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The Effect of Climate Variability on the Abundance of the Sandy Beach Clam (*Mesodesma mactroides*) in the Southwestern Atlantic

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ABSTRACT

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The yellow clam *Mesodesma mactroides* is a fast-growing, short-lived species that inhabits sandy beaches of the southwestern Atlantic Ocean (SAO). The purpose of this study was to relate interannual fluctuations of the yellow clam population in Uruguay to climate circulation anomalies in the SAO. Twenty-three years of clam abundance, as well as sea-surface temperature anomalies (SSTA), salinity, and wind stress anomalies (WSA) from oceanic reanalyses were used. Composites and linear regressions showed that the best scenario for high abundance of *M. mactroides* is characterized by cold and salty waters and onshore WSA on the Uruguayan Atlantic coast. These local WSA are part of a cyclonic configuration of WSA in the SAO that forces negative SSTA in the region. High and low *M. mactroides* abundance tended to occur along with La Niña and El Niño events in the equatorial Pacific Ocean, respectively. These results suggest that interannual fluctuations in *M. mactroides* abundance are not only locally but also remotely controlled by regional- and global-scale climate variability modes.

ADDITIONAL INDEX WORDS: *ENSO, composites, oceanic reanalyses, SODA, C-GLORS*.

INTRODUCTION

Exposed sandy beaches dominate the ice-free shores of all continents and provide important commercial resources in many areas (McLachlan *et al*., 1996). Many beaches, especially those of the dissipative type, support rich biotas, of which clams are often an important component, especially in terms of biomass (Defeo and McLachlan, 2005). Contractions or expansions in the geographic range of clams, as well as changes in their population structure, vary according to environmental settings. Indeed, direct environmental variables (*e.g.,* temperature, oxygen, grain size) have an unequivocal physiological influence on habitat suitability for benthic species (*e.g.,* Huntley and Scarponi, 2015; Peterson *et al.,* 2011). Recruitment tends to occur regularly in source areas and to be irregular or spasmodic in sink areas or marginal portions of the habitat (*i.e*. the habitat favorability hypothesis: Caddy and Defeo, 2003; Defeo *et al*., 2013). Thus, management of clam fisheries through harvest controls alone will be ineffective if these environmentally driven variations in abundance and habitat quality are not taken into account (Caddy, 2007).

The southwestern Atlantic Ocean (SAO) surface winds drive an open ocean circulation characterized by intense western boundary currents, with a poleward-flowing warm and salty Brazil Current and an equatorward-flowing cold and relatively fresh Malvinas Current (Peterson and Stramma, 1991). These two currents converge near 38°S, generating the highly energetic and productive Brazil/Malvinas Confluence (Machado, Barreiro, and Calliari*,* 2013; Olson *et al*., 1988). These currents in turn influence the continental shelf circulation (Piola *et al*., 2000). The Uruguayan shelf hydrography is characterized by a marked seasonality related to the southward displacement of the South Atlantic high-pressure cell during summer, with northward wind and shelf currents in winter and southward in summer (Möller *et al*., 2008; Strub *et al*., 2015). Interannual variability is strongly linked to El Niño–Southern Oscillation (ENSO). During El Niño years, positive sea-surface temperature anomalies (SSTA) and northerly wind stress anomalies (WSA) are observed in the SAO. In Uruguay, particularly in spring, precipitation, and consequently freshwater discharge, tends to increase, freshening waters along the coast. During La Niña years, the opposite condition tends to occur (*e.g.,* Barreiro, 2010).

The yellow clam *Mesodesma mactroides* Reeve, 1854 is a fast-growing, short-lived species (<4 y) found in sandy beaches of the SAO from Brazil (24° S) to Argentina (41° S) (Defeo, Jaramillo, and Lyonnet, 1992; Fiori and Defeo, 2006). Large interannual fluctuations in *M. mactroides* abundance have been observed in Barra del Chuy (Uruguay), even in the absence of fishing (Defeo *et al*., 2013; Ortega *et al*., 2016), suggesting a role for environmental conditions. Previous studies have shown that the distribution and abundance of *M. mactroides* appear to be modulated by recruitment pulses driven by environmental factors (Ortega *et al*., 2012). In the present paper, the response of *M. mactroides* at Barra del Chuy

