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Biogeographic Patterns in Life-History Traits of the Yellow Clam, *Mesodesma mactroides*, in Sandy Beaches of South America

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ABSTRACT

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Demographic and life-history attributes of the yellow clam, *Mesodesma mactroides,* were analyzed along exposed sandy beaches of the Atlantic coast of South America, from Brazil (32°S) to Argentina (41°S), covering most of its geographical range (24–41°S). Population features varied markedly within this range and exhibited systematic geographical patterns of variation. Abundance and growth/mortality rates significantly decreased from northern (Brazil and Uruguay) to southern (Argentina) populations. Snapshot information at the edge of its northern geographical range suggests a large-scale unimodal distribution pattern. Northern populations also had an extended or quasi-continuous recruitment season, whereas Argentinean populations had seasonal recruitment that became negligible at the southernmost edge of the range (41°S). Maximum individual sizes increased nonlinearly with latitude. This result, when considered together with density patterns, provided the second large-scale evidence of scaling of population density to body size in a sandy-beach population. Lifespan increased with latitude, ranging between 3 and >7 years. Length frequency-distribution analysis revealed marked intra-annual growth patterns for two populations located 7° latitude apart. Variations in water temperature explained large-scale differences in the demography and population dynamics of the yellow clam, and the high plasticity over latitudinal gradients leads to an adjustment of the phenotype–environment relationship. Long-term studies in Uruguayan beaches suggest that wide population fluctuations are the result of intertwined forces of environmental, density-dependent, and human-induced factors operating together at different spatiotemporal scales. As this species with planktonic larvae is structured as a metapopulation, future studies should incorporate a number of hierarchical scales to better understand macroscale variations in demographic patterns and life-history traits.

ADDITIONAL INDEX WORDS: *Macroecology, bivalves, yellow clam, sandy beaches.*

INTRODUCTION

Exposed sandy beaches dominate the ice-free shores of all continents and provide important recreational and commercial resources in many areas. Moreover, many beaches, notably those of the dissipative type (*sensu* SHORT, 1996), support rich biotas, of which clams often play a key ecological role, especially in terms of biomass (MCLACHLAN *et al.,* 1996).

Surprisingly, few studies have sought to document life-history variations exhibited by beach clam species across a geographical range, as well as potential explanations of the underlying mechanisms. In particular, there are few studies that investigate whether life-history characteristics undergo latitudinal changes (MCLACHLAN *et al.,* 1996). Because of the scale dependence, recent studies in sandy-beach macrofauna have been designed to incorporate a number of hierarchical scales to better understand macroscale variations in demographic patterns and life-history traits. This approach was useful to explain fluctuations in abundance at large spatial scales and to disentangle the relative importance of density-dependent and density-independent factors (CARDOSO and VELOSO, 2003; DEFEO *et al.,* 1997; LIMA *et al.,* 2000; SCHOEMAN and RICHARDSON, 2002). Such information also yields insights into the factors that determine the internal abundance structure of the geographic ranges of a species (BREWER and GASTON, 2003; CARDOSO and DEFEO, 2003).

The yellow clam, *Mesodesma mactroides* (Deshayes 1854), is an intertidal sandy-beach bivalve distributed along the warm–temperate southwestern Atlantic province of South America, from Santos Bay, Brazil (24° S), to Negro river, Argentina (41° S) (DEFEO *et al.,* 1993: Figure 1). This large species (up to 80 mm length) dominates, in terms of biomass, the macrofauna community on microtidal dissipative beaches all along this coastline (DEFEO *et al.,* 1992a). *Mesodesma mactroides* has been exploited in sandy beaches of Brazil, Uruguay, and Argentina by commercial and recreational harvesters since the 1940s, coinciding with the development of the canned industry (reviewed in DEFEO, 2003). Since the

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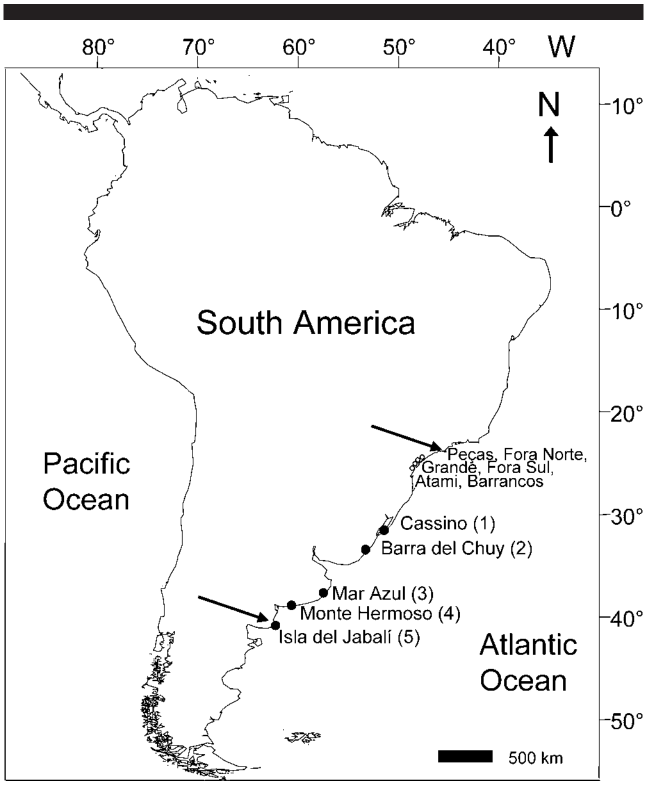

