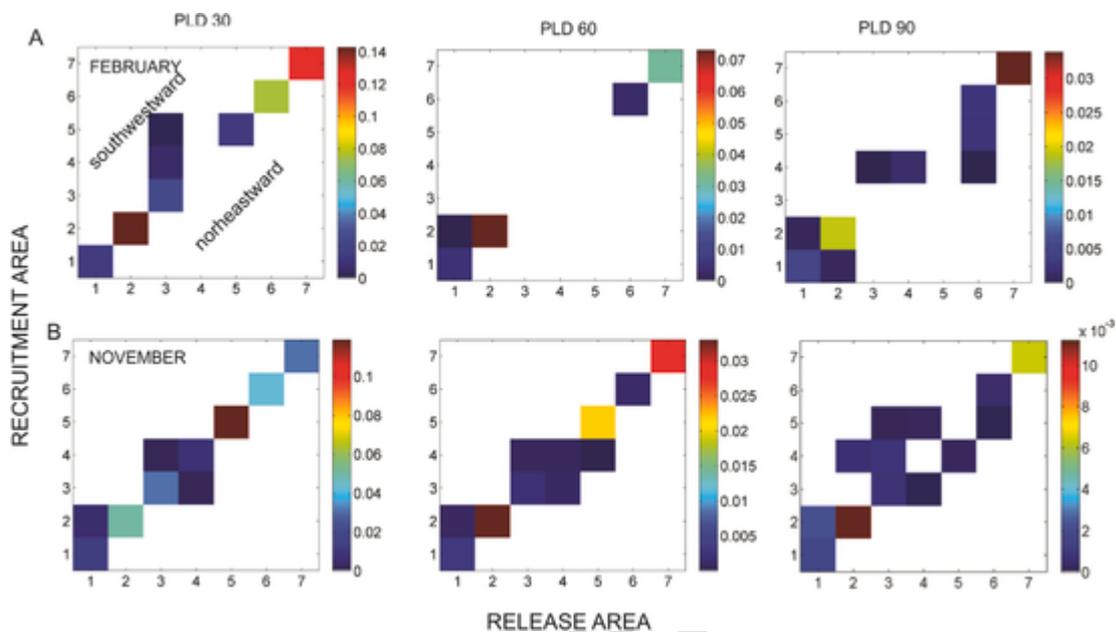


Fig. 3. Mean connectivity matrices for different months of larval release, A: February, B: November, and three planktonic larval duration (PLD in days) periods. Twelve years of simulations and three replicates (larvae released the same day, 1st of February and November) were averaged. Areas are numbered following Fig. 1. Connectivities above the diagonal indicate southwestward larval transport, and below the diagonal indicate northeastward transport (see upper-left in panel A). Connectivity is expressed as proportions in different color scales. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

material S1 A and B). The highest probabilities for self-recruitment were observed in area 2 and in recruitment area 7 for all PLDs (Fig. 3A, Supplementary material S1 A and B). Larval transport from release area 1 to recruitment area 2 had low probabilities, whereas along the portion of the coast south of the RdIP there was larval transport from area 3 to recruitment areas 4 and 5 at 30 PLD, and from release area 6 to recruitment areas 4 and 5 (90 days PLD) (Fig. 3A). There was no larval transport across the RdIP estuary or towards release area 7 (Fig. 3A, Supplementary material S1 A and B).

3.3. November larval release

For larvae released in November, there was self-recruitment for all areas at 30 days PLD, and for most areas at 60 and 90 days PLD (Fig. 3B). The highest connectivity probabilities were observed between release area 1 and area 2 (Fig. 3B). Along the coast south of the RdIP there was larval transport from release area 3 to 4, and vice versa (Fig. 3B). There was no larval transport towards area 7 (Isla del Jabalí), where there was only self-recruitment. Only in 2010 there was larval transport across the RdIP estuary from area 2 to recruitment area 4 (for 90 days PLD, Figs. 3B and 4, Supplementary material S1D for 85 days PLD). The probability of larval transport across the RdIP estuary from area 2 to area 4 was of the same order of magnitude than that of release area 3 to area 4 (Fig. 4).