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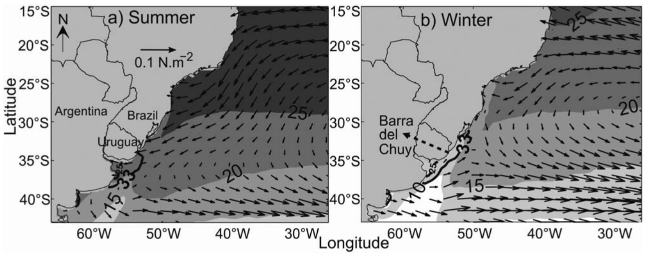

Figure 1. Mean sea-surface temperature (shades, °C) and wind stress (arrows, N m^{-2}) along *Mesodesma mactroides* distribution range in (a) summer and (b) winter for the period 1986–2008. Bold contours show 25 and 33 isohalines, representing the Rio de la Plata estuary mean limit and discharge influence, respectively. The dotted arrow shows Barra del Chuy Beach where sampling surveys were conducted. Data from C-GLORS.

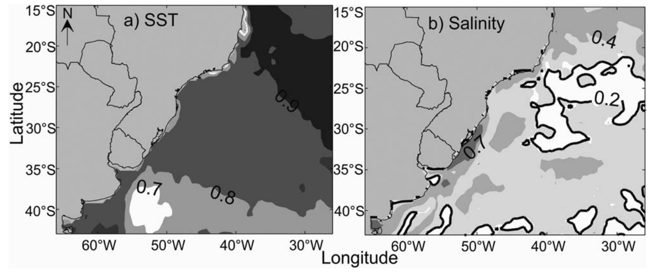

Figure 2. Pearson correlation coefficient values for the pixel-to-pixel linear regression comparing the SODA and C-GLORS reanalyses in the period 1986–2008 (monthly, $n = 276$) for: (a) sea-surface temperature (SST) and (b) sea-surface salinity. Each point in the grid is statistically significant ($p < 0.05$), except for those enclosed by bold contours. Reanalyses have similar evolution in the case of SST over the region, but in the case of salinity, correlation is high only over the southern Brazilian and Uruguayan shelf.

to regional atmospheric and oceanic anomalies is assessed, aiming to provide insights on interannual fluctuations in abundance and the potential influence of regional climate variability as a putative explanation of long-term patterns in clam abundance.

METHODS

This section provides information about Barra del Chuy beach and the sampling design of the yellow clam. The environmental data used from oceanic reanalysis and the statistical analysis used are also detailed.

Beach Description, Environmental Settings, and Data Collection

Mesodesma mactroides in Uruguay mainly occurs at Barra del Chuy beach (33°40′ S, 53°29′ W), a 22-km stretch of uninterrupted microtidal sandy beach with dissipative characteristics limited by two freshwater outlets, the Andreoni Canal and the Chuy Stream (Ortega *et al.*, 2013). Sea-surface temperature (SST) ranges from 12 to 24°C over the year and interannual variability is also high (2°C). Moreover, sea-surface salinity (thereafter salinity) strongly fluctuates, mainly due to the effect of the Andreoni Canal, the Chuy Stream, and the Rio de la Plata (RdlP) discharges. Mean wind direction is from NE in spring–summer and SW in autumn–winter, when RdlP discharge is also higher (Ortega and Martinez, 2007; Strub *et al.*, 2015; Figures 1, S1, and S2). *Mesodesma mactroides* is artisanally harvested with hand-gathering techniques in the intertidal zone of sandy beaches from Brazil, Uruguay, and Argentina (Defeo, 2003). In Uruguay, fishing started in the 1960s and evolved from an open-access system to a regulated fishery during the 1980s, and the fishery was closed because of overexploitation in April 1987. Two years after the closure, adult clam density increased by more than 400% and the fishery was reopened from December 1989 onward under a co-management framework (Defeo, 1996). This governance mode lasted until late 1994, when mass mortalities decimated populations of *M. mactroides* throughout its range (Ortega *et al.*, 2016). The fishery was reopened as a co-management system in 2008 after a partial recovery of the stock, using a precautionary approach that included very low harvesting levels (Gianelli, Martínez, and Defeo, 2015).