Figure 1. Geographic range of the yellow clam, *M. mactroides,* along sandy beaches of South America (indicated by arrows), highlighting the five sites fully analyzed in this study (●) and the six Brazilian ones only used to elucidate the shape of the distribution (○). The fully studied beaches are sequentially numbered in the north–south direction from 1 to 5.

mid-90s, the species has experienced mass mortalities throughout its biogeographic range (24–41° S) and it is presently at risk, probably with a critically endangered status (FIORI and CAZZANIGA, 1999). Thus, the challenge to conservation of the species is to segregate degrading anthropogenic events from natural processes. In this setting, it is critical to (1) address geographical trends in population dynamics and demography and (2) identify potential causes and mechanisms of change in life-history traits at geographic and local spatial scales. In this article, we assess latitudinal patterns in abundance, population structure, dynamics, and life-history traits of yellow clam, *M. mactroides,* populations in sandy beaches of South America.

MATERIALS AND METHODS

We collated information coming from five sandy beaches along the Atlantic coast of South America, between Brazil (Cassino: 32° S) and Argentina (Isla del Jabalí: 41° S). All analyzed beaches are microtidal, exposed to wave action and dissipative, with fine- to medium-grain sand and gentle beach-face slope (Table 1). A full characterization of physical properties of these beaches are described by GIANUCA (1983, 1985) for Brazil, DEFEO *et al.* (1992a, 1997) for Uruguay, and FIORI (2002) and OLIVIER *et al.* (1971) for Argentina. The lack of information for 24–32° S in Brazilian coasts precluded the integration of the full geographical distribution range of the species. However, information on yellow clam density coming from snapshots, provided by SOARES (2003, personal communication) for the northernmost edge of the range (*c*a. 25° S), was used to elucidate the distribution shape.

We only included information coming from studies with monthly samples taken at least for 1 year, with the exception of only one locality, Monte Hermoso (Argentina), which was sampled twice (Table 1). The sampling design was systematic, with transects set up perpendicular to the shoreline covering the whole across-shore yellow clam distribution. The yellow clams retained after sieving through 0.5-mm or 1-mm mesh were measured to the nearest 1-mm length. Large-scale variations in abundance were assessed in terms of density (ind/m^2) because most data extracted from the literature was expressed in this unit. When abundance was available as numbers per linear meter of beach or strip transect (IST, ind/m: DEFEO, 1998), conversion to density estimates was obtained by dividing IST values by the corresponding yellow clam distribution width in each beach. The species has been affected by several sources of impact that decimated its populations throughout the geographic range (DEFEO, 1996a; FIORI and CAZZANIGA, 1999; FIORI *et al.,* 2004b). Thus, large-scale patterns in abundance were depicted by selecting those years when the species was not affected by high harvesting

Table 1. *Sources of data and attributes of the exposed dissipative sandy beaches used for assessing macroscale patterns in life-history traits of the yellow clam,* M. mactroides. *Asterisks (*) denote data only included to infer the shape of the distribution range in Figure 4. Beaches from Brazil and Uruguay were categorized as mid temperate, whereas Argentinean beaches were defined as high-temperate. (a): Soares (2003, personal communication); (b) Borzone* et al. *(1996); (c) Souza and Gianuca (1995); (d) Gianuca (1983, 1985); (e) Defeo* et al. *(1992a, b); (f) Olivier* et al. *(1971); (g) Fiori (2002) and Fiori* et al. *(2004a).*

Beach Features	Peças*	Fora Norte*	Grande da Ilha do Mel*	Fora Sur*	Atami*	Barrancos*	Cassino	Barra del Chuy	Mar Azul	Monte Hermoso	Isla del Jabalí
Country†	Br	Br	Br	Br	Br	Br	Br	Uy	Arg	Arg	Arg
Latitude south	25°28′	25°31′	25°32′	25°34′	25°36′	25°37′	32°14′	33°45′	37°19′	38°59′	40°33′
Sampling duration (mo)	1	1	1	1	1	13	18	24	24	2	15
Beach width (m)	70	90	84–116	105	105	65–110	60	68	26	100	108
Sand size (mm)	0.15	0.14	0.14	0.15	0.14	0.12–0.20	0.18	0.15–0.22	0.20–0.35	0.21–0.32	0.20
Slope (%)	2.86	2.01	2.27	2.44	2.02	1.25–2.00	3.00	3.53	2.00–3.00	1.00–3.00	1.82
Data source	a	b	a, b	b	a, b	c	d	e	f	g	g

† Br = Brazil, Uy = Uruguay, Arg = Argentina.

rates or massive mortalities. Recruitment patterns were inferred from the frequency of occurrence of recruits (organisms less than 5 mm length) throughout a year. Longevity was approximated from the maximum observed age documented in the corresponding age–length key for each beach, whereas the maximum observed length was directly extracted from bibliographic sources. In this case, we based our analysis in the sampling periods detailed in Table 1 and, thus, we did not consider sporadic or eventual records documenting unusually large sizes (*e.g.,* GIANUCA, 1975).

