

Population structure, growth and production of the yellow clam *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) from a high-energy, temperate beach in northern Argentina

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Abstract The yellow clam *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) was once the most abundant intertidal species on the Atlantic coast of northern Argentina and an important commercial resource in South America. This study of a population inhabiting the intertidal zone of the sheltered-dissipative sandy beach Santa Teresita documents the species' population biology, including demographic structure, growth and production during December 2004 and December 2006, and adumbrates the critical state of *M. mactroides* at present. A total of 3,015 *M. mactroides* were collected and measured, whereas individuals were found with an anterior–posterior shell length between 2 and 64 mm. A von Bertalanffy growth function with an asymptotic length (L_{∞}) of 85 mm and a growth constant (K) of 0.47 year^{-1} was established from length–frequency distributions. The longevity of the species is estimated at approximately 6 years, and instantaneous mortality rate was about three times higher than

40 years ago. Besides, this study confirmed that the overall growth performance index (OGP) is habitat-specific and can be used to group *M. mactroides* and *M. donacium* from different areas into temperate and upwelling species. Furthermore, OGP is inversely correlated with the latitudinal distribution of *Mesodesma* populations. The intertidal biomass ranged between 0.06 and 0.07 g $AFDM \text{ m}^{-2} \text{ year}^{-1}$. Individual production was observed to be highest at 47 mm length ($0.35 \text{ g } AFDM \text{ m}^{-2} \text{ year}^{-1}$), and annual production ranged between 0.12 and 0.19 g $AFDM \text{ m}^{-2} \text{ year}^{-1}$, resulting in productivity values (P/B) between 1.84 and 2.93. The comparison of the results of the present study with those of growth studies conducted on *M. mactroides* 40 years ago revealed the following considerable differences in the population structure of *M. mactroides*, indicating the conservation status of this intertidal bivalve as endangered: (1) present growth rates are faster, but that the maximum length attained has decreased, (2) the numbers of individuals per square metre were many times higher in the past than in the present, (3) bivalves from the present work never reached the 'commercial size' of 60 mm and (4) 40 years ago, the population of *M. mactroides* was composed of up to three cohorts, whereas in this study, there was only one single cohort visible.

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Introduction

The world's open coastlines are dominated by almost 70% of sandy beaches (Bascom 1964; McLachlan and Brown 2006), at which 39% of the global human population are

living (within 100 km from the coast, CIESIN 2000). Exposed sandy beaches are one of the most dynamic environments, where sediment is being constantly moved by waves, winds and tides (McLachlan and Brown 2006). Previous investigations have demonstrated the influence of biological parameters (e.g. Defeo et al. 1992b; Defeo and de Alava 1995; Defeo 1996), as well as humans (e.g. Defeo 1998; Brazeiro and Defeo 1999), on the dynamics of populations and communities. However, physical parameters, mainly wave energy and particle size, are suggested as the main factors controlling the responses of the macrofaunal populations and communities (McLachlan et al. 1995, 1996). Rating systems for beach types (Short and Wright 1983) and beach exposure (McLachlan 1980) were used for a variety of previous studies investigating sandy beaches with contrasting morphodynamics (e.g. Souza and Gianuca 1995; Calliari et al. 1996; Gómez and Defeo 1999; Ricciardi and Bourget 1999; Jaramillo et al. 2000; Nel et al. 2001; Veloso and Cardoso 2001; de la Huz et al. 2002; Defeo and Martínez 2003; Laudien et al. 2003; Brazeiro 2005; Celentano and Defeo 2006; Delgado and Defeo 2007; Schlacher and Thompson 2008; Herrmann et al. 2009b). Due to the ability to absorb wave energy, the sandy beach ecosystem is one of the most debitable types of dynamic coastlines. The wave energy is used in driving surf-zone water movement, which transports sand offshore during storms and moves it back onshore during calms. Sandy beaches are greatly influenced by the transport of sand not only driven by waves but also by wind in the backshore and dunes. Most of the global sandy beaches are naturally backed by dunes (before the human influence, e.g. constructions in coastal dunes) and interact with them by supplying or receiving immense volumes of sand. Thus, sandy beaches are extremely dynamic environments where both mass of sand and water are always on the move (Komar 1998; Short 1999). Furthermore, the sandy beach ecosystem is characterized by sediment grains, which define the pore space between sediment particles. This so-called interstitial system is important as a habitat for organisms and for the filtration of seawater. The interstitial environment of sandy beaches is mainly controlled by the factors grain size, sorting, shape, packing, porosity, pore size and permeability (McLachlan and Turner 1994). The intertidal of sandy beaches is normally devoid of macroflora so that the microflora and detritus attain an important significance as a food resource for specimens living in this type of environment. The sandy beach flora is usually composed of benthic microalgae and surf-zone phytoplankton, both of which are regularly dominated by diatoms. Although surf clams are commonly the main primary consumers in soft bottom communities and can contribute up to 95% of the total biomass (McLachlan et al. 1981; Arntz and Fahrbach 1991; Ieno and Bastida 1998), sandy

beaches are inhabited by most phyla of invertebrates as interstitial forms or as members of the macrofauna, or both.