There was interannual variability in *M. mactroides* larval connectivity for larvae released in November (Fig. 4). Larvae released from area 1 only reached area 2 in 2004, 2007 and 2008 (Fig. 4), with the highest connectivity values in 2008 and a PLD of 30 days. There was also larval connectivity between area 3 and area 4 most of the years, while larval transport from area 4 to recruitment area 3 was observed only during 2003 and 2007 (Fig. 4).

3.4. Salinity and temperature effects on larval connectivity

Larval mortality due to low salinity did not decrease connectivity probabilities or alters the patterns of larval connectivity for larvae released in February (Figs. 3A and 5A). However, it affected the transport

across the RdIP in November. There was no larval transport from release area 2 to area 4 when larval mortality due to low salinity was considered (Figs. 3B and 5B).

The combined effects of high temperature and low salinity reduced drastically the connectivity, leading to self-recruitment in most areas. Larval connectivity was restricted only for larvae released in November from release area 1 to recruitment area 2 (Fig. 5D) in 2004, and from release area 2 to recruitment area 1 for 90 days PLD (not shown). For larvae released in February, there was connectivity only from release area 6 to recruitment area 5 (Fig. 5C).

3.5. Impact of ocean circulation on connectivity

The mean surface circulation in our area of study was characterized by a weak southwestward coastal flow during the austral spring and summer and a northeastward flow during the autumn (Supplementary material, S3). These flows did not promote larval transport towards area 7, since they were directed northeastward along the coast of Argentina (Supplementary material, S3). Interannual variations of surface currents, however, explained the main connectivity patterns observed. For instance, larval connectivity across the RdIP estuary was observed only for larvae released in November 2010, during the an intense La Niña event in our study period (Fig. 6A). This event was characterized by strong southwestward surface currents along the coast north of RdIP during the summer of 2011 (Supplementary material, S4).

The RdIP outflow presented substantial interannual variability. During the strong La Niña event in 2010, outflow values were approximately $20,000 \text{ m}^3\text{s}^{-1}$ in spring (Fig. 6B). Thus, lower RdIP and strong southwestwards surface currents allowed larval connectivity across the estuary for larvae released in November 2010. Hence, a combination of the strength and direction (southwestwards) of surface currents and winds (Supplementary material S5) during the following summer, together with RdIP low discharge during the strong La Niña event, favored the larval transport across the estuary for a PDL of 90 days. The impact of the low discharge, associated to its effects in circulation patterns, favored this larval transport across the RdIP. However, when con-