Information on growth parameters of *M. mactroides* came from published sources (GIANUCA, 1985; OLIVIER *et al.,* 1971) and our own results (DEFEO *et al.,* 1992b; FIORI and MORSÁN, 2004). The length–age keys for all populations were used to recalculate growth parameters of the von Bertalanffy growth function (VBGF) using nonlinear fitting through the quasi-Newton method:

$$Lt = L_\infty[1 - e^{-K(t-t_0)}], \quad (1)$$

where L_∞ is the asymptotic length, K is the curvature parameter, and t_0 is the computed age at length zero. In the case age–length key for yellow clam at Cassino (Brazil), a biannual periodicity of growth formation was assumed following DEFEO *et al.* (1992b). The lack of raw data precluded the statistical comparison of growth curves through likelihood ratio tests. Thus, the growth index phi prime, $\phi' = 2 \log_{10}(L_\infty) + \log_{10}(K)$ was used to assess growth performance (PAULY and MUNRO, 1984). Growth rates (GR) were also estimated for this purpose as follows (SPARRE and VENEMA, 1995):

$$GR_t = L_\infty K - L_\infty L_t, \quad (2)$$

where L_t is shell length at age t.

Seasonal growth patterns of yellow clams were determined by analyzing the monthly length frequency distributions (LFDs) for Barra del Chuy (33°45′ S, Uruguay) and Isla del Jabalí (40°33′ S, Argentina), for which data were entirely available. To this end, we reassessed our database to fit the generalized von Bertalanffy growth function (GVBGF: GAYANILO and PAULY, 1997), by maximum likelihood:

$$L_t = L_\infty[1 - e^{-K(t-t_0)+(KC/2\pi)\sin 2\pi(t-WP)-(KC/2\pi)\sin 2\pi(t_0-WP)}], \quad (3)$$

where C accounts for the intensity of seasonal growth oscillation, and WP is the time of the year with slowest growth. In order to build the age–length key needed for fitting Equation (3), we identified and separated normal components in the LFDs (grouped by 4 mm) using the Bhattacharya method and a separation index >2 as criterion to separate contiguous normal components (GAYANILO and PAULY, 1997). As we followed each cohort through its entire life span, we were able to assign absolute ages to relative ones (lengths) and thus to build an age–length key, following the methodology proposed by GÓMEZ and DEFEO (1999).

Total mortality (Z) values extracted from the literature came from age or length structured catch curves, which provide unbiased and comparable mortality estimates (PAULY *et al.,* 1995). In both cases, the linearized negative exponential model was given by $\ln(n) = a - Zt$, n being the number of clams, a the regression intercept, and t the age in each cohort. Z estimates for each beach coming from different years were included as separate entities to perform statistical analyses. Data extracted from the reference sources allowed us to reassess Z estimates for the Argentinean beaches Mar Azul (OLIVIER *et al.,* 1971) and Isla del Jabalí (FIORI, 2002). Z estimates for Barra del Chuy (Uruguay) and Monte Hermoso (Argentina) were obtained from DEFEO *et al.* (1992b) and MORSÁN and FIORI (unpublished), respectively. With the exception of Monte Hermoso, two estimates per beach were available.

Large-scale patterns in life-history characteristics were defined using latitude (centesimal units) and mean annual surf water temperature as independent variables. Even though the relationship between them was negative and highly significant ($r = -0.99$; $p \ll 0.001$), both variables were used to depict large-scale patterns. In general, temperature was measured during sampling time at the surf zone, and mean annual values were obtained as the average of individual estimates. Additional information was taken from the reference sources. The relationships between biotic and abiotic variables were modeled by linear and nonlinear fitting procedures, selecting the model with the best goodness of fit.

RESULTS

Density of the yellow clam, *M. mactroides,* varied widely between the five analyzed beaches. The density recorded for Cassino, Brazil (*ca.* 2700 ind/m^2: 32° S) was 32 times higher than that at Monte Hermoso, Argentina (83 ind/m^2: 39° S). Thus, density (D) exponentially increased with mean surf water temperature ($r = 0.97$; $P \ll 0.01$) and decreased with latitude (LAT) according to a monotonically decreasing exponential function of the form ($r = -0.99$; $p < 0.001$: Figure 2a):

$$D = 1.81e^{10}[e^{(-0.49LAT)}]. \quad (4)$$

Recruitment switched from markedly seasonal in high-temperate Argentinean beaches (*e.g.,* less than 1 mo/y) to continuous (12 mo/y) in midtemperate ones, notably the Brazilian Cassino beach, and thus the occurrence of yellow clam recruits within a year linearly decreased with latitude ($r = -0.96$; $p < 0.0007$; Figure 2b) or increased with temperature ($r = 0.97$; $p < 0.0003$).