The yellow clam *Mesodesma mactroides*¹ Reeve,² 1854 (Bivalvia: Mesodesmatidae), also known as ‘almeja amarilla’ in Argentina and Uruguay, is a peculiar species (Parodiz 1942; Stuardo 1964). As one of the most common bivalves of South America (Defeo 1989), it inhabits intertidal Atlantic sandy beaches from tropical (23°S Ilha Grande, Rio de Janeiro State, Brazil) to temperate latitudes (40°S Isla del Jabalí, Province of Buenos Aires, Argentina) (Rios 1994; Fiori and Morsán 2004). Thus, its distributional range covers about 1,800 km South Brazilian sandy beaches, 22 km in Uruguay and 375 km in Argentina. A suspension-feeder, the yellow clam is the only *Mesodesma* species occurring throughout the Argentinean intertidal (Olivier et al. 1971). It cooccurs in the north of Argentina with the sympatric and numerically dominant surf clam *Donax hanleyanus* (Herrmann 2009). During the 1940s and 1950s, *M. mactroides* was an important economic resource in Argentina. A maximum exploitation of 1,079 tonnes was reached in 1953, but the fishery was closed in 1956 following a stock crash (Coscarón 1959) from which the population never recovered. Abundances were decimated further by subsequent mass mortality events in March 1993 due to a red tide incident (Odebrecht et al. 1995), in the 1990s due to an unknown cause (Fiori and Cazzaniga 1999) and most recently as a likely result of heavy metal pollution (Thompson and Sánchez de Bock 2007). Illegal extractions and the impact of tourism may also be contributing factors in the failure of the species to make a recovery (Bastida et al. 1991). Although there are a number of recent studies on populations of *M. mactroides* from Uruguay (e.g., Defeo 1989; Defeo et al. 1986, 1988b, 1991, 1992c; Brazeiro and Defeo 1999; Lima et al. 2000), the last Argentinean study is 40 years old (Olivier et al. 1971). The aim of this study is to estimate contemporary population parameters and production and to make comparisons with data from the historical study. Additionally, this study aims at examining the possible influence of physical and biological factors on the yellow clam growth and to compare observed population parameters with those of other members of the genus from elsewhere.

¹ *M. mactroides* reference specimens were deposited in the collections of the ‘Museum für Naturkunde der Humboldt-Universität zu Berlin’ and the ‘Museo Argentino de Ciencias Naturales—Bernardino Rivadavia’ under the reference numbers ZMB/Moll.104643 and MACN-In37513, respectively.

² In previous studies, Deshayes 1854 was cited spuriously as the author who first described *M. mactroides*. However, this description was not published by Deshayes but by his colleague Reeve; thus, the corresponding author of *M. mactroides* is Reeve 1854 (see Reeve 1854; Deshayes 1855).

Materials and methods

Study area

This study was carried out at the three south Atlantic beaches Santa Teresita (36°32'S, 56°41'W), Mar de las Pampas (37°19'S, 57°00'W) and Faro Querandí (37°29'S, 71 57°07'W) (Fig. 1), whereby we want to underline that *M. mactroides* was insignificantly abundant at the last two mentioned locations during the entire sampling period. Consequently, the population structure, growth and production of the intertidal yellow clam were studied during alternate spring tides only at Santa Teresita. According to McLachlan's (1980) rating scale for exposure and Short and Wright's (1983) classifications of beach types, Santa Teresita can be classified as sheltered and dissipative (for detailed physical parameters see: Herrmann 2009). This is an open ocean beach receiving continuous wave action and is subject to semidiurnal tides, with a maximum tide range of 1.6 m; spring tides average 1.7 m and mean neap tides 0.2 m. The sea surface temperature (SST) varies between 11°C in winter and 23°C in summer. The study site is composed of good–moderate fine sand, with a mean particle diameter of 2.26 phi (Herrmann 2009). The well-drained and oxygenated sandy beach of Santa Teresita is affected by a freshwater seepage and a southward current that brings water masses from the 290-km-long and up to

220-km-wide estuary of the Río de la Plata and is thus characterized by a mean salinity of 31.

Sampling and laboratory procedures

Quantitative sampling of *M. mactroides* was carried out at monthly intervals from December 2004 to December 2006, using a series of stations located at 4-m intervals along a transect running perpendicular to the shoreline from the spring tide high water mark to the spring tide low water mark. At each station, three replicate sand samples (40 × 40 cm) were excavated to 50 cm depth using a stirring corer and sieved individually on a 1-mm mesh. To obtain monthly length–frequency distributions, the maximum anterior–posterior shell length (*apSL*) of yellow clams retained on the mesh was measured to the nearest 0.1 mm using a digital vernier calliper (Mitutoyo, model 500-161U). For biomass analysis, monthly sub samples of 35 specimens were collected and stored in 70% ethanol. To estimate shell-free wet mass (*SFWM*), soft tissues were removed and weighed after blotting on filter paper in the laboratory. Samples were subsequently dried to constant mass at 70°C, weighed again to determine shell-free dry mass (*SFDM*) and ignited in a muffle furnace at 550°C for 5 h in order to estimate ash-free dry mass (*AFDM*).

Growth, growth performance, lifespan and mortality

A series of 25 length–frequency distributions provided the basic information for growth estimates. A von Bertalanffy growth function (*VBGF*) (von Bertalanffy 1938) was fitted to the data using the electronic length–frequency analysis 'ELEFAN I' routine of the FISAT II program package (Gayaniilo et al. 2005):

$$L_t = L_\infty \left[1 - e^{-K(t-t_0) + \left(\frac{KC}{2\pi}\right) \sin 2\pi(t-t_s) - \left(\frac{KC}{2\pi}\right) \sin 2\pi(t_0-t_s)} \right], \quad (1)$$

where L_t is the *apSL* (mm) at time t , L_∞ is the asymptotic maximum *apSL* (mm), K (year^{-1}) is the curvature parameter, C is a constant defining the degree of seasonal oscillation (ranging from 0 indicating continuous nonoscillating growth, to 1 when growth comes to a complete halt at the 'winter point' (*WP*)), t_0 is the theoretical age at zero length (year) and t_s is the initial point of oscillation in relation to $t = 0$ and the *WP*. The different subroutines of ELEFAN I (K -scanning) were used to identify the *VBGF* that best fitted the monthly size–frequency data, using the R_n value as a criterion of fit.

