

Distribution pattern, density and growth of the stout razor clam *Tagelus plebeius* in a South-west Atlantic estuarine system

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The population biology of the stout razor clam Tagelus plebeius is poorly understood, despite the species' current wide distribution, and the potential use of its Holocene shell deposits to infer past environmental and ecological conditions. This study investigates distribution and growth pattern of T. plebeius in the south-western Atlantic Mar Chiquita Coastal lagoon (37°32'S 57°19'W), Argentina. The population includes the oldest individuals (up to 27 years) reported so far with shell length up to 77.9 mm. A von Bertalanffy model with $L_{\infty} = 67.60$ mm (95% CI = 64.55; 70.64), $k = 0.181$ year⁻¹ (CI = 0.142; 0.218), and $t_0 = -0.77$ (CI = -1.46; -0.08) best described their individual growth for the whole population. The higher density, growth rate k , t_0 and maximum age and lower L_{∞} were in the low intertidal rather than in the medium intertidal, but there were no differences in density and age between medium and high intertidal. Given the results and the current knowledge on the effects of different factors influencing this species, we conclude that the distribution pattern and shell growth observed in our study reflect a response to metabolic necessities in combination with a strong influence of biological interactions.

Keywords: *Tagelus plebeius*, razor clam, growth, age, Mar Chiquita Coastal Lagoon

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INTRODUCTION

The determination of individual age and growth rate is one of the key parameters for stock assessment (e.g. Lai *et al.*, 1996; Orensanz & Jamieson, 1998). Growth, production and physiological activity in bivalve species can be affected by abiotic factors such as temperature (e.g. Green, 1973; Jones *et al.*, 1989; Dekker & Beukema, 1999), substrate characteristics (e.g. Pratt, 1953; Pratt & Campbell, 1956; Urban, 1998), variations in salinity (e.g. Morton, 1978; Vincent *et al.*, 1994; Kube *et al.*, 1996) and food availability (e.g. Beukema & Desprez, 1986; Beukema & Cadée, 1991; Arneri *et al.*, 1998). Moreover, population processes such as density-dependence (e.g. Weinberg, 1998; Dekker & Beukema, 1999; Gutiérrez & Defeo, 2003) and interaction processes (trophic and non-trophic such as presence of predators, parasitism, ecological engineers) can also affect growth rate (e.g. Nakaoka, 2000; Beal, 2006; Lomovasky *et al.*, 2006). In this sense, along an intertidal gradient, the effects of environmental stress on shell growth seem to outweigh those of biological interactions at higher zones (Reise, 1998; Gosling, 2003; Cognie *et al.*, 2006), while the relationship is opposite at lower intertidal levels (Bartol *et al.*, 1999; Bologna & Heck, 1999). Thus, knowledge of the biological characteristics, distribution

patterns, abundance and growth across the intertidal range constitutes additional information for sustainable management of exploited intertidal bivalve populations.

The stout razor clam *Tagelus plebeius* (Lightfoot, 1786) is a euryhaline species that inhabits tidal flats with cohesive sandy silt sediments along the American Atlantic coast from Cape Cod, Massachusetts (42°N, USA; Leal, 2002) to the Northern Argentinean Patagonia (San Matías Gulf, 41°S, Argentina; Olivier *et al.*, 1972a, b). Their shells are ubiquitous in Holocene estuarine deposits of central South America (1340 to 3850-year B.P.; Fasano *et al.*, 1982; Schnack *et al.*, 1982) and are often used as indicators of palaeoenvironmental conditions (see Golfieri *et al.*, 1998; Iribarne & Botto, 1998; Iribarne *et al.*, 1998; Aguirre & Farinati, 1999). This suspension-feeding species (Holland & Dean, 1977a; Arruda *et al.*, 2003) is a deep burrowing species that inhabits permanent burrows (up to 0.70 m depth) showing vertical movements through each semidiurnal tidal cycle, but not showing intertidal migration (Holland & Dean, 1977b). Current knowledge of *T. plebeius* biology and ecology is limited to a few localities in Argentina (Mar Chiquita coastal lagoon: Cledón *et al.*, 2004; Lomovasky *et al.*, 2005, 2006; Addino *et al.*, 2010, 2016; Bahía Blanca estuary: Addino *et al.*, 2015), Brazil (Canal do Calunga, Maceió: Viégas, 1982; São Sebastião: Abrahão & Amaral, 1999; Arruda *et al.*, 2003; Abrahão *et al.*, 2010; Cachoeira river estuary: Ceuta & Boehs, 2012; Ceara river estuary: de Farias & Rocha-Barreira, 2012; Caraguatatuba Bay: da Silva *et al.*, 2015), and the USA (North Inlet estuary, Holland & Dean, 1977a, b).