The maximum observed yellow clam length ($L_{\max}$) varied from 69 mm in the northernmost population Cassino (32° S) to 82 mm in Isla del Jabalí (41° S), increasing asymptotically with latitude according to the following nonlinear model (Figure 2c):

$$L_{\max} = 81.72[1 - e^{-0.32(LAT-26.39)}]. \quad (5)$$

This model, which explained 96% of the variance ($p < 0.0002$) and had the best goodness of fit among all fitted models, has a biological interpretation as follows: 81.72 mm is the maximum expected yellow clam length, 0.32 is the curvature parameter estimate that measures how fast the species approaches the maximum length and 26.39 (latitude in centesimal units: *ca.* 26°23′ S) could be interpreted as the theoretical northern end of the species distribution. The disagreement between this estimate and the observed northernmost limit (24° S) could be explained by the lack of information in

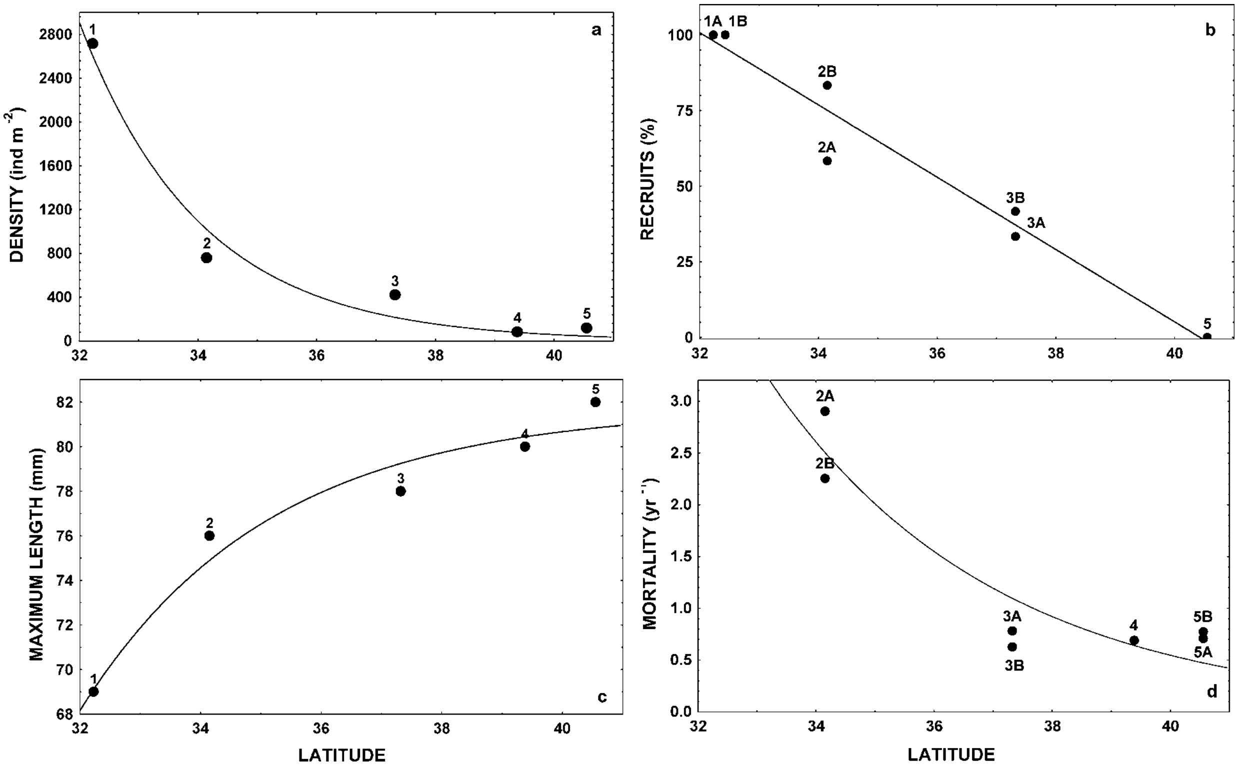

Figure 2. *Mesodesma mactroides.* Relationship between latitude (centesimal units) and (a) density (Equation [4]), (b) recruitment, quantified through the number of months in a year that individuals <5 mm appeared in the samples, (c) maximum observed length (Equation [5]), and (d) mortality (Equation [6]). The model with the best goodness of fit is shown in each case. Numbers beside each point refer to the corresponding beaches as in Figure 1. Associated letters refer to different years analyzed for the same beach.

Brazilian beaches from 32° S to 24° S. $L_{\max}$ linearly decreased with water temperature ($r = -0.93$; $p < 0.02$). Combining the results provided by Equations (4) and (5), a clear density-dependent response of the yellow clam body size to density emerged, with a highly significantly negative relationship between both variables ($r = -0.94$; $p < 0.007$).