To measure growth performance, the growth index phi prime (ϕ') defined as:

$$\phi' = 2 \log_{10}(L_\infty) - \log_{10} K \quad (2)$$

was used. This criterion was chosen because the negative correlation between K and L_∞ invalidates comparisons



Fig. 1 Map of the three study sites at the Argentinean Atlantic coast: Santa Teresita (S), Mar de las Pampas (M) and Faro Querandí (F). Filled circle indicates the southernmost distribution of *M. mactroides* at Isla del Jabalí. Dotted areas indicate northern and southern sandy beaches of the Province of Buenos Aires where major *M. mactroides* populations existed in 1953–1956 (Coscarón 1959)

based on individual parameters (Pauly and Munro 1984). Finally, the overall growth performance index

$$OGP = \log\left(K[L_\infty]^3\right), \quad (3)$$

which represents growth rate at the point of inflexion of the size–growth curve (Pauly 1979), was calculated to compare growth of *M. mactroides* with other surf clam species.

The theoretical lifespan (t_{\max}) was estimated by an inverse of the von Bertalanffy growth equation, considering maximum shell length as 95% of the asymptotic length (Taylor 1958):

$$t_{\max} = \frac{[\ln L_{95\%} - \ln(L_\infty - L_{95\%})]}{K}, \quad (4)$$

where $L_{95\%}$ represents 95% of the maximum shell length recorded during field sampling.

Total mortality (Z) was calculated for 2005 and 2006 separately from length-converted catch curves (Pauly 1995) yielded by the ELEFAN II routine of the FISAT program (Gayaniilo et al. 2005). Z was estimated by:

$$\ln(N) = g - Z \cdot t, \quad (5)$$

where N is the number of individuals, g is the regression intercept, Z (year^{-1}) is the unbiased mortality estimate, and t is the estimated age (year) for each cohort (Pauly 1995).

Biomass and production

To compare biomass of *M. mactroides* with values for other species, all published values retrieved were converted to *AFDM* (according to Brey et al. 1988), whereby a conversion factor of 0.186 (*SFWM* to *AFDM* for ethanol [70%] preserved *M. mactroides*) was empirically determined. Parameters of the relationship between length and ash-free dry mass (*AFDM*) of *M. mactroides* were estimated by regression analysis

$$M = aL^b, \quad (6)$$

where M is the *AFDM* (g), L is the shell length of the size class (mm), and a and b are constants. *AFDM* was determined for 400 specimens of all size classes sampled between December 2004 and December 2006.

Total annual productivity was calculated for the *M. mactroides* belt at Santa Teresita (January–December 2005 and January–December 2006) using the mass-specific growth rate method (Crisp 1984; Brey 2001) from size–mass relationships, the size–frequency distribution obtained from all pooled samples and the *VBGF*:

$$P = \sum N_i M_i G_i (\text{g AFDM m}^{-2} \text{ year}^{-1}), \quad (7)$$

where N_i and M_i are the average abundance of animals (number m^{-2}) and mean individual *AFDM* in length class i , respectively, and G_i is the mass-specific growth rate:

$$G_i = bK \left[\left(\frac{L_\infty}{L_i} \right) - 1 \right] (\text{year}^{-1}), \quad (8)$$

where b is the exponent of the size–mass relation, K , L_∞ are *VBGF* parameters and L_i is the mean size in class i .

Mean annual biomass was estimated as

$$\bar{B} = \sum N_i M_i (\text{g AFDM m}^{-2}), \quad (9)$$

and annual P/\bar{B} ratios of the *M. mactroides* population were calculated from annual total production P and mean annual biomass \bar{B} .

Statistical analysis

Temporal differences of the population abundance and mean *OGP* were analysed statistically by one-way ANOVA using the software package SPSS version 17.0 (2008). Differences were considered significant at a level of $\alpha = 5\%$ (Zar 1999).

Results

No *M. mactroides* populations were discovered south of Santa Teresita during the sampling period. Only a few single individuals were recorded at Mar de las Pampas (August 2005: 31 ind. m^{-2}) and Faro Querandí (August 2005: 19 ind. m^{-2} ; March, April and October 2005: 6 ind. m^{-2} and February 2006: 6 ind. m^{-2}) meaning that population parameters and production could not be estimated for these two last mentioned areas.

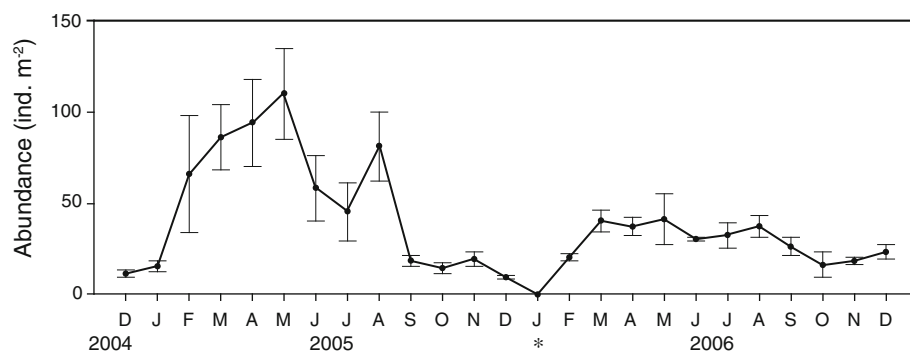
Population structure

Greatest abundance was recorded in May 2005, with 110 ± 25 ind. m^{-2} (mean \pm SE) and absolute abundance peaked at 543 ind. m^{-2} (size class 2–4 mm) in April 2005 (Fig. 2). Distinct cohorts were apparent in the length–frequency distributions obtained (Fig. 3). In both years, a single new cohort was observed during February. New cohorts were tracked for up to 11 months in which they reached *apSLs* of 27 mm in 2005 and approximately 35 mm in 2006 before disappearing, after which new recruits appeared.