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Given the current knowledge about the effects of biological interactions on this species, we expect distinct patterns of individual growth in *T. plebeius* across an intertidal system. For example the differences in morphometric characteristics related to the presence of the intertidal burrowing crab *Neohelice granulata* (a co-habiting species, Lomovasky *et al.*, 2006), to parasitism by the gymnophallid metacercariae (Lomovasky *et al.*, 2005; Addino *et al.*, 2010), and to the presence of salt marsh plants *Spartina alterniflora* (Addino *et al.*, 2015) are important. Given this evidence, we hypothesize that the density pattern and individual growth may respond to metabolic necessities of this species determining differential recruitment and mortality, albeit modulated by trophic (e.g. predation, parasitism, competition) and non-trophic (e.g. ecosystems engineering) biological interactions. Accordingly, we expect highest density and growth rates at the low intertidal level. Thus, the aims of the present study are to evaluate the distribution pattern, density and growth of the stout razor clam *T. plebeius* across intertidal in Mar Chiquita Coastal Lagoon estuarine system.

MATERIALS AND METHODS

Study area, sampling procedure and sediment characteristics

The study was performed between January 2003 and March 2004 in the Mar Chiquita Coastal Lagoon (37°32'S 57°19'W; Argentina). This is a brackish water area of about 46 km² with muddy sediments and low tidal amplitude (<1 m, Fasano *et al.*, 1982). Sampling was conducted in a tidal flat area located along 3 km of shoreline from the lagoon inlet at seven different sites (Figure 1). At each site, samples were taken at three tidal levels parallel to the shore with similar

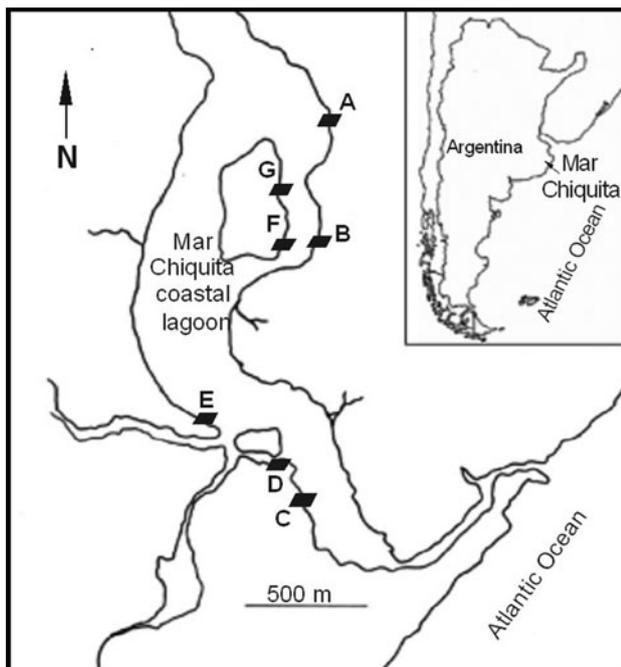


Fig. 1. The seven sampling sites in the Mar Chiquita Coastal Lagoon, Argentina, South-west Atlantic.

exposure time: low intertidal level (LIL) 0.40 m above mean low tide (thereafter amlt), medium intertidal level (MIL) 0.55 m amlt and high intertidal level (HIL) 0.75 m amlt.

Five sediment samples (cores of 5 cm diameter and 35 cm depth) were collected at each site and tidal level in January 2004. Organic matter content (OMC) of ~10 g subsamples was determined as the difference between dry weight (80°C to constant weight) and the ash weight (450°C for 8 h). Grain size frequency distribution was obtained by sieving a dried 400 g subsample through a series of five screens (screen sizes: 2000, 500, 250, 125, 62 µm). The null hypothesis of no difference in OMC and each grain size fraction along intertidal levels was evaluated by one-way ANOVA with a posteriori Tukey test (Zar, 1999).

Tagelus plebeius distribution pattern, size structure and shell morphology

At each site the density of *Tagelus plebeius* was estimated by counting siphon holes on the sediment surface, a measure that approximates the number of bivalves reasonably well and is not disruptive to the intertidal environment (see Holland & Dean, 1977a; Iribarne *et al.*, 1998). Between five to ten randomly placed replicates of 0.25 m² area were examined at each site and tidal level. The null hypothesis of no difference in the density of *T. plebeius* between intertidal levels was then tested by Kruskal–Wallis non-parametric analysis (Zar, 1999) with multiple comparisons of mean ranks of all groups, as the assumptions for a parametric test were not fulfilled.

At each site, 30–100 bivalves (N = 2491) were collected by excavating the sediment using a shovel. Shell length (L; the anterior-posterior axis), height (H; from the umbo to the ventral margin), width (W; all with precision ± 0.1 mm), total Mass (TM) and shell mass (SM) were determined (precision ± 0.01 g). Then, the internal tissues were dried at 70°C to constant mass in order to obtain the shell free dry mass (SFDM; precision ± 0.001 g). The relations between H, L, W, TM, SM and SFDM were fitted to the best model (linear or exponential).