Yellow clams were obtained from seasonal surveys carried out in Barra del Chuy beach during 23 consecutive years (1986 to 2008). A systematic sampling design was used by setting 22 equidistant transects perpendicular to the shoreline. Along each transect, sampling units were obtained with a corer 28.2 cm in diameter and 40 cm in depth at 4-m intervals, starting at the sand dunes and continuing seaward until two consecutive sampling units yielded no yellow clams (Lima, Brazeiro, and Defeo, 2000). Specimens were measured (maximum valve length) and counted, covering the full range of individual sizes (1 to 76 mm). Annual abundance was estimated by averaging seasonal estimates of the number of individuals per strip transect (ind.m^{-1}) following Defeo (1996).

Environmental Data and Statistical Analysis

The Uruguayan coast is a very poorly environmentally sampled region, which hampers the identification of local environmental conditions that modulate the interannual abundance of *M. mactroides*. However, since coastal variability responds to regional patterns of atmospheric and oceanic circulation, reanalysis data could be used to determine the main anomaly patterns associated with clam abundance. The Simple Ocean Data Assimilation (SODA 2.1.6) reanalysis (Carton and Giese, 2008) and Global Ocean Physics Reanalysis (C-GLORS) (Storto, Masina, and Navarro, 2016) were used. Both reanalyses assimilate a historical archive of hydrographical profiles supplemented by ship intake measurements, moored hydrographical observations, Argos drifters, and remotely sensed SST and sea level to an ocean general circulation model. Annual averages from 1986 to 2008 of wind stress, SST, and salinity in the SAO (15–45°S and 65–25°W) were used, and the corresponding anomalies were calculated by subtracting the mean of the study period. SODA has horizontal resolution of 0.5° × 0.5° and C-GLORS 0.2°× 0.25° near Barra del Chuy. The main differences between the SODA and C-GLORS are grid size, the data assimilation method used, and the number of observations assimilated in each interpolation. C-GLORS assimilates a larger number of observations for the salinity field. A correlation analysis between C-GLORS and SODA data revealed that, for SST, all grid points had values higher than 0.7 ($p < 0.05$) (Figure 2a). On the other hand, for salinity there was no significant

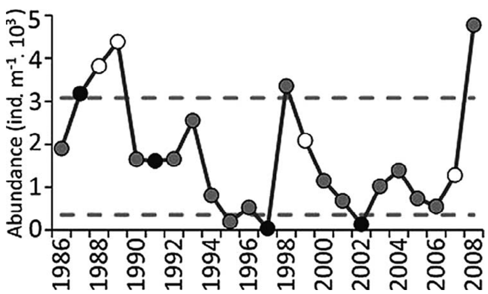

Figure 3. Long-term variations in abundance of *Mesodesma mactroides* in Barra del Chuy (Uruguay) estimated from sampling surveys conducted between 1986 and 2008. Dotted lines show the mean long-term abundance ± 1 standard deviation, which was used for the classification of composites. Black circles indicate years with a beginning of a moderate or strong El Niño event; white circles show years with a beginning of a moderate or strong La Niña event. Gray circles indicate neutral ENSO years. Large interannual variability in clam abundance is observed. Minimums of abundance tend to occur mainly during an El Niño year. Data from ENSO 3.4 index.

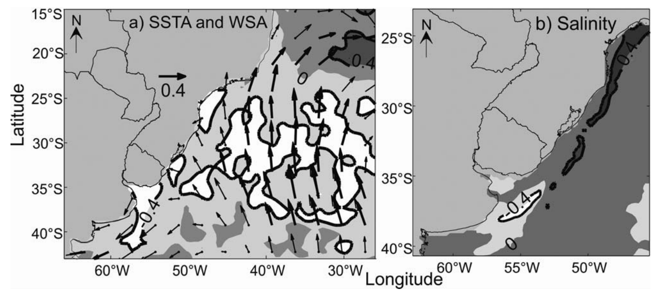

Figure 4. Pearson correlation coefficient values between abundance of *Mesodesma mactroides* in Barra del Chuy (Uruguay) and annual mean anomalies of: (a) sea-surface temperature (SSTA, in shades, °C) and wind stress (WSA, in arrows, N m^{-2}) and (b) sea-surface salinity. Bold contours and bold arrows indicate significant regions ($p < 0.05$). Low abundance is correlated with negative SSTA and southerly WSA over a large region between 25 and 40°S. At the same time, increased abundance is related to salty conditions over the Uruguayan shelf and diluted waters to the south of the Rio de la Plata outlet. Environmental data from (a) SODA and (b) C-GLORS.