Growth, longevity and mortality

During the 25-month study period 3,015 *M. mactroides* were collected and measured at Santa Teresita: 2,142 ind. in the first year and 873 ind. in the second year. The smallest recorded individual (*apSL* 2 mm) was found in winter (September 2005), and the largest specimen (*apSL* 64 mm) was found in summer (February 2005). The

Fig. 2 Population abundance of *M. mactroides* from December 2004 to December 2006 at Santa Teresita. * *M. mactroides* was not abundant during sampling in January 2006. Error bars: standard error (SE)



estimated VBGF of the *M. mactroides* population at Santa Teresita with the growth parameter $K = 0.47$ (year⁻¹) and $L_{\infty} = 85$ mm (*apSL*) are shown in Fig. 4. The corresponding ϕ' index (3.53) and *OGP* (5.46) are compared with those of *Mesodesma* growth parameters, calculated from different areas. Parameter $C = 0.10$ indicated weak seasonal variation in growth, with lowest growth rates occurring in winter ($WP = 0.7 \sim$ mid-August). The calculated lifespan (t_{max}) of *M. mactroides* was 6.19 years, and the instantaneous mortality rate (Z) was 3.01 year⁻¹ in 2005 and 2.57 year⁻¹ in 2006.

Biomass and production

The observed relationship between length and calculated *AFDM* of *M. mactroides* $M_{(AFDM)} = (9.44 \times 10^{-6}) \times L_{(mm)}^{2.83}$ ($N = 606$, $r^2 = 0.98$) was used for production estimates.

Annual abundance of *M. mactroides* (mean \pm SE) was 48 ± 13 ind. m⁻² in 2005 and 29 ± 3 ind. m⁻² in 2006. Within the *Mesodesma* belt, these abundance values represent an average annual biomass \bar{B} of 0.07 g *AFDM* m⁻² year⁻¹ (2005) and 0.06 g *AFDM* m⁻² year⁻¹ (2006) (Fig. 5b–c). Individual production increased to its highest value at 47 mm length (0.35 g *AFDM* m⁻² year⁻¹) and decreased thereafter (Fig. 5a). The distribution of total annual production P and abundance among the size classes are illustrated in Fig. 5b–c. Annual production ranged between 0.12 and 0.19 g *AFDM* m⁻² year⁻¹, and P/\bar{B} ratios were between 1.84 and 2.93.

Discussion and conclusion

Population structure

Comparison of historical data (Olivier et al. 1971) with present situation, both diagrammed in Fig. 3, showed considerable differences in the population structure of *M. mactroides*. The number of individuals was many times higher in

1968 compared to 2005 (up to 53 times higher in December), suggesting a much smaller reproduction success nowadays during spring time, which represents one of the two spawning seasons per year (Herrmann et al. 2009a). Not merely the number of individuals can be registered as a great difference between the historical population and the recent one, but rather the bivalves in 1968 reached a much higher *apSL*. Studied individuals from the present work never reached the 'commercial size' of 60 mm (Coscarón 1959); indeed, only three individuals with *apSL* of >60 mm were recorded in the entirety of the study period. Furthermore, the analysis of Fig. 3 showed up to three cohorts in the past population structure, whereas in the current study it was found only one single cohort of *M. mactroides*. However, since Herrmann et al. (2009b) reported variations in the reproductive biology of the wedge clam *D. hanleyanus*, depending on different beach morphodynamics, it cannot be excluded that also the population structure of *M. mactroides* can be diversified between beaches with contrasting morphodynamics, for which the comparison between populations of *M. mactroides* from Mar Azul (historically) and Santa Teresita (presently) only can point out a tendency.

Growth and growth performance

The data presented here confirm that *M. mactroides* is a fast-growing species ($K = 0.47$; $\phi' = 3.4$) and fall in line with estimates from previous studies of Argentinean and Uruguayan populations ($K = 0.3$ – 0.9 ; $\phi' = 3.3$ – 3.8 ; Table 1). However, changes in growth parameters are evident when the recent values (Table 1, no. 1) are compared with those of Olivier et al. (1971) (Table 1, no. 9). In 1968–1970, *M. mactroides* showed a lower growth constant ($K = 0.28$ vs. 0.47), indicating that yellow clam growth was slower four decades ago, but that eventual maximum length was almost even compared to the present ($L_{t(1968-1970)} = 84$ mm; $L_{t(2005-2006)} = 85$ mm). Our values are in conformity with estimated maximum shell length of *M. mactroides* from previous studies in Argentina (Olivier et al. 1971: 84 mm) and Uruguay (Defeo et al. 1992a: 100 mm).