Internal shell growth pattern and growth rate of *T. plebeius*

Subsamples for growth analysis were obtained from each area and tidal level (N = 626). Individual age was inferred from internal shell growth bands (following Richardson, 2001) of the left valve. Each valve was embedded in polyester resin and sectioned along the axis of maximum growth in height (H) using a Bosch GDC 34 saw with a diamond blade. The cross-sections were polished on lapidary wheels using grits of 400, 600, 1200, 2400 and 4000 grade, and etched 14 min using 0.5% DE-CAL agent. Acetate peel replicates of the cross-sectioned surfaces were produced following Rhoads & Lutz (1980) and examined microscopically. The number of internal translucent bands and the corresponding length were recorded as age-length data (following age validation in next section).

The von Bertalanffy growth model was fitted to the shell length-at-age data using:

$$L_t = L_\infty(1 - e^{-k(t-t_0)})[\text{mm}, y]$$

where L_{∞} is the asymptotic length, k is the growth constant, t the age and t_0 the age at zero length. To fit the model to the data, the maximum likelihood method was used (following Edwards, 1992; Hilborn & Mangel, 1997).

Additionally, in order to compare the growth across intertidal levels, the von Bertalanffy k , t_0 and L_{∞} parameters from each intertidal level were compared by pair-wise comparisons using the Likelihood ratio test (Cerrato, 1990), and bivariate confidence limits (CI) for k , t_0 and L_{∞} were built using profile likelihood (see Hilborn & Mangel, 1997).

Timing of growth band formation

Under stereomicroscopy, the internal shell growth bands can be identified as translucent and opaque bands (Jones *et al.*, 1990). If major growth bands were formed annually, then one winter growth line (translucent band) should have been formed in the shell part grown during one year. Thus, the annual formation of internal shell growth bands was verified by a one-year tagging-recapture field experiment. Sixty individuals of varying size (40.5–63.25 mm L) were collected from MIL, measured and marked with numbered plastic labels adhered to the surface of the periostracum. The animals were then returned to the intertidal area and allowed to bury each in an individual enclosure consisting of a PVC tube (10 cm diameter and 50 cm height) open in the top that was vertically buried in the sediments. The wall of these tubes was perforated to allow for the horizontal flow of water through the enclosure. After one year the animals were recovered, the increment in length was determined, the internal shell growth pattern was examined using the acetate peel technique (see above) and the number of translucent and opaque growth bands formed during the experimental time was registered.

Additionally, the annual band formation (see Results section) was confirmed using trace element profiles derived by laser ablation – inductively coupled plasma – mass spectrometry (LA-ICP-MS) at Bremen University (Bremen, Germany). A shell was embedded in polyester resin and sectioned along the axis of maximum growth in height (H) and polished on lapidary wheels as described above. The section was rinsed with deionized water and allowed to dry in a clean hood. Shell material was ablated by a Finnigan 266 nm laser probe (settings: laser energy 1.0 mJ, pulse rate 5 Hz, beam diameter 40 μm) using helium as sample gas in the ablation cell (0.4 l min^{-1}) and subsequent addition of argon as make-up gas (0.8 l min^{-1}). The isotopes ^{43}Ca and ^{88}Sr were measured by a ThermoFinnigan (plasma power 1200 W, low resolution, 160 ms dwell time per isotope). We used the NIST610 glass standard reference for external calibration (Pearce *et al.*, 1997); external reproducibility for Sr/Ca of this standard was 1–2%. Samples were collected ($N = 120$) with an average distance of 65 μm along the growth trajectory until an annual band was reached that was too narrow to collect four or more samples. Every five samples the NIST610 standard was measured and a new calibration line established in order to compensate for instrument drift. The calculated Sr/Ca ratios were related to the position of the translucent and opaque bands in the shell and a t -test was made to test the null hypothesis of no difference in the mean Sr/Ca ratios between translucent and opaque bands (Zar, 1999).

RESULTS

Sediment characteristics

Sediments of the different sites differed in a wide variety of physical properties.

Table 1. Granulometry of the different sampling sites in Mar Chiquita Coastal Lagoon.