The nonlinear fitting of the VBGF to the age-length keys extracted from the literature explained more than 94% of the variance ($0.94 < r^2 < 0.99$), and all parameters were highly significant ($p < 0.01$), except t_0 at Barra del Chuy (Table 2, Figure 3a). The life span drastically decreased with latitude, ranging from *ca.* 3–4 years in Cassino (Brazil) and Barra del Chuy (Uruguay) to almost 8 years in Argentinean beaches. Following the classic inverse relationship between individual size, longevity, and growth rates, yellow clams at southern Argentinean beaches showed significantly lower growth rates (Figure 3b) than northern beaches, with the growth index ϕ' decreasing linearly with latitude (Figure 3c) and increasing

Table 2. *Growth parameters estimated by nonlinear models for the five populations of* M. mactroides *(age–length data from Olivier* et al., *1971; Gianuca, 1983, 1985; Defeo* et al. *1992; and Fiori and Morsán, 2004). With the exception of* t_0 *at Barra del Chuy, all the parameters fitted for the five populations were significant (*$p < 0.01$*). Results of the nonlinear fitting of the GVBGF are shown for Barra del Chuy and Isla del Jabalí.*

	Growth Parameters						
Beach*	L_∞ (mm)	K (year^{-1})	t_0 (year)	C	WP	R^2	ϕ
VBGF							
Cassino (Br)	68.33	1.31	−0.25			0.99	3.79
Barra del Chuy (Uy)	75.86	0.87	−0.01			0.99	3.70
Mar Azul (Arg)	82.71	0.31	−1.37			0.99	3.32
Monte Hermoso (Arg)	70.42	0.54	−0.36			0.99	3.43
Isla del Jabalí (Arg)	77.73	0.42	−0.51			0.99	3.40
GVBGF							
Barra del Chuy (Uy)	73.14	1.11	0.17	1.00	0.34	0.97	3.77
Isla del Jabalí (Arg)	74.50	0.61	−0.38	1.00	0.57	0.96	3.55

* Br = Brazil, Uy = Uruguay, Arg = Argentina.

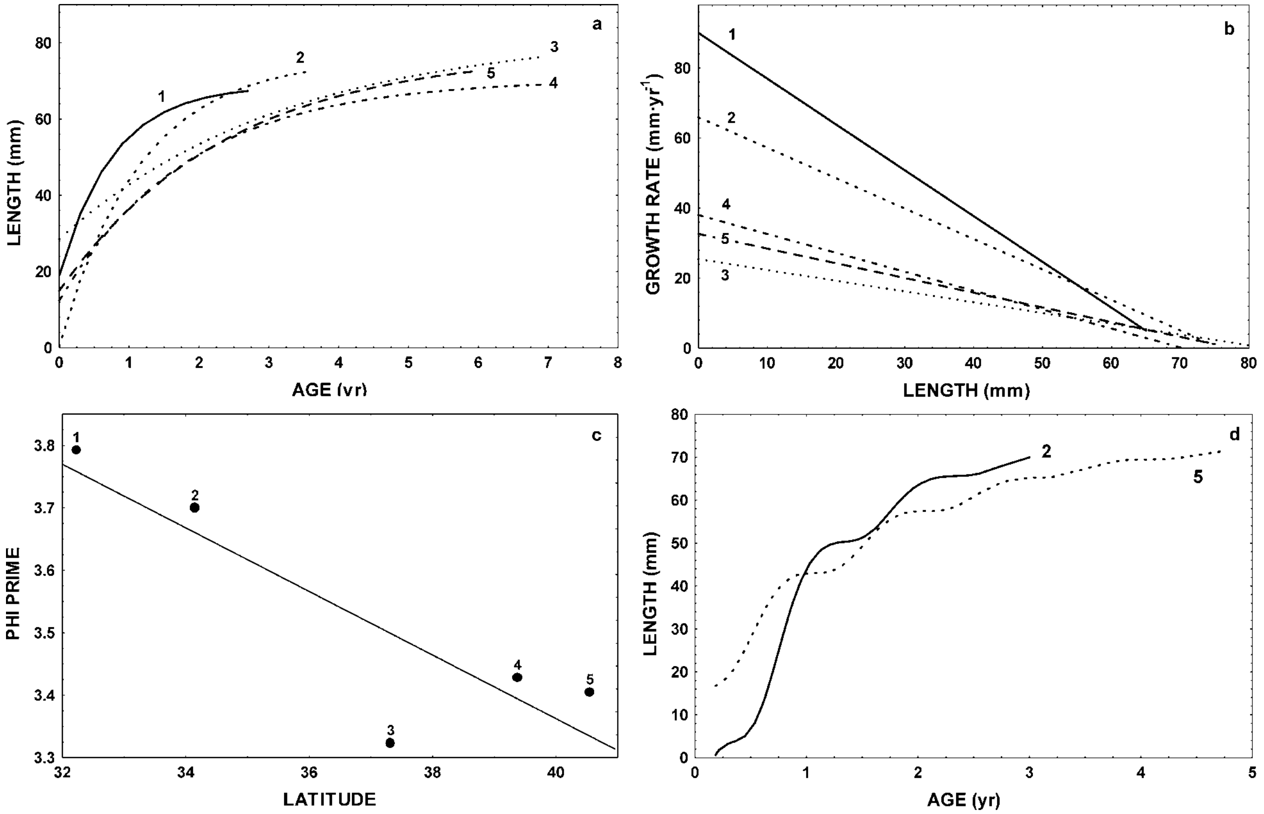

Figure 3. Latitudinal variations in growth indicators of *M. mactroides*: (a) growth curves resulting from nonlinear fitting of Equation (1), (b) growth rates estimated by Equation (2), (c) growth performance index ϕ', and (d) seasonal curves (Equation [3]) fitted for Barra del Chuy (2) and Isla del Jabalí (5) populations. Numbers beside each point refer to the corresponding beaches, following Figure 1.

with water temperature of the surf zone ($r = 0.90$; $p < 0.04$). LFD analyses, together with the nonlinear fitting of the GVBGF (Equation [3]) to modal sizes, showed growth seasonality for two clam populations situated *ca.* 7° latitude apart (Barra del Chuy and Isla del Jabalí). In both cases, yellow clams showed intense intra-annual growth oscillations ($C = 1$), stopping growth ($0.34 < WP < 0.57$) between late autumn and winter (Table 2, Figure 3d). The combination of K and L_∞ estimated from the GVBGF determined higher ϕ' values than those derived from the classic VBGF (Table 2).