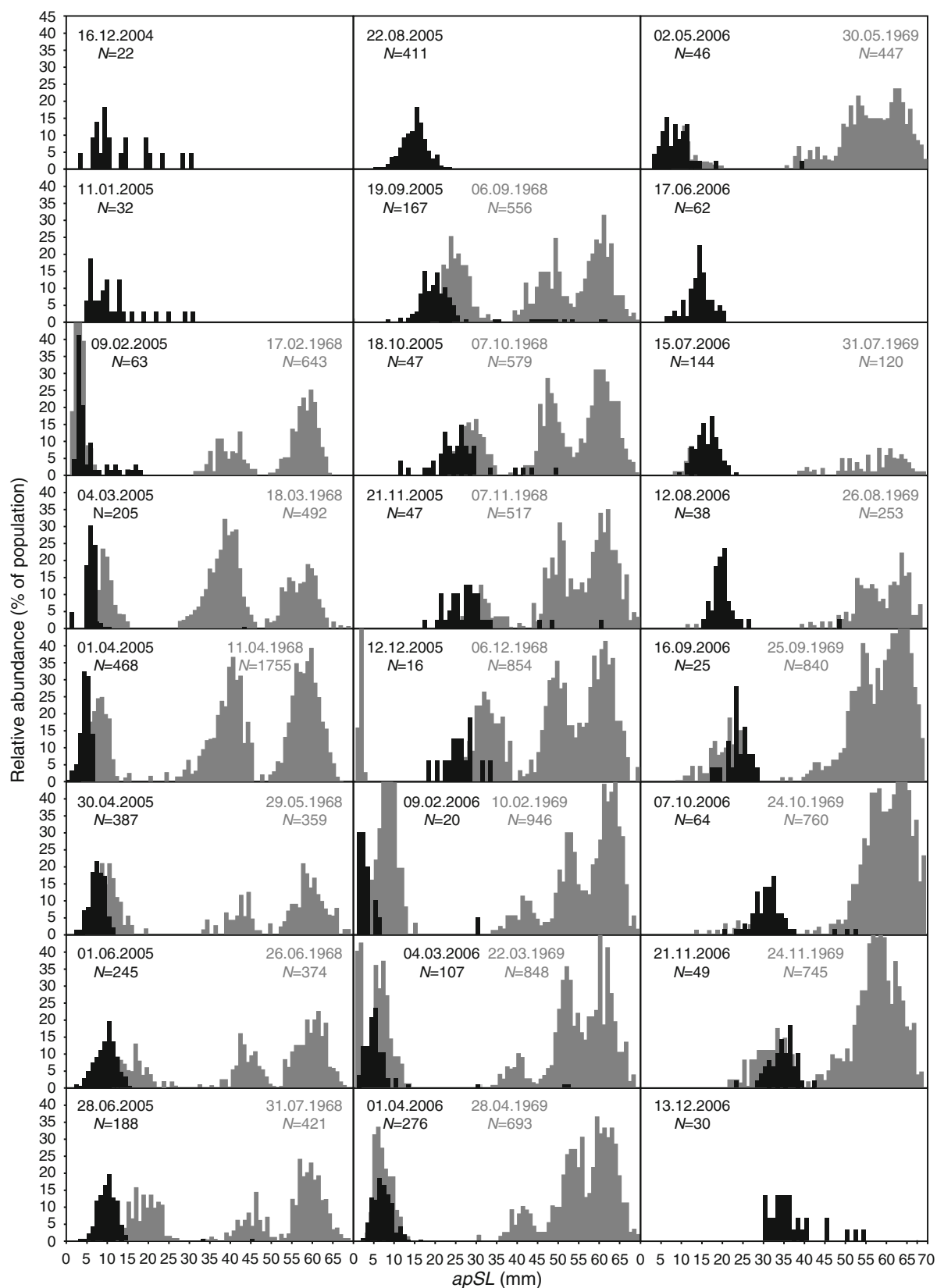


Fig. 3 Monthly length–frequency distribution of *M. mactroides* collected between December 2004 and December 2006 at Santa Teresita (black histograms) compared with historical data from Olivier et al. (1971) sampled between 1968 and 1969 at Mar Azul (grey histograms)

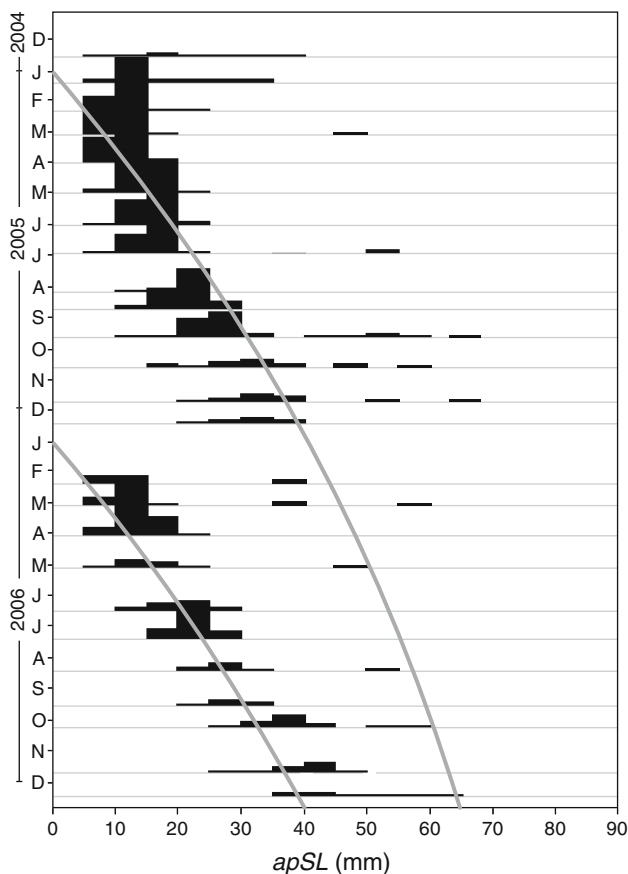


Fig. 4 The VBGF (grey lines) of *M. mactroides* was estimated with the FISAT program from monthly length–frequency data (black histograms) for the period December 2004 to December 2006

While Defeo et al. (1992c) observed strong seasonal variation ($C = 1.0$) in growth rates for a *M. mactroides* population in Uruguay, the variation documented by Fiori and Morsán (2004) was low ($C = 0.45$), and Olivier et al. (1971) recorded no seasonal variations for this species from the Argentinean coast. In support of these latter findings, the present study estimated $C = 0.1$.

Nonlinear growth functions such as the VBGF are difficult to compare, and several authors (e.g., Pauly 1979; Munro and Pauly 1983; Moreau et al. 1986; Laudien et al. 2003; Herrmann 2009) have demonstrated the suitability of composite indices of overall growth performance (OGP) for inter- and intraspecific comparisons for various clam species. OGP is proportional to the maximum rate of body mass increase during a lifetime, i.e. mass increase at the inflexion point of the VBGF. Few values of maximum body mass can be found in the literature and maximal mass is proportional to L_{∞} . The OGP value of 5.46 (Table 1, no. 1) obtained for *M. mactroides* in this study conforms with the values of 5.22 (Olivier et al. 1971) and 5.30 (Fiori and Morsán 2004) calculated from data sets of previous studies on Argentinean populations of the same species and also