correlation between reanalyses in the study region of the SAO (Figure 2b). Highest correlations (above 0.7) were observed over the Uruguayan and southern Brazilian shelf. Thus, for SST both SODA and C-GLORS were used, whereas C-GLORS was used for salinity because it assimilates more observed data and better represented the RdlP's complex dynamics.

The spatial dependence between annual variations in abundance of *M. mactroides* in Barra del Chuy and annual mean anomalies at each grid point in the SAO were assessed using Pearson correlation coefficient values. Statistical significance was determined by a Student's t test ($\alpha = 0.05$). Composites were also used to study the behavior of environmental variables associated with yellow clam abundance:

$$C(h)_l = \overline{X(h)_l} - \overline{X_n} \quad (1)$$

where $C(h)_l$ = composite associated with (high-) low-abundance years, $\overline{X(h)_l}$ = mean of enviromental anomalies during (high-) low-abundance years, $\overline{X_n}$ = mean of enviromental anomalies during neutral-abundance years. (High-) low-abundance years are those (above) below $\mu \pm \sigma$, whereas neutral years are those between $\mu \pm \sigma$, the mean abundance ± its standard deviation, respectively (Figure 3). The significance of the composite was determined using the difference of means test ($\alpha = 0.05$) following section 6.6 of Von Storch and Zwiers (2001). To explore the potential relationship between abundance of *M. mactroides* and SSTA in the SAO and tropical Pacific and Atlantic oceans, composites were constructed using the optimum interpolation SST data set of Reynolds *et al.* (2002) with a horizontal resolution of 1° × 1°.

RESULTS

Long-term variations in abundance of *M. mactroides* in Barra del Chuy (Uruguay) are observed (Figure 3). The spatial pattern of the correlation between *M. mactroides* abundance in Barra del Chuy and SSTA and WSA shows that increased yellow clam abundance is associated with an SSTA pattern characterized by negative and positive anomalies south and of 20° S, respectively, as well as with a cyclonic configuration of WSA in the SAO. Along the Uruguayan coast, a locally significant negative correlation between clam abundance and SSTA is observed ($p < 0.05$) together with a positive, although nonsignificant, correlation with an onshore WSA configuration in Barra del Chuy (Figure 4a).

Composites show overall linearity in the structure of the regional anomalies associated with high yellow clam abundance years (Figure 5). Positive and negative SSTA north and south of 20°S are observed respectively, concurrently with a cyclonic configuration of WSA in the SAO during high-abundance years. An opposite behavior during low-abundance years is found in the open ocean, with negative and positive SSTA north and south of 20° S, respectively, accompanied by an anticyclonic configuration of WSA in the SAO. Over the Uruguayan and southern Brazilian shelves, the SSTA composites for high- and low-abundance years are not opposite: the SSTA in the shelf near Barra del Chuy is about –0.8°C ($p <$

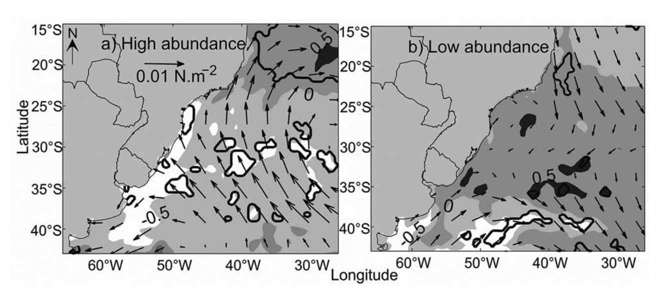

Figure 5. Composite associated with: (a) high and (b) low annual values of *Mesodesma mactroides* abundance in Barra del Chuy (Uruguay) for the period 1986–2008. Mean sea-surface temperature anomalies (SSTA) are shown in shades (°C) and mean wind stress anomalies (WSA) in arrows (N m^{-2}). Bold contours enclose significant SSTA regions ($p < 0.05$). Only high-abundance cases are significantly related to environmental anomalies over the shelf. No significant regions are observed for WSA. SSTA and WSA data from SODA.