Site	Intertidal level	Mean grain size (mm)	Median grain size (mm)	Very coarse sand (>2 mm)	Coarse sand (2–0.5 mm)	Medium sand (0.5–0.25 mm)	Fine sand (0.25–0.125 mm)	Very fine sand (0.125–0.062 mm)	Silt-clay (<0.062 mm)	Mean Organic matter (%)
A	Low	0.20	0.0935	4.8 (0.8)	1 (0.3)	1 (0.3)	26.7 (2.8)	32.1 (2.4)	35 (3.6)	3.52
	Medium	0.13	0.0935	1.4 (0.9)	0.6 (0.2)	0.6 (0.2)	24.6 (2.8)	33.8 (5.7)	39.1 (6.5)	3.49
	High	0.12	0.0935	1 (0.5)	0.7 (0.1)	0.7 (0.1)	21.8 (2.1)	40.4 (1.5)	35.3 (1.6)	3.29
B	Low	0.27	0.0935	7.7 (1.9)	2.7 (0.7)	2.7 (0.7)	17.5 (2.6)	25.8 (2)	45.3 (4.6)	3.69
	Medium	0.19	0.0935	3.8 (0.3)	2.1 (0.3)	2.1 (0.3)	21.8 (1.7)	29.2 (2)	42.4 (3.4)	3.18
	High	0.19	0.0935	3.7 (1.2)	2.2 (0.3)	2.2 (0.3)	23.4 (4.7)	31.1 (3.3)	38.8 (5.4)	3.24
C	Low	0.40	0.1875	2.9 (1.2)	17.1 (2.8)	17.1 (2.8)	25.3 (4.2)	9.3 (1)	30.9 (4.5)	3.23
	Medium	0.43	0.1875	2.1 (1.2)	19.3 (3.5)	19.5 (3.3)	31.8 (6.5)	7 (1.8)	18 (4.8)	2.01
	High	0.48	0.1875	2.6 (1.5)	23.1 (11.4)	19 (4.7)	32.3 (7.5)	8.5 (1.5)	10.1 (4.2)	1.51
D	Low	0.10	0.031	0.6 (0.5)	1.7 (0.6)	1.7 (0.6)	13.3 (4)	17.6 (5.3)	64.6 (10)	5.38
	Medium	0.12	0.031	0.6 (0.1)	2.1 (0.8)	2.1 (0.8)	17 (1.5)	23.2 (2.5)	54.9 (2.7)	3.58
	High	0.20	0.0935	1.6 (0.2)	6 (1.7)	6 (1.7)	21.9 (1.1)	16.6 (0.9)	48 (2.6)	3.43
E	Low	0.36	0.0935	7.7 (2.3)	7.2 (1.8)	7.2 (1.8)	30 (4.7)	20.3 (2.5)	32.1 (8.4)	3.04
	Medium	0.44	0.1875	11.9 (3.6)	7.5 (1.2)	7.5 (1.2)	27.7 (3.3)	23.1 (1.7)	26.8 (2.8)	3.01
	High	0.36	0.0935	9.1 (2.5)	6.4 (2.1)	6.4 (2.1)	23.1 (3.9)	16.8 (3.4)	42.5 (6)	3.04
F	Low	0.095	0.031	0.8 (0.6)	0.6 (0.3)	0.6 (0.3)	17 (2.6)	21.4 (3.3)	59.7 (6)	4.66
	Medium	0.15	0.0935	1.9 (1.3)	1.5 (0.5)	1.5 (0.5)	25.2 (3.5)	26.1 (3.5)	44.3 (5)	3.10
	High	0.15	0.0935	2 (0.4)	1.8 (0.1)	1.8 (0.1)	21.4 (1.8)	29 (2.6)	44.9 (4.5)	3.17
G	Low	0.24	0.0935	6.4 (1.5)	2.6 (0.9)	2.6 (0.9)	17.6 (1.6)	23.9 (1.5)	48.4 (3.7)	4.03
	Medium	0.14	0.0935	1.2 (0.8)	1.2 (0.4)	1.2 (0.4)	30.6 (1.6)	29.8 (4.8)	36.5 (4.8)	3.57
	High	0.24	0.0935	3.3 (1.8)	5.2 (6.8)	5.2 (6.8)	29.2 (3.8)	26.6 (5)	34.7 (5.4)	3.58

Values for sediment fractions are expressed in percentage.