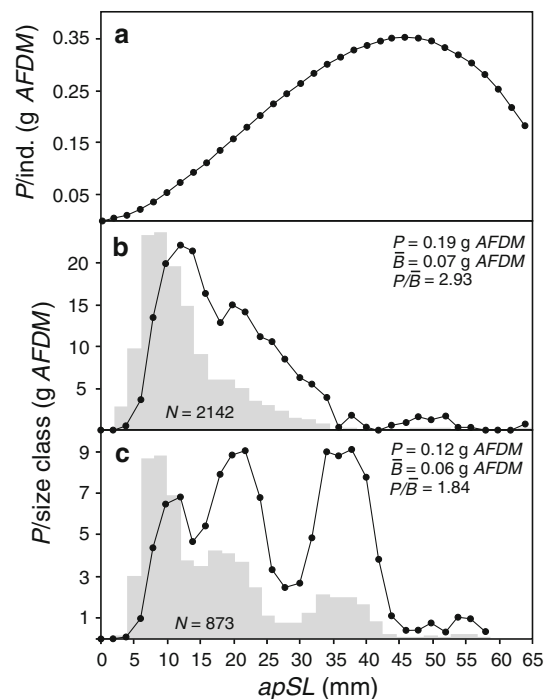


Fig. 5 Distribution of annual somatic individual (a) and population production at Santa Teresita for 2005 (b) and 2006 (c). Mean abundance (grey areas = 100%) for the different length classes of *M. mactroides* is also given

with the value of 5.28 for a population of *M. donacium* from the Peruvian sampled after an El Niño (EN) event (Arntz et al. 1987). It can be assumed that SST and food availability are key factors affecting growth and aspects of population dynamics such as production, reproduction, recruitment and mortality. The relatively high values of OGP from Uruguay (Fig. 6, no. 10–13) and Peru (before and during an EN event, Fig. 6, no. 14–15), suggest a negative correlation with latitude (Fig. 7: $y = 6.77 - 0.04x$, $r = 0.94$, $P < 0.05$, $N = 12$). This trend provides support to the latitudinal gradient hypothesis of marine invertebrates (Defeo and Cardoso 2002), which predicts a positive correlation between body size and latitude: populations from subtropical beaches exhibited higher growth and mortality rates and shorter lifespans than those of temperate beaches. However, this observation would be better understood if growth studies on several populations could be linked to quantitative and qualitative data regarding phytoplankton. Results compiled from several studies of two different *Mesodesma* species confirmed the hypothesis of Laudien et al. (2003) that OGP is habitat-specific (Fig. 6). OGP is lowest (5.22–5.81, group A) for *M. mactroides*-populating temperate regions and highest (6.33, group B) for *M. donacium* of an upwelling area. Mean OGPs of the two groups were significantly different (ANOVA, $F_{1,14} = 21.716$, $P < 0.05$). Climate anomalies

Table 1 *M. mactroides* from the present study (1) in comparison with studies on two South American mesodesmatids and their variation in growth performance with the von Bertalanffy growth parameter K (year^{-1}) and L_{∞} (mm) as well as the standard growth index ϕ' and the *OGP*

No.	Species	Country	Area	Lat.	Long.	Ca	K	L_{∞}	ϕ'	<i>OGP</i>	Source
1	<i>M. mactroides</i> ^{a,d}	Argentina	Santa Teresita	36°32'S	56°41'W	A	0.47	85.00	3.53	5.46	Present study
2	<i>M. mactroides</i> ^{a,d}	Argentina	Costa Chica	36°31'S	56°41'W	A	0.43	84.00	3.48	5.41	Luzzatto (2007)
3	<i>M. mactroides</i> ^{b,d}	Argentina	Monte Hermoso	38°59'S	61°15'W	A	0.48	74.66	3.43	5.30	Fiori and Morsán (2004)
4	<i>M. mactroides</i> ^{c,d}	Argentina	Monte Hermoso	38°59'S	61°15'W	A	0.54	70.42	3.43	5.28	Fiori and Morsán (2004)
5	<i>M. mactroides</i> ^{a,d}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.49	78.42	3.48	5.37	Fiori and Morsán (2004)
6	<i>M. mactroides</i> ^{a,d}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.47	79.13	3.47	5.37	Fiori and Morsán (2004)
7	<i>M. mactroides</i> ^{b,d}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.59	72.77	3.49	5.36	Fiori and Morsán (2004)
8	<i>M. mactroides</i> ^{c,d}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.42	77.73	3.40	5.30	Fiori and Morsán (2004)
9	<i>M. mactroides</i> ^c	Argentina	Faro Querandí	37°29'S	57°07'W	A	0.28	83.76	3.29	5.22	Olivier et al. (1971)
10	<i>M. mactroides</i> ^{c,f}	Uruguay	La Coronilla–Barra del Chuy	33°39'S	53°28'W	A	0.90	75.47	3.71	5.59	Defeo et al. (1992b)
11	<i>M. mactroides</i> ^{a,d}	Uruguay	La Coronilla–Barra del Chuy	33°39'S	53°28'W	A	0.84	75.00	3.67	5.55	Defeo et al. (1992b)
12	<i>M. mactroides</i> ^{a,d}	Uruguay	La Coronilla–Barra del Chuy	33°39'S	53°28'W	A	0.82	83.00	3.75	5.67	Defeo et al. (1992a)
13	<i>M. mactroides</i> ^{a,e}	Uruguay	La Coronilla–Barra del Chuy	33°39'S	53°28'W	A	0.64	100.00	3.81	5.81	Defeo et al. (1992a)
14	<i>M. donacium</i> ^{a,d}	Peru	Santa Mariadel Mar	12°20'S	76°50'W	B	1.13	124.00	4.24	6.33	Amtz et al. (1987) → before EN
15	<i>M. donacium</i> ^{a,d}	Peru	Santa Mariadel Mar	12°20'S	76°50'W	B	0.38	110.00	3.66	5.70	Amtz et al. (1987) → during EN
16	<i>M. donacium</i> ^{a,d}	Peru	Santa Mariadel Mar	12°20'S	76°50'W	B	0.32	84.00	3.35	5.28	Amtz et al. (1987) → after EN