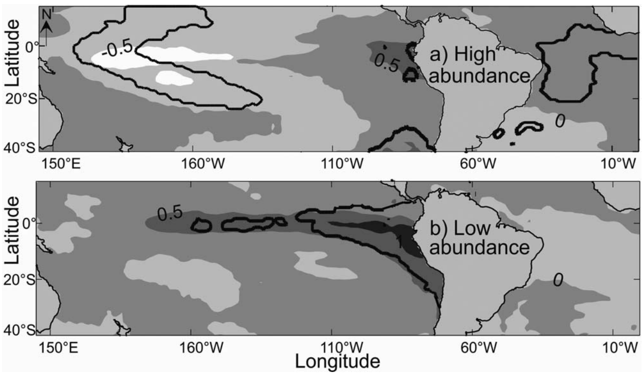

Figure 6. Composite associated with: (a) high and (b) low annual values of *Mesodesma mactroides* abundance in Barra del Chuy (Uruguay) for the period 1986–2008. Shades show mean sea-surface temperature anomalies (SSTA, °C). Bold contours enclose significant regions ($p < 0.05$). High-abundance years are characterized by cold conditions in the central equatorial Pacific, whereas low-abundance years show SSTA typical of El Niño. SSTA data from Reynolds *et al*. (2002).

0.05) for high-abundance years but only 0.3°C (not significant) for low-abundance ones, respectively (Figure 5).

Salinity anomalies show significant negative and positive correlation ($p < 0.05$) south and north of the RdlP outlet, respectively, meaning higher *M. mactroides* abundance associated with fresher waters south of the RdlP outlet and saltier waters along the Uruguayan and southern Brazilian shelves (Figures 4b and S3). Moreover, the composite for low-abundance years shows fresher waters along Barra del Chuy ($p < 0.05$, not shown). The composite for high yellow clam abundance years shows no significant salinity anomalies. Composites of global SSTA show that low yellow clam abundance years coincide with warm conditions in the equatorial Pacific (mean ENSO 3.4 index >0.5°C, $p < 0.05$). On the other hand, high abundance years are characterized by a relatively cold western-central equatorial Pacific and warm conditions next to Peru, as well as with a warm equatorial Atlantic (mean ENSO 3.4 index <0°C, Figure 6).

DISCUSSION

The results of this study provide evidence of the role of regional climate on abundance fluctuations of the sandy beach clam *M. mactroides*. The current analysis extends the work of Ortega *et al*. (2012), who found a significant negative correlation between annual mean yellow clam abundance and SSTA near Barra del Chuy. By considering a larger area and more environmental variables, the following patterns were detected: (1) atmospheric circulation anomalies associated with the SSTA pattern in the region; (2) an increase in abundance of *M. mactroides* in Uruguay associated with cold periods in the SAO; (3) a relationship between clam abundance and ENSO events, with high and low *M. mactroides* abundance periods during La Niña and El Niño events in the equatorial Pacific Ocean, respectively; and (4) a positive trend in abundance in relation to high salinity.

The best scenario for high-abundance years of *M. mactroides* was characterized by a cyclonic configuration of WSA in the SAO, with cold and salty waters and onshore WSA in Barra del Chuy. It is worth stressing that the cyclonic configuration of WSA in the SAO that accompanies an increase in clam abundance has a much larger spatial scale than the study site, thus affecting a large oceanic region. It is hypothesized that these atmospheric circulation anomalies increase and decrease the oceanic heat loss south and north of 20° S respectively, leading to the observed SSTA dipole in the open ocean (Barreiro *et al*., 2004). Dynamic processes on the shelf may further modify this large-scale thermodynamic forcing, increasing the influence of local SSTA in yellow clam abundance (see Figure 5).