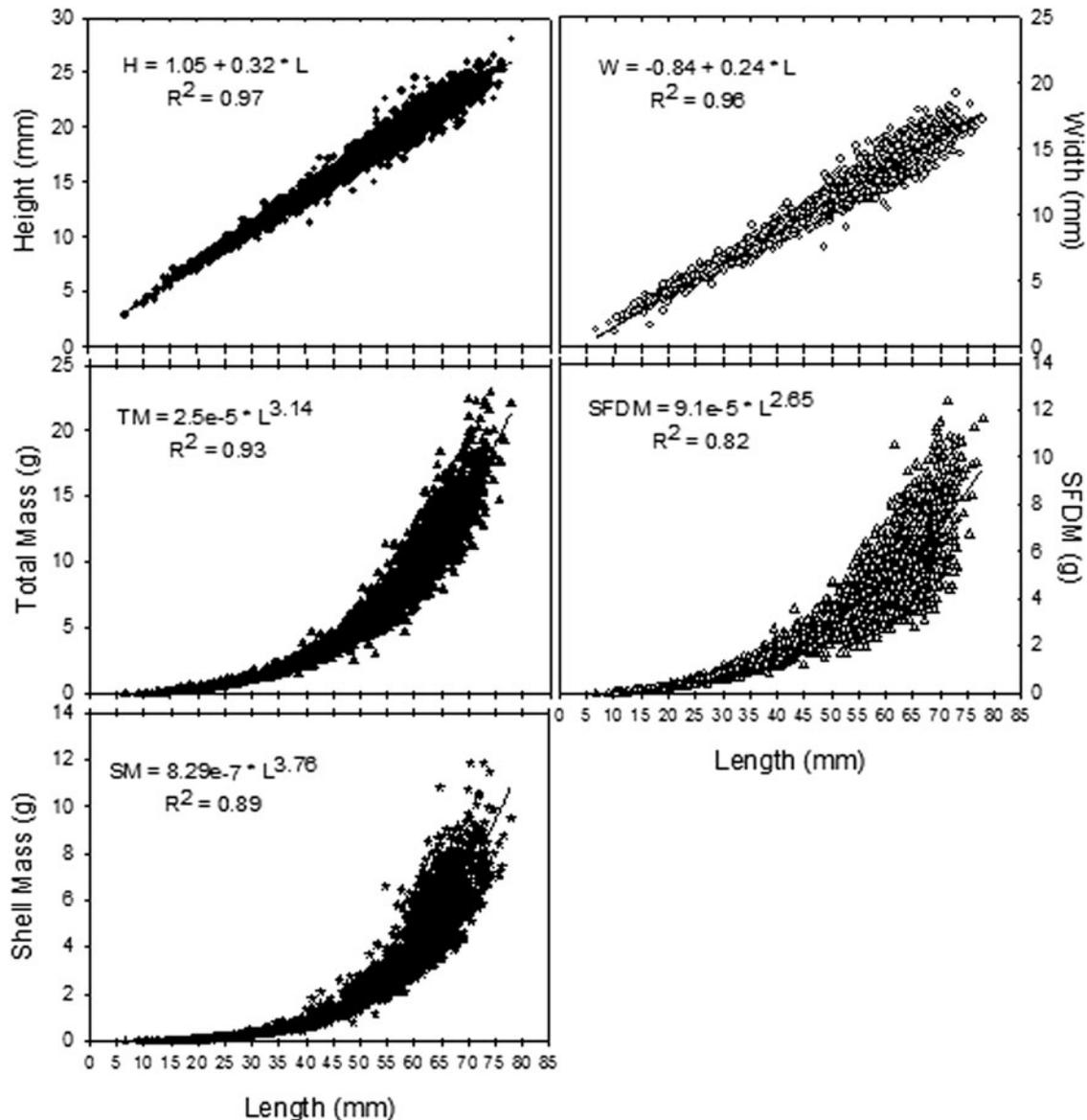


Fig. 2. Morphological relationships in *Tagelus plebeius*.

Median grain size diameter varied from 0.031 to >0.1875 mm, mean silt-clay content from 10.1 to 64.6% and the OMC from 1.51% in sandy sediments to 5.38% in the muddiest sediments (Table 1). Sediment organic matter content (OMC) was higher at LIL compared with MIL and HIL (3.94%, SD = 0.99 compared with 3.13%, SD = 0.82 and 3.04%, SD = 0.73 respectively, $P < 0.05$). The silt and clay sediment fraction <62 μm showed the same pattern as OMC ($P < 0.05$).

Tagelus plebeius distribution pattern, size structure and shell morphology

The density of *T. plebeius* was higher at LIL with 61.18 individuals m^{-2} (95% CI = 54.34; 68.05) compared with MIL (mean = 23.54 ind m^{-2} , CI = 15.76; 31.32) and HIL (mean = 27.14 ind m^{-2} ; CI = 12.15; 42.14; $H_{(2;133)} = 60.35$, $P < 0.05$). Shell length ranged from 6.71 to 77.93 mm with

a mean of 52.19 mm; SD = 14.40. The morphological relationships are shown in Figure 2.

Tagelus plebeius individual growth

The internal shell cuts under stereoscopy and acetate peels technique under microscopy showed a pattern of alternating broad opaque and narrow translucent bands (Figure 3). The umbo is not well defined in this species thus, the internal growth bands showed a parallel pattern in this area (Figure 3B). It was possible to follow each translucent internal growth band from the umbo throughout the shell section (Figure 3C, D) to the point where it crosses the outer shell layer to form an external ring on the shell surface (Figure 3E, F). In the ventral (most recent) part of the valve, the internal growth bands were situated closer to the shell edge and more narrowly spaced (individuals > 40 mm L). These bands were clearly visible in acetate peels but very difficult to identify on the exterior shell surface.