The instantaneous rate of total mortality (Z) varied between 2.91/y in Barra del Chuy to 0.64/y in Mar Azul, with values almost five times higher for northern populations than for southern ones. Consequently, Z significantly decreased with latitude according to the following monotonically decreasing exponential function ($r^2 = 0.87$; $p < 0.0003$: Figure 2d):

$$Z = 38{,}040e^{-0.28LAT}. \qquad (6)$$

Given the inverse relationship between temperature and latitude, Z exponentially increased with temperature ($r = 0.95$; $p < 0.0002$). These results suggest an unambiguous trend for yellow clams to have higher mortalities at higher densities in midtemperate sandy beaches with higher surf water temperatures than in southern ones.

DISCUSSION

Life-history traits of yellow clam, *M. mactroides,* exhibited systematic geographical patterns of variation: abundance, growth, and mortality rates significantly decreased from northern (Brazil and Uruguay) to southern (Argentina) populations, whereas longevity and individual sizes increased in the same direction. Northern populations also had an extended or quasi-continuous recruitment season, whereas southern populations located at higher latitudes had markedly seasonal recruitment that became negligible at the southernmost edge of the range (41° S). These macroecological patterns derived from beach-specific intensive studies (at least one year of monthly sampling) are in agreement with general latitudinal patterns that predict larger body sizes and life spans together with lower mortality rates at higher latitudes than in lower ones (see *e.g.,* ATKINSON and SIBLY, 1997; JENSEN, 1996; PAULY, 1980).

Data from the five sandy beaches intensively analyzed here suggest that density of *M. mactroides* exponentially decreased from midtemperate (Brazil and Uruguay) to high-temperate (Argentina) beaches. The increase in density from Isla del Jabalí (41° S, southernmost edge of the range) to Cassino (32° S, northern limit of coverage), apparently suggest a ramped-north distribution shape (*sensu* SAGARIN and

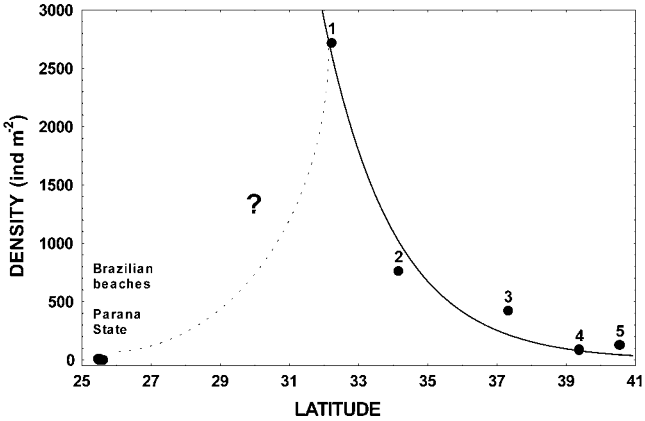

Figure 4. Hypothetical shape of the distribution range of *M. mactroides* based on modeled (continuous line) and expected (dashed line) trends, the latter inferred from observed data toward the northern distribution limit.

GAINES, 2002). However, snapshot information provided by SOARES (2003, personal communication: Table 1) indicates a sharp decline in yellow clam density (*i.e.,* lower than 5 ind/m^2) in dissipative beaches of Parana State (25°30′–25°50′ S) for the northernmost edge of the range in Brazil. This suggests a large-scale unimodal distribution pattern (Figure 4), with the highest abundance at the center of the range (Barra del Chuy and Cassino), decreasing toward both edges of the range. Our hypothesis is supported by two additional studies performed close to the northern end of the yellow clam distribution in truly dissipative beaches (Table 1): (1) SOUZA and GIANUCA (1995) did not find yellow clams during a 13-month sampling period in the dissipative Barrancos beach (25°37′ S, Parana State, Brazil), even though the typical sympatric suspension feeders *Donax hanleyanus* and *Emerita brasiliensis* were present, and (2) BORZONE *et al.* (1996) did not find yellow clams in a comprehensive study that involved sampling on 10 beaches also in Parana State, Brazil (25°30′–25°50′ S), including at least four dissipative beaches with the same physical features that characterize the suitable habitat for *M. mactroides* (Table 1). This evidence suggests that 25°30′ S could be close to the northernmost distribution edge of the range (Figure 4).