A higher abundance of *M. mactroides* associated with negative SSTA in Barra del Chuy and all along the southern Brazilian shelf was identified. Moreover, whereas composites suggest that cold years are a trigger for high abundance, warm years do not necessarily negatively affect the yellow clam population. This preference for cold conditions may reflect the Antarctic origin of the species (von Ihering, 1907). Low clam abundance could be explained by other variables like the remote influence of El Niño, which has been already identified as a driver of mass mortalities in clams of the same genus along the Pacific coast (Ortega *et al*., 2012). Of the three years with low abundance, two (1997 and 2002) occurred during the beginning of an El Niño event and the other one (1995) was preceded by the mass mortality event that occurred in November 1994. The link between El Niño and low-abundance years could also be related to increased rainfall in the RdlP basin that leads to a higher river discharge and, consequently, fresher waters along the coast. High-abundance years, on the other hand, are mainly La Niña years with onshore WSA, coming mainly from the SE, that push the plume against the Argentinean coast. This is consistent with laboratory observations that showed reduced or no clam survival exposed to low salinity for a few days (Sauco *et al*., 2013). This is also in agreement with the fact that no yellow clam populations are found in sandy beaches of the RdlP estuarine region. It is worth pointing out, however, that no significant correlation between abundance and salinity along the coast was detected, possibly because the large coastal variability of this variable is not captured by the reanalysis. In addition to the increased freshwater discharge, El Niño events have been shown to promote cyclogenesis in the region (Gan and Rao, 1991), which may induce increased beach erosion and sea-level change (Ortega *et al*., 2013), causing habitat degradation and potential mass stranding and mortality of benthic organisms.

High yellow clam abundance years in Barra del Chuy were associated with wind stress having a SE (onshore) direction. These onshore winds favor the advection of sub-Antarctic waters over the shelf during cold periods, and could promote blooms of surf phytoplankton that accumulate in the surf zone. Indeed, the passage of cold fronts associated with onshore winds favor the accumulation and growth of the surf zone diatom *Asterionellopsis glacialis* (Odebrecht *et al.,* 2010 and references therein), which is the main food source of *M. mactroides* (Lercari, Bergamino and Defeo, 2010). This is consistent with observations made at Cassino Beach (Brazil), which is located in the same ecoregion (250 km NE of Barra del Chuy) with similar beach orientation and morphodynamics (Odebrecht *et al.,* 2010). This supports high yellow clam abundance during cyclonic atmospheric events, which represents a regional weakening of the semipermanent subtropical high pressure in the SAO, favoring the passage of cold fronts in the region. High yellow clam abundance years were also modulated by ENSO (see also Lima, Brazeiro and Defeo, 2000). Clam abundance could be negatively affected by increasing SSTA, favoring warm-water species such as the wedge clam *Donax hanleyanus* and the mole crab *Emerita brasiliensis*, which are subordinate competitors for space and food in this suspension-feeding guild (Defeo *et al*., 2013; Ortega *et al*., 2012).

Several studies have used reanalysis to assess the role of environmental factors in marine populations (*i.e*. Bertrand *et al*., 2008; Maunder *et al*., 2006; Pacariz, Westerberg, and Björk, 2014), though it still remains infrequently used. In this paper, oceanic reanalyses were useful to determine the environmental configuration associated with ecological processes and allowed the identification of large-scale patterns in atmospheric and oceanic conditions as putative explanatory factors of long-term fluctuations in abundance of *M. mactroides*. This could set the basis for future research efforts in modeling the abundance and spatial distribution of shellfish, which should be taken into account by fisheries management schemes.

CONCLUSIONS

The best scenario for high abundance of *M. mactroides* is characterized by a cyclonic configuration of WSA in the SAO, with cold and salty waters and onshore WSA in the Uruguayan Atlantic coast (Figures 4 and 5). On the other hand, low abundance tends to occur during El Niño years, due to high SSTA and fresher waters along the coast resulting from increased rainfall in the RdlP basin that leads to a high runoff (Figures 3 and 6). These results suggest that the interannual fluctuations in *M. mactroides* abundance are not only locally but also remotely controlled by regional- and global-scale climate variability modes.