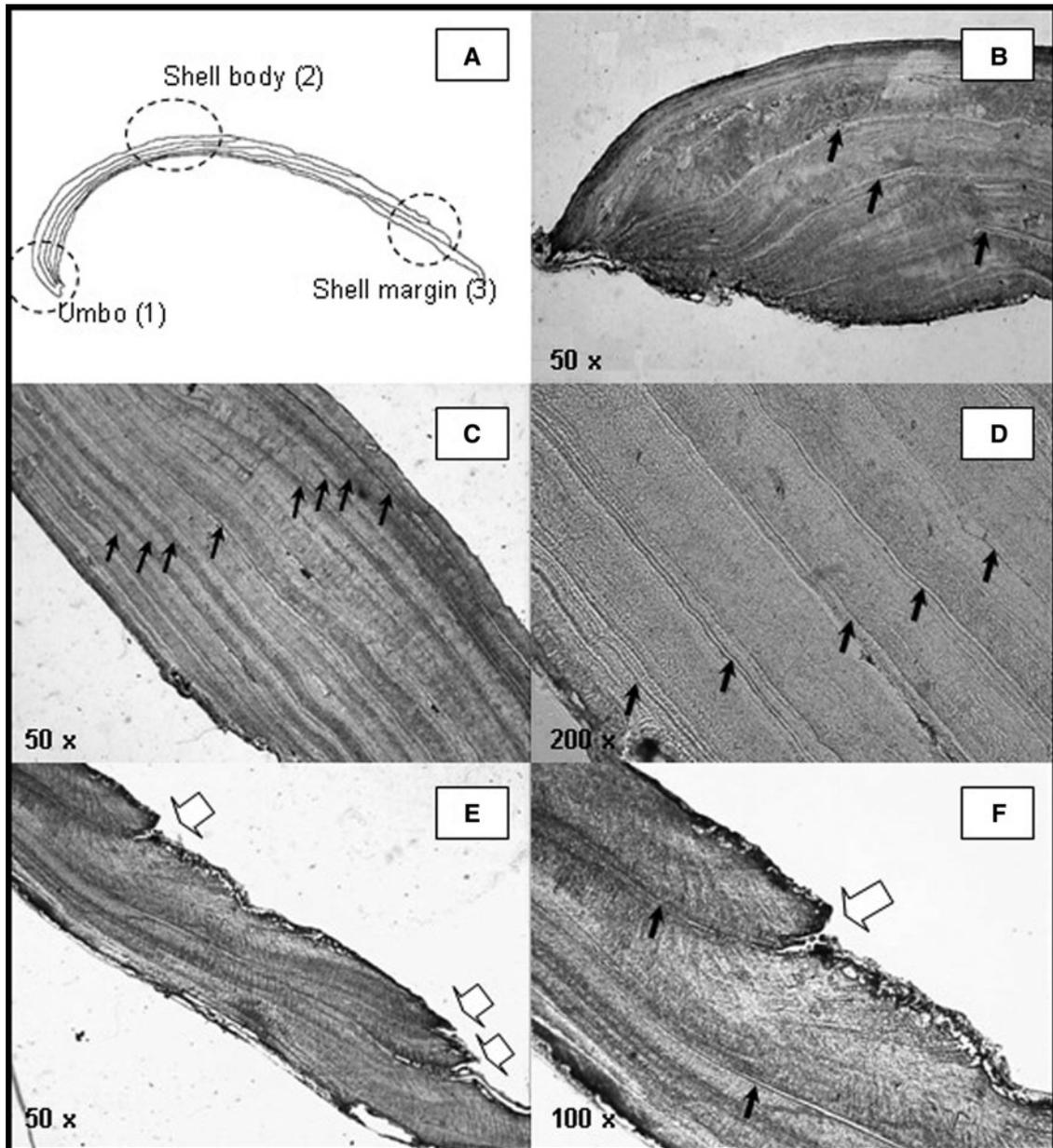


Fig. 3. (A) Scheme of the shell cross section of *T. plebeius* and acetate peels from (B) umbo, (C, D) body shell, (E, F) shell margin showing the internal growth bands all the way along a cross shell section (black arrows: translucent growth bands) and the point where translucent growth bands cross the outer shell layer to form an exterior ring on the shell surface (white arrows: exterior rings).

A von Bertalanffy model with $L_{\infty} = 67.60$ mm (95% CI = 64.55; 70.64), $k = 0.181$ year⁻¹ (CI = 0.142; 0.218) and $t_0 = -0.77$ (CI = -1.46; -0.08; $N = 626$) described individual growth in the whole population best (Figure 4). The oldest animal found was 27 years old.

The comparison of the von Bertalanffy parameters from the three intertidal levels (Table 2), showed lower L_{∞} at LIL than at MIL and HIL, lower k at MIL than at LIL and HIL, and higher t_0 at LIL than at MIL (Likelihood ratio test, $P < 0.05$; Table 3). The maximum age was higher at LIL (27 years old) than at MIL and HIL (23 years old).