Large-scale variations in coastal physiognomy could explain the pattern found: Cassino beach takes part of a continuously (640 km) exposed, dissipative, and microtidal (astronomic tides $\approx$ 0.5 m) sandy-beach stretch extending from Rio Grande do Sul (Southern Brazil: *ca.* 29° S) to northeastern Uruguay (Barra del Chuy: 33°45′ S). These sandy beaches have fine sands, gentle slopes, heavy wave action, and a wide surf zone (CALLIARI *et al.,* 1996), together with a high primary production (DEFEO and SCARABINO, 1990), mainly originated from surf diatom blooms, and as such have been defined as semiclosed ecosystems (*sensu* MCLACHLAN, 1980). These beaches constitute a suitable habitat for the yellow clam. Changes in coastal physiognomy occur northward to this sandy-beach chain: intermediate and reflective beaches, estuaries, and embayments prevail over dissipative beaches between 29° and 24° S (DEFEO and DE ALAVA, 2005). SOARES (2003), in a worldwide analysis, showed that dissipative beaches were far more frequently found in temperate than in subtropical and tropical Atlantic South America. The fact that the species inhabits only dissipative, semiclosed ecosystems throughout its range suggests that the hypothesis of differential food availability (*sensu* DEFEO and CARDOSO, 2002) should also be of relevance in explaining the disappearance of yellow clams in well-developed dissipative beaches of Brazil close to 25° S, but with lower primary production than in dissipative systems located between 32° and 40° S. This indicates that location in a particular part of the range is not a prior indicator of habitat suitability for the yellow clam. Thus, macroscale variations in coastal physiognomy ultimately interact with large-scale environmental variables, notably temperature, to determine the northern end of the yellow clam distribution. This is in agreement with recent findings showing that large-scale variations in abundance in sandy-beach populations do not necessarily vary smoothly from the central region to range boundaries because of spatial variations in habitat quality (CARDOSO and DEFEO, 2004). However, as the portion of the range from 32° to 26° S has been severely undersampled, the elucidation of the exact shape of the species distribution pattern within the range is still unclear (Figure 4).

Recruitment patterns switched from continuous in the Brazilian beach Cassino to markedly seasonal in southern Argentinean beaches. In most cases, few recruits appear in winter, suggesting reduced spawning and recruitment during colder months (DEFEO *et al.,* 1992b). Indeed, two main spawning periods were observed for Uruguayan (MASELLO, 1987) and Argentinean populations (OLIVIER *et al.,* 1971): one between October and December, and a second one from February to April (late summer). The southernmost edge of *M. mactroides*' range, Isla del Jabalí, exhibited null recruitment (Figure 2b; see also FIORI, 2002), 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, dispersal could have a direct impact on yellow clam abundance and distribution among different subpopulations and its overall persistence in the whole metapopulation (DEFEO, 1996b).

We provide the second large-scale evidence of an inverse relationship between density and body size (in this article represented by individual length) for a sandy-beach population. Body size explained a significant amount of variation in population density at a large spatial scale. DEFEO and CARDOSO (2004) found the same pattern for the mole crab, *Emerita brasiliensis,* but the authors used the universally accepted rule that relates density with individual body weight (MARQUET *et al.,* 1990). However, assuming the classic proportionality between individual length L and mass W (*i.e.,* $W = aL^b$), our pattern could be valid also in a theoretical context. Both the mole crab and the yellow clam are dominant in terms of biomass in sandy-beach communities, and thus fluctuations in scaling could be attributed to intraspecific rather than to interspecific effects.

Growth and mortality of the yellow clam, *M. mactroides,* showed marked latitudinal gradients throughout its range.

Yellow clams at midtemperate beaches had higher growth and mortality rates and shorter life spans than at high-temperate beaches. These geographic trends were significantly related to variations in temperature. The increase in growth intensity toward northern beaches was also registered in other sandy-beach species of the Atlantic coast of South America, as females of the mole crab, *Emerita brasiliensis* (DEFEO and CARDOSO, 2002, 2004), and the isopod *Excirolana braziliensis* (CARDOSO and DEFEO, 2004). The significant latitudinal trends in growth rates unambiguously indicate that *M. mactroides* has a better growth performance in northern latitudes than in southern ones. The large-scale variation in ϕ' could be considered an expression of variability in the growth potential of the species on a geographic scale. In this setting, it is hypothesized that organisms at higher latitudes achieve larger sizes by delaying maturity and thus they should be able to allocate more resources to reproduction and somatic growth than in tropical beaches, thereby modifying population growth rates.

Growth of *M. mactroides* was seasonal in two midtemperate populations located 7° latitude apart, one at the theoretical center of the range (Barra del Chuy) and the other at its southernmost edge (Isla del Jabalí). High intra-annual variation in temperature, commonly observed in midtemperate Atlantic sandy beaches, could explain this growth seasonality, as has been already documented for isopods (DE ALAVA and DEFEO, 1991), amphipods (GÓMEZ and DEFEO, 1999), anomurans (DEFEO *et al.,* 2001), and clams (DEFEO *et al.,* 1992b; FIORI, 2002) inhabiting sandy beaches at these latitudes.