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LITERATURE CITED

Barreiro, M., 2010. Influence of ENSO and the South Atlantic Ocean on climate predictability over Southeastern South America. *Climate Dynamics*, 35(7–8), 1493–1508.

Barreiro, M.; Giannini, A.; Chang, P., and Saravanan, R., 2004. On the role of the South Atlantic atmospheric circulation in tropical Atlantic variability. *In:* Wang, C.; Xie, S.P., and Carton, J.A. (eds.), *Earth's Climate: The Ocean–Atmosphere Interaction*. Washington, D.C.: Wiley, pp. 143–156.

Bertrand, S.; Dewitte, B.; Tam, J.; Díaz, E., and Bertrand, A., 2008. Impacts of Kelvin wave forcing in the Peru Humboldt Current system: Scenarios of spatial reorganizations from physics to fishers. *Progress in Oceanography*, 79(2), 278–289.

Caddy, J.F., 2007. *Marine Habitat and Cover: Their Importance for Productive Coastal Fishery Resources*. Paris: UNESCO, Oceanographic Methodology Series, 249p.

Caddy, J.F. and Defeo, O., 2003. *Enhancing or Restoring the Productivity of Natural Populations of Shellfish and Other Marine Invertebrate Resources*. Rome: FAO Fisheries, *Technical Paper*, 448p.

Carton, J.A. and Giese, B.S., 2008. A reanalysis of ocean climate using Simple Ocean Data Assimilation (SODA). *Monthly Weather Review*, 136(8), 2999–3017.

Defeo, O., 1996. Recruitment variability in sandy beach macrofauna: Much to learn yet. *Revista Chilena de Historia Natural*, 69, 615–630.

Defeo, O., 2003. Marine invertebrate fisheries in sandy beaches: An overview. *Journal of Coastal Research*, 35(19), 56–65.

Defeo, O. and McLachlan, A., 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: A multi-scale analysis. *Marine Ecology Progress Series*, 295, 1–20.

Defeo, O.; Castrejón, M.; Ortega, L.; Kuhn, A.M.; Gutiérrez, N.L., and Castilla, J.C., 2013. Impacts of climate variability on Latin American small-scale fisheries. *Ecology and Society*, 18(4), 30.

Defeo, O.; Jaramillo, E., and Lyonnet, A., 1992. Community structure and intertidal zonation of the macroinfauna on the Atlantic coast of Uruguay. *Journal of Coastal Research*, 8(4), 830–839.

Fiori, S. and Defeo, O., 2006. Biogeographic patterns in life-history traits of the yellow clam, *Mesodesma mactroides*, in sandy beaches of South America. *Journal of Coastal Research,* 22(4), 872–880.

Gan, M.A. and Rao, V.B., 1991. Surface cyclogenesis over South America. *Monthly Weather Review*, 119(5), 1293–1302.

Gianelli, I.; Martínez, G., and Defeo, O., 2015. An ecosystem approach to small-scale co-managed fisheries: The yellow clam fishery in Uruguay. *Marine Policy*, 62, 196–202.

Huntley, J.W. and Scarpon D., 2015. Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: Implications for the stratigraphic paleobiology of biotic interactions. *Paleobiology*, 41, 134–143.

Lercari, D.; Bergamino, L., and Defeo, O., 2010. Trophic models in sandy beaches with contrasting morphodynamics: Comparing ecosystem structure and biomass flow. *Ecological Modelling,* 221, 2751–2759.

Lima, M.; Brazeiro, A., and Defeo, O., 2000. Population dynamics of the yellow clam *Mesodesma mactroides*: Recruitment variability, density-dependence and stochastic processes. *Marine Ecology Progress Series*, 207(9), 97–108.

Machado, I.; Barreiro, M., and Calliari, D., 2013. Variability of chlorophyll-a in the Southwestern Atlantic from satellite images: Seasonal cycle and ENSO influences. *Continental Shelf Research*, 53, 102–109.

Maunder, M.N.; Hinton, M.G.; Bigelow, K.A., and Langley, A.D., 2006. Developing indices of abundance using habitat data in a statistical framework. *Bulletin of Marine Science*, 79(3), 545–559.