Timing of growth band formation

From the 60 individuals introduced in the tagging-recapture experiment only 31 survived after one year not showing

individual migration across intertidal levels. Analysis of all surviving individual confirmed that one translucent growth band and one opaque growth band were formed each year. The Sr/Ca ratio ranged from 1.55 to 3.69 mmol mol⁻¹ along the measurement transect, with higher values located at the translucent growth bands (mean = 2.66; SD = 0.34 mmol mol⁻¹) compared with the samples from the opaque bands (mean = 2.31; SD = 0.36 mmol mol⁻¹) (t -test₁₁₈ = 2.92; $P < 0.05$; Figure 5).

DISCUSSION

The population of *Tagelus plebeius* from Mar Chiquita coastal lagoon consisted of individuals of up to 27 years old, with shells up to 77.93 mm length. Comparison of density and

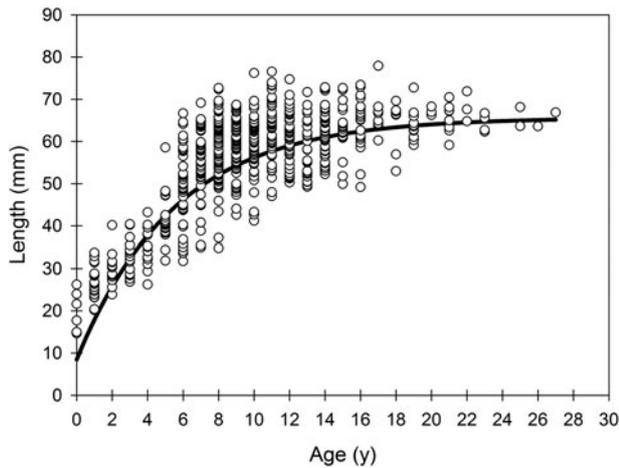


Fig. 4. Size-at-age data and corresponding von Bertalanffy growth curve in *Tagelus plebeius* from Mar Chiquita coastal lagoon.

growth parameters and maximum age between intertidal levels showed higher density, growth rate k , t_0 and maximum age and lower L_∞ at LIL than at MIL, associated with no difference in density and age between MIL and HIL.

Higher density of *T. plebeius* are commonly associated with muddy sediments of high organic content (e.g. Holland & Dean, 1977a; Abrahão & Amaral, 1999; Lomovasky *et al.*, 2006; this study), while populations associated with sandy and muddy-sandy sediments show lower densities (Abrahão *et al.*, 2010; de Farias & Rocha-Barreira, 2012). The sediment characteristics could be an indicator of environmental stability and food availability for suspension feeding species, which are facilitated by fine sediments and high OMC (da Silva *et al.*, 2015). Similarly, a higher growth index was associated to finer sand but higher OMC in different localities from Brazil (da Silva *et al.*, 2015). The sediment at all sites sampled in the present study was composed of >10% silt-clay, reaching 64% in some areas. Thus, the whole tidal flat is composed of sandy-muddy and muddy sediments such as described at North Inlet estuary, South Carolina (33°20'N 79°10.0'W, USA) where these more stable sediments facilitate *T. plebeius* (Holland & Dean, 1977a).

This study showed that *T. plebeius* has a pattern of alternating broad opaque and narrow translucent growth bands observed in internal shell cuts under stereoscopy and acetate peels under microscopy, which represent alternating periods of fast and slow shell growth respectively. Elevated Sr/Ca ratios along a shell coincide with translucent bands formed during winter as confirmed by our annual field experiment. This inverse relationship between Sr/Ca ratios and water temperature may render Sr/Ca a suitable indicator of the seasonal formation of growth bands in *T. plebeius*, as found in some further species with aragonite shells (Dodd, 1965; Surge &

Table 3. Results of Likelihood ratio test for pair-wise comparison for k , L_∞ and t_0 parameters between different intertidal levels.

Intertidal levels	H_0	Likelihood ratio test	
		$\chi^2_{(df=2)}$	P-value
Low-medium	$L_{\infty 1} = L_{\infty 2}$	9.93	0.0016*
	$k_1 = k_2$	7.94	0.0048*
	$t_{01} = t_{02}$	4.49	0.0340*
Low-high	$L_{\infty 1} = L_{\infty 2}$	4.07	0.0430*
	$k_1 = k_2$	1.39	0.2372
	$t_{01} = t_{02}$	0.69	0.4040
Medium-high	$L_{\infty 1} = L_{\infty 2}$	3.38	0.066
	$k_1 = k_2$	4.22	0.040*
	$t_{01} = t_{02}$	3.31	0.069

Asterisks indicate a significance of $P < 0.05$.

Walker, 2006), but not in all species analysed so far (see Palacios *et al.*, 1994; Freitas *et al.*, 2005; Gillikin *et al.*, 2005; Schöne *et al.*, 2011).