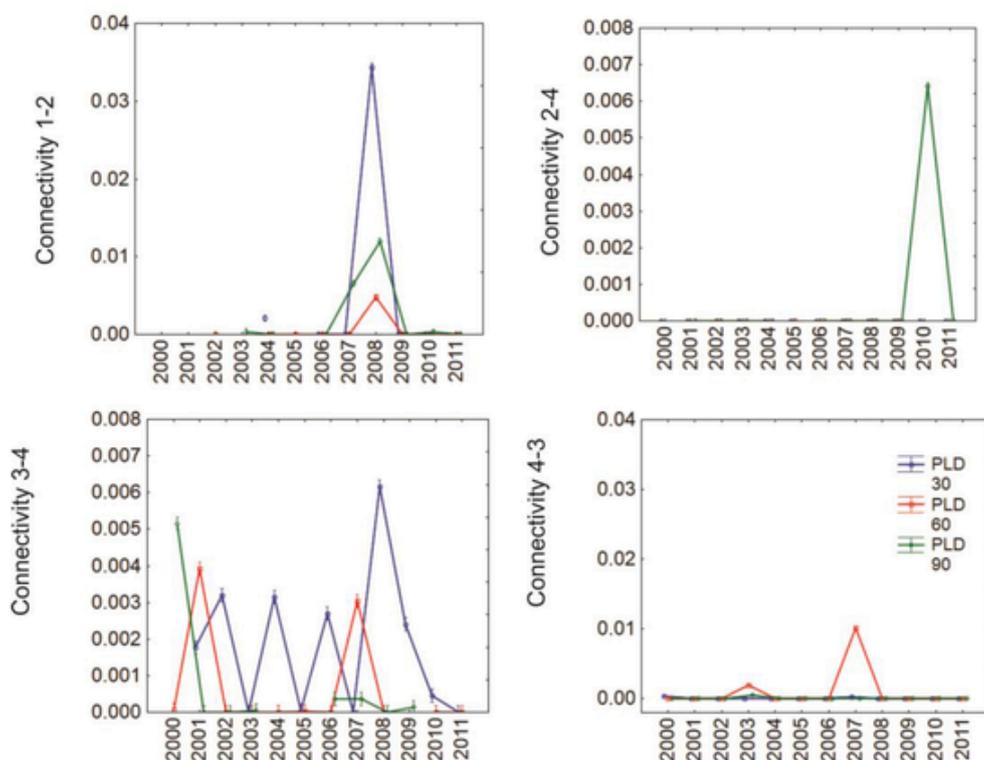


Fig. 4. Yellow clam *M. mactroides* larval connectivity time series between sandy beach recruitment areas for larvae released in November and planktonic larval durations (PLD) of 30, 60 and 90 days. Areas are numbered following Fig. 1. ROMS outputs started on April 2000, and therefore time series of summer connectivity start in 2001. Connectivity is presented from release area number # towards recruitment area #. Note the different Y-axis scales. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

sidering larval mortality due to low salinity, there was no larval transport across the RdIP.

4. Discussion

Here we simulated the *Mesodesma mactroides* larval dispersal along the Atlantic coast of South America using an IBM/ROMS coupled model, which considers salinity and temperature effects on large-scale connectivity patterns. Larval transport across RdIP estuary occurred during the strongest La Niña event of the period of study and only for larvae released in November 2010. Larval mortality due to warm waters modified connectivity patterns, showing three main larval sources: areas 1 (Cassino), 2 (Barra del Chuy) and 6 (Monte Hermoso).

Larval transport across the RdIP estuary was restricted to larvae released from Barra del Chuy (release area 2) to Punta Médanos (recruitment area 4). This transport occurred during spring of 2010, which was a strong La Niña event characterized by below average RdIP discharges and northeasterly winds (Matano et al., 2014) that generated a coastal flow that allowed the observed larval transport. In the Atlantic coast of Uruguay, the best scenario for the high yellow clam abundance is characterized by cold and salty waters and onshore wind stress anomalies, in agreement with the occurrence of La Niña events (Manta et al., 2017). These local wind stress anomalies are part of a cyclonic configuration of wind stress anomalies in the SAO, which forces negative sea surface temperature anomalies in the region (Manta et al., 2017).

Interannual fluctuations in *M. mactroides* abundance in the coast of Uruguay appear to be remotely controlled by regional and global-scale climate variability modes (Manta et al., 2017). For the Argentine coast, the shell mass condition index of the yellow clam is negatively correlated to the Oceanic Niño Index (Risoli et al., 2020). Our results showed important interannual variability in larval connectivity southwestward larval transport across the RdIP was favored during the strong La Niña event in late 2010 (see Fig. 4). In a climate change scenario, stronger

and more frequent La Niña events are expected to occur (Cai et al., 2015), and therefore more frequent larval transport across the RdIP estuary could be expected.

When larval mortality due to low salinity was considered in the model, there was no larval exchange across the RdIP estuary. Salinity-induced mortality of modelled larvae also substantially decreased transport success for the eastern oyster, *Crassostrea virginica*, in the Choptank and little Choptank rivers (Chesapeake Bay, Spires, 2015). The results presented here are in agreement with studies that showed that river plumes and fronts impose constraints to larval transport and connectivity (Gilg and Hilbish 2003; Ayata et al., 2010). For example, the larval exchange of *Mytilus edulis* in the shelf off southwest England, in the eastern North Atlantic Ocean can be restricted in summer if an oceanographic front develops between two populations (Gilg and Hilbish 2003). Empirical results show that the RdIP seems to function as a biogeographic barrier to the crab *Armases rubripes* (Luppi et al., 2003) However, authors mention this barrier is not absolute: it hinders, but does not entirely prevent, the dispersal of crab larvae. Additionally, genetic analysis (Ituarte et al., 2012) found that the genetic structure of the SW Atlantic estuarine crab *Neohelice granulata* could be divided into two distinct groups due to a limited gene flow between southern and northern regions as a consequence of larval dispersal patterns. Authors suggested that coastal currents in the vicinity of the RdIP likely act as a barrier to dispersal within the species range.