McLachlan, A.; Dugan, J.E.; Defeo, O.; Ansell, A.D.; Hubbard, D.M.; Jaramillo, E., and Penchaszadeh, P., 1996. Beach clam fisheries. *Oceanography and Marine Biology: An Annual Review*, 34, 163–232.

Möller, O.O., Jr.; Piola, A.R.; Freitas, A.C., and Campos, E.J., 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. *Continental Shelf Research*, 28(13), 1607–1624.

Odebrecht, C.; Bergesch, M.; Rörig, L., and Abreu, P.C., 2010. Phytoplankton interannual variability at Cassino Beach, Southern Brazil (1992–2007), with emphasis on the surf zone diatom *Asterionellopsis glacialis*. *Estuaries and Coasts*, 33(2), 570–583.

Olson, D.B.; Podestá, G.P.; Evans, R.H., and Brown, O.B., 1988. Temporal variations in the separation of Brazil and Malvinas Currents. *Deep Sea Research Part A. Oceanographic Research Papers*, 35(12), 1971–1990.

Ortega, L. and Martínez, A., 2007. Multiannual and seasonal variability of water masses and fronts over the Uruguayan shelf. *Journal of Coastal Research*, 23(3), 618–629.

Ortega, L.; Castilla, J.C.; Espino, M.; Yamashiro, C., and Defeo, O., 2012. Effects of fishing, market price, and climate on two South American clam species. *Marine Ecology Progress Series*, 469, 71–85.

Ortega, L.; Celentano, E.; Delgado, E., and Defeo, O., 2016. Climate change influences on abundance, individual size and body abnormalities in a sandy beach clam. *Marine Ecology Progress Series*, 545, 203–213.

Ortega, L.; Celentano, E.; Finkl, C., and Defeo, O., 2013. Effects of climate variability on the morphodynamics of Uruguayan sandy beaches. *Journal of Coastal Research*, 29(4), 747–755.

Pacariz, S.; Westerberg, H., and Björk, G., 2014. Climate change and passive transport of European eel larvae. *Ecology of Freshwater Fish*, 23(1), 86–94.

Peterson, A.T.; Sorberon J.; Pearson R.G.; Anderson R.P.; Martinez-Meyer E.; Nakamura M., and Araujo, M.B., 2011. *Ecological Niches and Geographic Distributions*. Princeton, New Jersey: Princeton University Press, 316p.

Peterson, R.G. and Stramma, L., 1991. Upper-level circulation in the South Atlantic Ocean. *Progress in Oceanography*, 26(1), 1–73.

Piola, A.R.; Campos, E.J.D.; Möller, O.O., Jr.; Charo, M., and Martínez, C., 2000. The subtropical shelf front off eastern South America. *Journal of Geophysical Research*, 105, 6565–6578.

Reynolds, R.W.; Rayner, N.A.; Smith, T.M.; Stokes, D.C., and Wang, W., 2002. An improved *in situ* and satellite SST analysis for climate. *Journal of Climate*, 15(13), 1609–1625.

Sauco, S.; Gómez, J.; Barboza, F.R.; Lercari, D., and Defeo, O., 2013. Modified whole effluent toxicity test to assess and decouple wastewater effects from environmental gradients. *PloS ONE*, 8(6), e66285.

Storto, A.; Masina, S., and Navarra, A., 2016. Evaluation of the CMCC eddy-permitting global ocean physical reanalysis system (C-GLORS, 1982–2012) and its assimilation components. *Quarterly Journal of the Royal Meteorological Society,* 142(695), 738–758.

Strub, P.T.; James, C.; Combes, V.; Matano, R.P.; Piola, A.R.; Palma, E.D.; Saraceno, M.; Guerrero, R.; Fenco, H., and Ruiz-Etcheverry, L.A., 2015. Altimeter-derived seasonal circulation on the southwest Atlantic shelf: 27°–43°S. *Journal of Geophysical Research: Oceans*, 120(5), 3391–3418.

von Ihering H., 1907. *Les mollusques fossils du tertiare et du crétacé supérieur de l'Árgentine*. Buenos Aires: Anales del Museo de Buenos Aires, 611p.

Von Storch, H., and Zwiers, F.W., 2001. *Statistical Analysis in Climate Research*. Cambridge, U.K.: Cambridge University Press, 494p.