Climate areas (Ca): temperate (A) and upwelling (B) species. Code numbers (No.) are equivalent to Fig. 7

^a Age estimated from length–frequency distributions

^b Age estimated from external growth rings

^c Age estimated from size at age data

^d Values obtained by the application of ELEFAN

^e Values obtained by the application of SLCA

^f Values obtained by the application of CAST

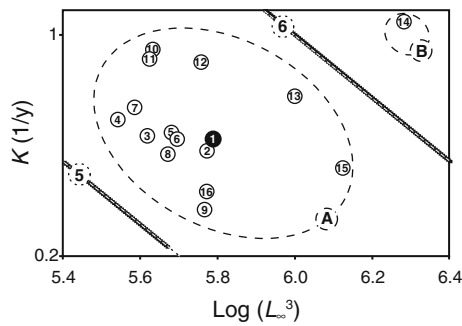


Fig. 6 Auximetric grid comparing the *OGP* of the Argentinean *M. mactroides* from the present study (●) with several *Mesodesma* populations from different areas (white circles). Plot indicates two groups: temperate (A) and upwelling species (B), indicated by dashed contours. Dotted diagonal lines show equal values of *OGP* (numbers in dotted circles). For keys and data sources, see Table 1

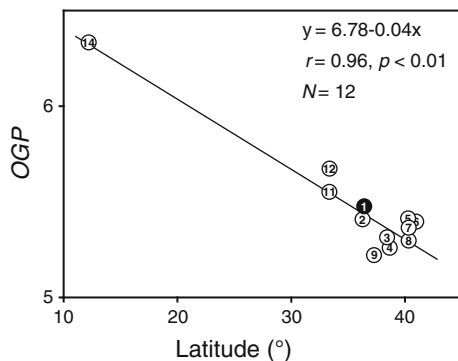


Fig. 7 *OGP* of *M. mactroides* from the present study (●) estimated from length–frequency data and obtained from ELEFAN, compared with several *Mesodesma* populations from different latitudes. For comparing values, see Table 1

may be detected with the help of the auximetric grid, as indicated by the lower *OGP* for the upwelling surf clam *M. donacium* sampled in Peru during and shortly after EN (1982/1983, Fig. 6, no. 15–16) compared to data from normal upwelling years (Fig. 6, no. 14) (Arntz et al. 1987).

Biomass and production

Annual intertidal biomass of the *M. mactroides* population at Santa Teresita ranged between 0.06 and 0.07 g *AFDM* m⁻² year⁻¹ and production varied between 0.12 and 0.19 g *AFDM* m⁻² year⁻¹. Unfortunately, comparable information on the species from elsewhere is very scarce. To the best of our knowledge, no study of this kind has been carried out in Brazil. Defeo (1985) estimated a biomass of 133 g *AFDM* m⁻² (converted from *SFWM* values published) for the Uruguayan *M. mactroides* population, while four decades ago the biomass of Argentinean *M. mactroides* was estimated at 323 g *AFDM* m⁻² (Olivier et al. 1971, calculated

from published *SFWM* data). Thus, the once-prominent role of this primary consumer in the ecosystem appears to be reduced. The individuals observed during the present study were small compared to the records of Olivier et al. (1971), in which individuals of commercial size (>60 mm) were found throughout the year. The reason may be a change in environmental conditions, which has impacted directly on food supply. Biomass data ranging from 141 to 546 g *AFDM* m⁻² year⁻¹ for the similar-sized surf clam *D. serra*, which occupies a similar ecological position in the Benguela-upwelling system (Laudien et al. 2003) lead us to hypothesize that environmental conditions off Argentina may have been more favourable with regard to major primary production four decades ago. Indeed, changes in the environmental conditions of the Argentinean coast are implicated in a study of historical SSTs (Bava et al. 1999). The authors reported that EN 1992 evoked negative SST anomalies throughout the south western Atlantic. However, a detailed understanding of the collapse of the Argentinean *M. mactroides* population would require analysis of further historical climate and phytoplankton data.

Lifespan and mortality

There is some controversy concerning longevity estimates for *M. mactroides*. Olivier et al. (1971) estimated a maximum age of ~8 years for the Argentinean yellow clam population, using length–frequency analysis. In contrast, Defeo et al. (1988a) suggested a lifespan of ~3.5 years for Uruguayan *Mesodesma* populations, derived by the interpretation of shell growth rings. Length–frequency analysis of the current data set yields a lifespan of ~6 years, an intermediate estimate within the range of the aforementioned extremes.

The instantaneous mortality rate (*Z*) for the Argentinean *M. mactroides* was higher in the present study (2.57–3.01 year⁻¹) compared to calculations (0.85 year⁻¹) from Olivier et al. (1971), but fits well with mortality rates for the same species from Uruguayan beaches (Defeo et al. 1992c: 2.26–2.91 year⁻¹). Arntz et al. (1987) also found similar mortality rates (*Z* = 2.5 year⁻¹) for the closely related *M. donacium* inhabiting Peruvian sandy beaches. Found differences in mortality rates indicate that the Argentinean *M. mactroides* population this day is much more stressed than 40 years ago. Factors inducing this stress are possibly engendered by ecological (e.g. mass mortality events) and environmental aspects (e.g. changing beach morphodynamics by human impacts).

Ecological aspects

The carnivorous gastropod *Olivancillaria vesica auricularia*, a known predator of surf clams in Brazilian sandy

beaches (Marcus and Marcus 1959; Gianuca 1985; Rocha-Barreira de Almeida 2002), also attacks *M. mactroides* and *D. hanleyanus* at Santa Teresita (V. S. Teso, pers. communication). Predator-prey relationship tests revealed escape behaviour in both clams, when approached by the snail. Surf clams sought refuge even without direct contact, excavating themselves within 10 s in order to escape with the next wave (M. Herrmann, unpublished data).