Mean direction of surface currents restricted larval exchange across the RdIP most of the years, and larval mortality due to low salinity decreases the modelled probability of yellow clam larval connectivity across the RdIP. The RdIP estuary is included within the RdIP marine ecoregion, which is located between Rio Grande (Brazil) and Uruguay-Buenos Aires shelf ecoregions (Spalding et al., 2007). Therefore, our results reinforce the perception that reduced dispersal of sandy beach macrofauna favors isolation among ecoregions (Barboza and Defeo 2015).

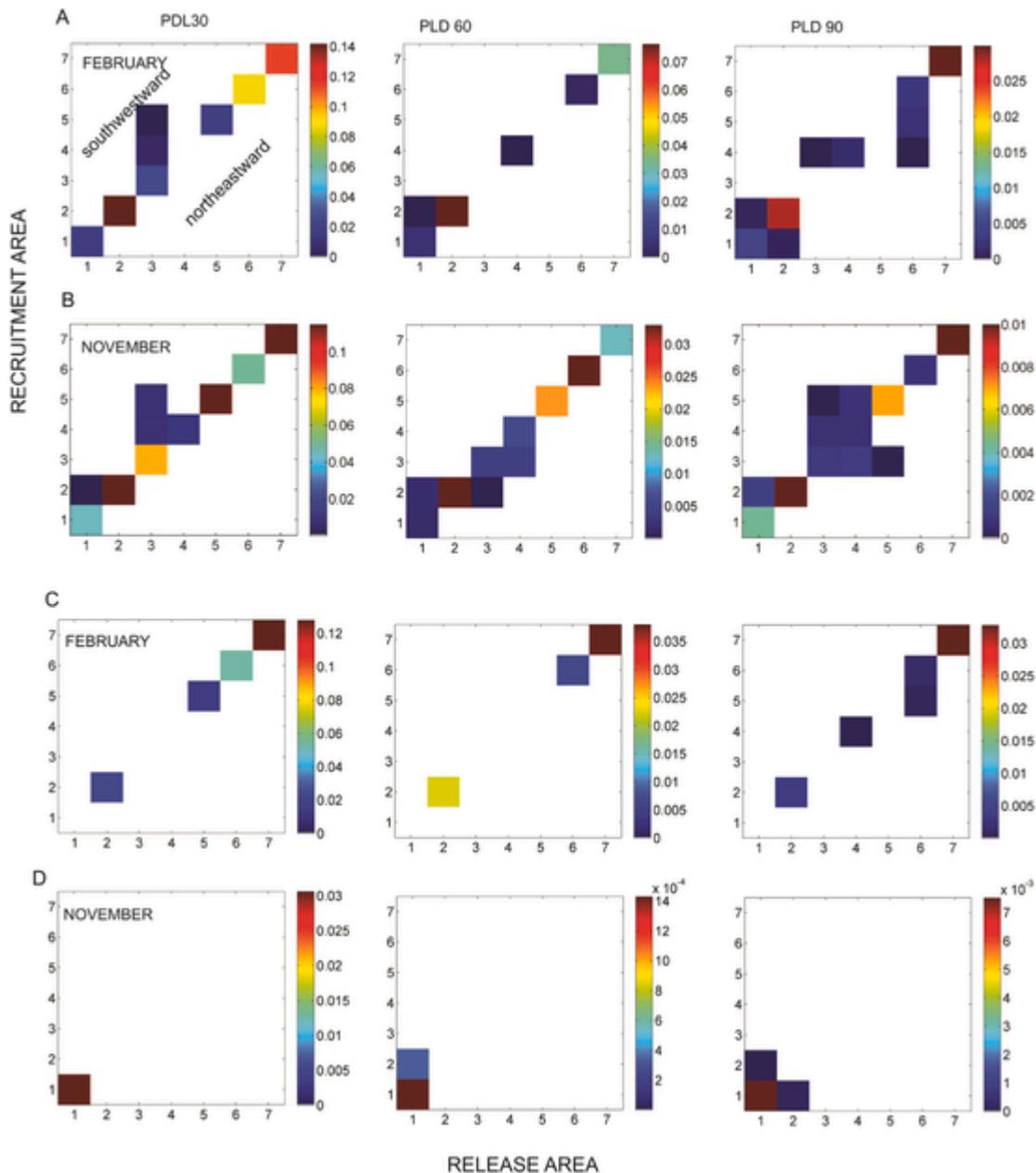


Fig. 5. Mean connectivity matrices for larval connectivity in the yellow clam *M. mactroides*, corrected for larval mortality due to low salinity for larvae released in February (A) and November (B), and corrected by larval mortality due to low salinity and high temperature in February (C) and November (D). Connectivities above the diagonal indicate southwestward larval transport, and below the diagonal indicate northeastward transport (see upper-left in panel A). Connectivity is expressed as proportions in different color scales. Note the different scales in color bar (right side of each panel). Twelve years of simulations and three replicates (larvae released the same day) were averaged. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Simulation results showed that there was larval transport among all release/recruitment areas of the Argentine coast (south of RdIP), except for Isla del Jabalí (area 7), which is the southernmost limit of *M. mactroides* distribution (Fiori and Defeo 2006). In the Argentine shelf, numerical simulations, satellite, and