Mortality of the yellow clam significantly increased with density toward sandy beaches located in the northern part of its distribution range (Brazil and Uruguay), where individual sizes are smaller, growth rates faster, and life span shorter than in southern beaches. Higher growth and mortality rates at the north could probably result from increasing metabolic rates determined by higher oxygen consumption at high water temperatures (MOREAU, 1987). Thus, the increase in reproductive investment in northern, midtemperate beaches, inferred from the more extended reproductive and recruitment periods, could compensate for the higher mortality rates. *Excirolana armata* inhabiting subtropical Brazilian beaches also showed a shorter life span (25°30′ S; SOUZA, 1998) than populations in temperate Uruguayan beaches (33°45′ S; DE ALAVA and DEFEO, 1991). Similar large-scale patterns in life-history traits were found for the mole crab, *Emerita brasiliensis* (DEFEO and CARDOSO, 2002, 2004), and the isopod *Excirolana braziliensis* (CARDOSO and DEFEO, 2003, 2004).

Human-induced impacts or episodic disturbance agents could alter the macroecological patterns depicted here for *M. mactroides.* A long-term study, including experimental manipulation of fishing effort, based on the closure of the fishery in Uruguay (DEFEO, 1996a, 1998), demonstrated that human-induced, biotic, and abiotic factors significantly affected fine-scale demographic parameters, such as age-specific survival probability and fertility, as well as coarse-scale demographic parameters, such as age composition, elasticity to demographic parameters, and population growth rate (BRAZEIRO and DEFEO, 1999; LIMA *et al.,* 2000). Massive natural mortality events have also been documented as stochastic sources of demographic variability in *M. mactroides* throughout its range, decimating its populations along thousands of km of South American beaches (FIORI *et al.,* 2004b). This was also observed for the surf clam, *Mesodesma donacium,* along Pacific sandy beaches of South America (ARNTZ *et al.,* 1987). Another source of mass mortality affecting populations at a mesoscale (*i.e.,* within a single beach) can be stranding of intertidal organisms at high beach levels due to unpredictable short-term storm surges and barometric tides (DEFEO, 2003).

The above-mentioned long-term, large-scale field experiments suggested that wide fluctuations in the Uruguayan yellow clam population are the result of intertwined forces of exogenous, environmental, density-dependent, and human-induced factors operating together at different spatial and temporal scales (LIMA *et al.,* 2000). Moreover, the open nature of *M. mactroides,* which is structured as a metapopulation, imposes additional restrictions on our ability to assess fluctuations in abundance with some degree of confidence. Indeed, the yellow clam has a complex life cycle defined by planktonic larvae and a benthic adult phase decoupled in time and space. High variable mortality and dispersion rates of the planktonic phase make prediction of recruitment to the benthic life of sandy shores highly uncertain and difficult to quantify (DEFEO, 1996b). This will also depend on the pattern of connectivity (larval replenishment and gene flow) between components of a metapopulation (source–sink dynamics), which, in *M. mactroides,* is still uncertain (MARINS and LEVY, 1999). Even though this issue has been explicitly recognized for managing sandy-beach populations (DEFEO *et al.,* 1993), there are no examples in which the source–sink metapopulation theory (see ORENSANZ and JAMIESON, 1998) has been applied to identify the patterns of connectivity between components of sandy-beach metapopulations (reviewed in DEFEO, 2003). This deserves future long-term and large-scale studies on the subject. Because of the scale dependence, future studies on the yellow clam should be designed to incorporate a number of hierarchical scales to better understand macroscale variations in demographic patterns and life-history traits.

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☐ RESUMEN ☐

La almeja amarilla, *Mesodesma mactroides,* es un bivalvo intermareal característico de las playas de arena de la costa atlántica sudamericana. Su área de distribución se extiende desde el sur de Brasil (24° S) hasta Argentina (41° S). En este artículo presentamos un análisis macroespacial de las características de su ciclo de vida, demografía y dinámica poblacional a lo largo de casi todo su rango de distribución (32–41°S). Las propiedades poblacionales de almeja amarilla exhibieron claros patrones biogeográficos. La abundancia y las tasas de crecimiento y mortalidad disminuyeron significativamente de norte (Brasil y Uruguay) a sur (Argentina). Información adicional a este estudio, tomada en el límite norte del rango geográfico, permite sugerir que el patrón de distribución macroespacial de la almeja amarilla es unimodal. El reclutamiento fue casi continuo en las poblaciones del norte, marcadamente estacional en las del sur y casi ausente en el extremo austral del rango (41° S). La talla máxima individual aumentó en forma no lineal con la latitud. Este resultado, en conjunto con los patrones de densidad, hizo evidente una relación inversa de macroescala entre la densidad y el tamaño corporal. La longevidad aumentó con la latitud de 3 a más de 7 años. El análisis de las distribuciones de frecuencia de tallas reveló una marcada variabilidad intra-annual en el crecimiento para dos poblaciones separadas unos 7° de latitud. Las variaciones en la temperatura del agua explicaron los patrones demográficos y dinámico-poblacionales de macroescala de la especie, en la cual el ajuste del fenotipo en relación con el ambiente denota su alta plasticidad en el gradiente latitudinal. Evidencias experimentales y observacionales de largo plazo en playa de Uruguay sugieren que las poblaciones de almeja amarilla están controladas por la acción conjunta de factores denso-dependientes y ambientales. Dado que la almeja amarilla posee larva planctónica y está estructurada como una metapoblación, estudios futuros deberán incorporar una serie de escalas jerárquicas para entender las fluctuaciones de macroescala en los patrones demográficos y características de su historia de vida.