From previous investigations (e.g., Olivier et al. 1971; Penchaszadeh and Olivier 1975; Bastida et al. 1991), it is well-known that intertidal sandy beach communities of northern Argentina were inhabited by large co-existing populations of the surf clams *M. mactroides* and *D. hanleyanus*. However, the significant negative correlation between the abundances of *D. hanleyanus* (data taken from Herrmann 2009) and *M. mactroides* (Fig. 8) at Santa Teresita in 2005 suggests that the timing of abundance peaks of *D. hanleyanus* may be related to periods of low *M. mactroides* abundance. Penchaszadeh and Olivier (1975), Dadon (2005) and Defeo and de Alava (1995) observed similar inverse correlations between *D. hanleyanus* and *M. mactroides* abundance on Argentinean and Uruguayan beaches. Furthermore, surf clam populations from the Peruvian Pacific coast also showed the same relationship, and abundances of *Emerita analoga* and *D. marincovich* (formerly *D. peruvianus*) increased coincidentally with the collapse of *M. donacium* populations (Penchaszadeh 1971; Tarazona et al. 1985; Arntz et al. 1987). Defeo and de Alava (1995) hypothesized that interspecific competition for space and food might explain the relationship between *D. hanleyanus* and *M. mactroides*. Olivier et al. (1971) supported this by describing overlapping trophic niches of the two species and predicted that limited food availability might soon impact on *M. mactroides*. However, results in the present study suggest that the two surf clam species do not compete for resources at Santa Teresita. The fact that abundances of *D. hanleyanus* and *M. mactroides* populations were previously much higher than at present (Olivier et al. 1971; Penchaszadeh

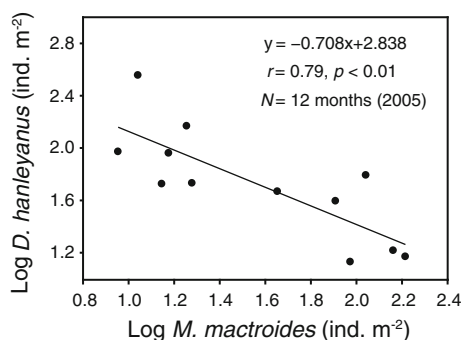


Fig. 8 *M. mactroides*–*D. hanleyanus* linear correlation of abundances (Log ind. m⁻²) from 2005 at Santa Teresita

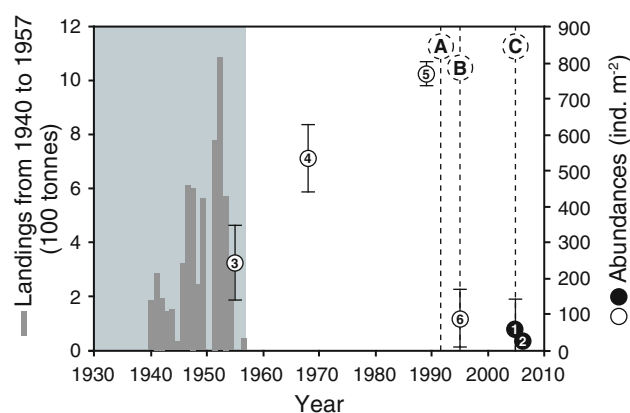


Fig. 9 Population trends in the Argentinean surf clam *M. mactroides*: mean abundances from the present study (1: 2005; 2: 2006) compared with historical records (3: Coscarón 1959; 4: Olivier et al. 1971; 5: Bastida et al. 1991; 6: Mabrugaña 1997) and landing data (histogram: Coscarón 1959). (A) indicates mass mortality of *M. mactroides* in South America (in March 1993: Odebrecht et al. 1995), (B) and (C) unexplained mass mortality events in Argentina (in November 1995: Fiori and Cazzaniga 1999; in September 2004: Thompson and Sánchez de Bock 2007, respectively). Grey area shows the period when *M. mactroides* was commercially fished, the white area is the period when the clam fishery was closed

and Olivier 1975) makes food availability an even less likely limiting factor in the current scenario.

This said, the balance between these two species appears to have been disturbed following mass mortality events affecting *M. mactroides* in March 1993 (Odebrecht et al. 1995), November 1995 (Fiori and Cazzaniga 1999) and September 2004 (Thompson and Sánchez de Bock 2007) (Fig. 9). *D. hanleyanus*, which was not affected by the mass mortality events, took over immediately as the dominant species, but failed to reach the former abundance of *M. mactroides*. Similar changes in the structure of Peruvian shallow sandy beach communities have been ascribed to EN. Arntz et al. (1987) observed that *D. marincovich* (formerly *D. peruvianus*) prevailed over *M. donacium* immediately after EN but, like Argentinean *D. hanleyanus*, never matched the abundance of the previously dominant *M. donacium*.

Environmental aspects

Another hypothesis explaining the recent dominance of *D. hanleyanus* over *M. mactroides* is a change in granulometry. Penchaszadeh and Olivier (1975) reported that sediment characteristics are principle factors in the distribution of surf clams. Olivier et al. (1971) also described substratum sensitivity in *M. mactroides*, although the clams are able to penetrate into sediments with a wide spectrum of grain sizes. The present study found *M. mactroides* almost exclusively at the fine sand locality Santa Teresita

where mean grain size was 0.21 mm (results from granulometric analysis are given in Herrmann 2009).

The present study found no evidence for along-shore migration in *M. mactroides*, although abundances are seen to vary considerably a given location. Additional random sampling south and east of the transect did not reveal greater abundances than those recorded at the monthly stations. Further random sampling with a dive corer (Rumohr and Arntz 1982) in the highly dynamic wave-breaking zone confirmed that unlike Peruvian *Donax* populations *D. hanleyanus* did not extend into the surf zone.

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