direct current observations indicate a northeastward mean flow over shelf south of $\sim 40^{\circ}\text{S}$ (Ruiz Etcheverry et al., 2016; Lago et al., 2019). Consequently, southwestwards larval transport towards Isla del Jabalí is not promoted by the mean circulation. Similar results were reported by Franco et al. (2015), who showed that the dominant semidiurnal tidal currents and the mean N-NE flow on the inner-middle Patagonian shelf are the main mechanisms preventing particles released in an IBM to reach the southern area. However, recent observations suggest that sudden changes in along-shore winds can induce intense current reversals, lasting between 3 and 14

days (Lago et al., 2019). These events are driven by synoptic atmospheric systems and could favor sporadic larvae transfer to area 7. These results reinforce the perception that synoptic variability may affect larval pools in coastal areas (Satterthwaite et al., 2020).

When larval mortality due to high temperature was included in the model, there was larval connectivity only between areas 1 and 2 for larvae released in November and from release area 6 to recruitment area 5 for larvae released in February. These results provide additional support to the negative impact of ocean warming over this species at the warming hotspot developed in the SAO (Franco et al., 2020; Gianelli et al., 2021). Raventos et al. (2021) showed that increasing temperature in the Mediterranean Sea results in considerable reduction in the dispersal potential of temperate fish, which could isolate populations as waters warm. Therefore, sensitivity to warming is critical in metapopu-

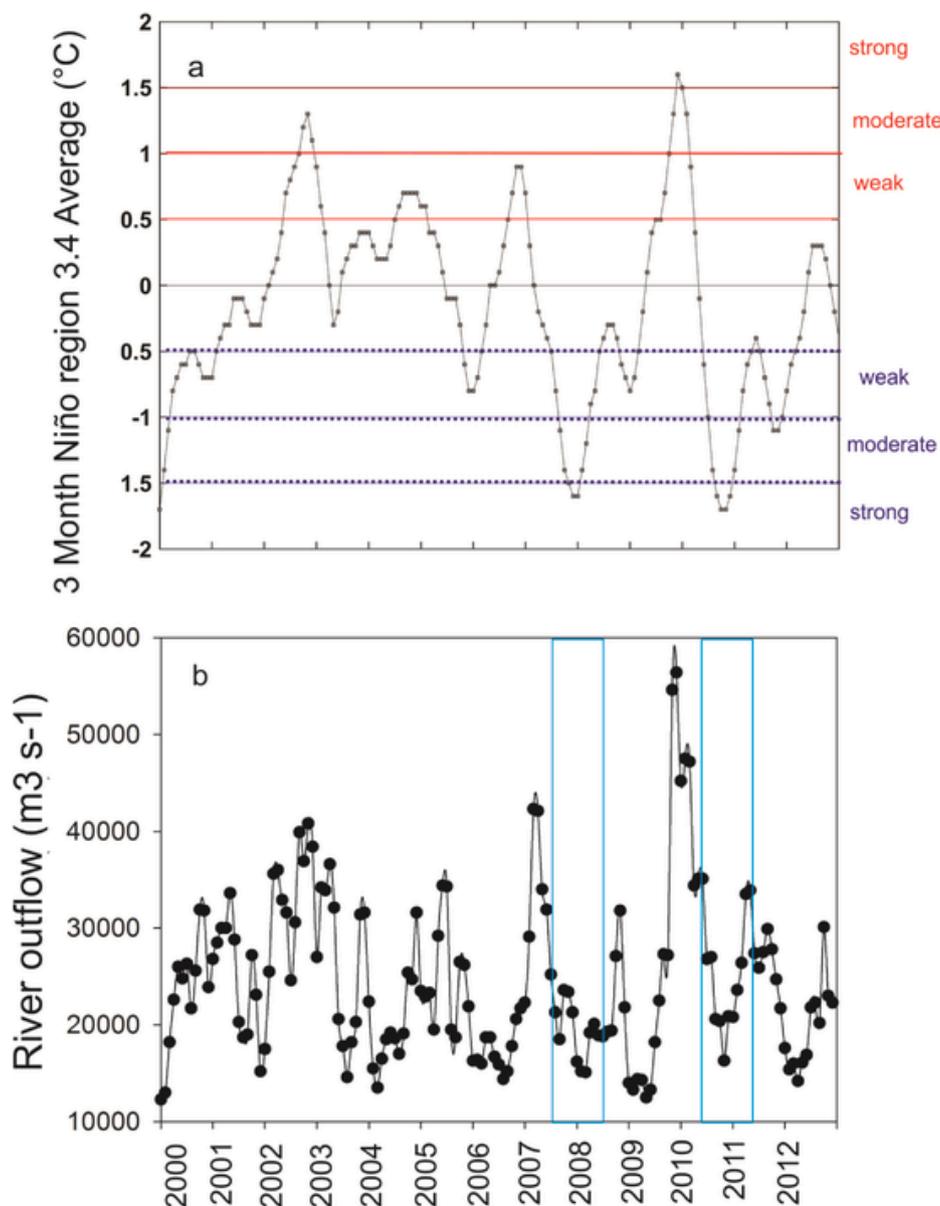


Fig. 6. A) Monthly oceanic Niño index (ONI) for the analyzed period. Dashed blue lines indicate La Niña events and red lines El Niño events. Thresholds are broken down based on absolute SST anomalies as follows: weak 0.5 to 0.9 °C, moderate 1.0 to 1.4 °C, and strong 1.5 to 1.9 °C. B) Monthly RdIP outflow: strong La Niña episodes are highlighted in light blue. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

lations like the yellow clam, because local variable conditions can alter the capacity of the species to foster a large-scale recovery from pulse (e.g., El Niño) or press (e.g., climate change) disturbances (Cowen et al., 2006; Treml et al., 2008).

Our results suggest that yellow clam populations from areas 1 (Cassino), 2 (Barra del Chuy) and 6 (Monte Hermoso) should be protected to provide larvae to other areas. This research reinforces the importance of addressing connectivity issues when managing metapopulations as the yellow clam, as also suggested for managing other transboundary resources, such as the spiny lobster in the Caribbean (Kough et al., 2013). The design of marine reserve networks currently incorporates changes in larval connectivity due to potential reductions in planktonic larval duration associated with ocean warming (Álvarez-Romero et al., 2017). This has utmost importance for the yellow clam in the SAO, which encompass an ocean warming hotspot that could further restrict larval connectivity between populations. This cool-water species has suffered temperature-dependent mass mortalities through-

out its geographic range (Ortega et al., 2016) and could be considered as a threatened species. Reduced dispersal success due to high water temperature will further lower recruitment, with implications for fishery stocks (Bashevkin et al., 2020). As the yellow clam is subject to small-scale fisheries that are critical for the livelihood of local communities (Gianelli et al., 2021), our results have strong management and conservation implications. A regional perspective to address connectivity patterns among populations is a pressing, short-term need.

Author statement

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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.

Acknowledgements

EM acknowledges the financial support from Comisión Académica de Postgrado (CAP, Uruguay) Postdoctoral grant and Agencia Nacional de Investigación e Innovación (ANII) Grant Fondo Clemente Estable (FCE 3_2020_1_162359). Financial support was also provided by the Inter-American Institute for Global Change Research (grants CRN 3070 and SGP-HW 017), which is supported by the US National Science Foundation, and by Comisión Sectorial de Investigación Científica de Uruguay (CSIC Grupos ID 32).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2022.105591>.

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