The maximum lifespan of 27 years in the recent Mar Chiquita population is much higher than values reported for fossil shells from the same location (8 years, Isla & D'Andrea, 1993) and from different sites in Brazil, below 3 years at Enseada Beach (23°43'S 45°25'W) in São Sebastião (Abrahão *et al.*, 2010), and at Camaroeiro Beach (23°S 45°W) in Caraguatatuba Bay (da Silva *et al.*, 2015). However, those studies evaluated growth rate and maximum age using shell size frequency analyses (Abrahão *et al.*, 2010; da Silva *et al.*, 2015) and external growth rings (Isla & D'Andrea, 1993). Both methods are highly prone to underestimate age in long-lived species where annual growth increments may become quite small. In such cases, analysis of internal shell growth bands is the appropriate approach (Rhoads & Lutz, 1980; Richardson, 2001). Hence, only a proper re-analysis of the shells used in the previous studies will show whether we are dealing with an increase of maximum lifespan with decreasing ambient temperature, as observed in other bivalve species (e.g. Lomovasky *et al.*, 2008, 2011), or with a distinct underestimation of individual age in the previous studies. Although the difference between our analysis and those previously reported may lead to the hypothesis of changes in growth rate, we believe that it is most likely due to deficiencies of the used techniques.

Processes governing benthic populations along an intertidal gradient in soft sediment substrates had been studied in different systems (e.g. Peterson & Beal, 1989; Nakaoka, 2000; Beal, 2006), in general determining a distribution pattern for bivalve species of higher density and higher shell growth rate in the low intertidal compared with the medium and high intertidal levels (Holland & Dean, 1977b; Marsden & Weatherhead, 1999; Gosling, 2003) related to physiological stress and/or biological interactions. In this sense, *T. plebeius*

Table 2. Parameters of the general von Bertalanffy growth function with confidence limits (CI) at alpha 0.05 in *Tagelus plebeius* from the low, medium and high intertidal levels.

Intertidal level	L_∞ (mm) (CI)	k (y^{-1}) (CI)	t_0 (y) (CI)	n	L_{max} (mm)	Age_{max}
Low	64.96 (62.96; 66.97)	0.214 (0.167; 0.262)	-0.20 (-1.04; 0.64)	229	76.23	27
Medium	73.96 (65.40; 82.51)	0.131 (0.081; 0.180)	-1.51 (-2.63; -0.39)	159	77.93	23
High	68.1 (65.11; 71.09)	0.184 (0.147; 0.221)	-0.585 (-1.204; 0.035)	238	72.67	23

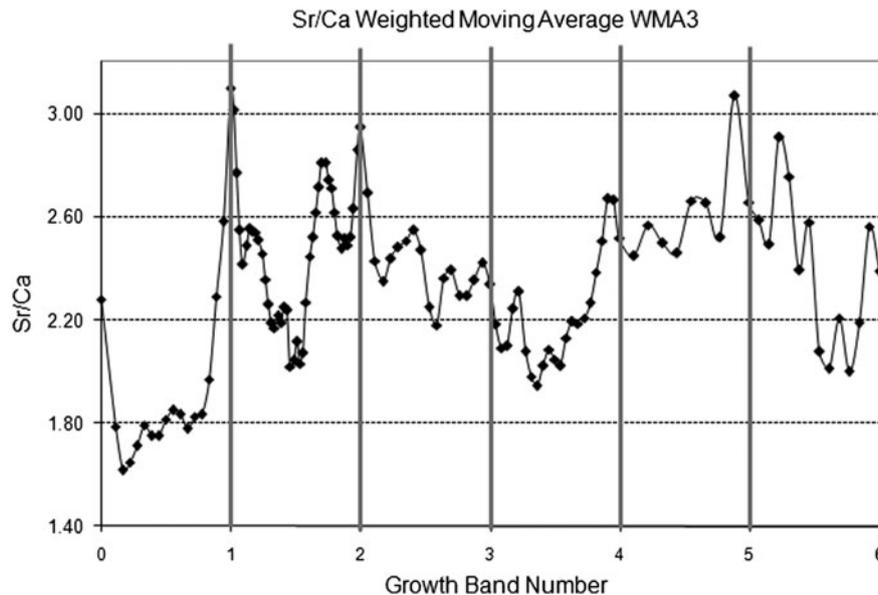


Fig. 5. Analysed Sr/Ca ratios from an individual of *Tagelus plebeius* 6 years old related to the position of translucent growth bands.

showed higher density at LIL than at MIL and HIL and this was correlated with higher percentage of OMC and muddy sediments at LIL (Lomovasky *et al.*, 2006 and this study). Similar results were found in the North Inlet estuary located near Georgetown, South Carolina (33°20'N 79°10'W) with higher density of *T. plebeius* in low intertidal (<200 ind m⁻²) and low density in the high intertidal (<5 ind m⁻²) (Holland & Dean, 1977a), and in other filter feeder bivalves inhabiting intertidal areas (e.g. Crosby *et al.*, 1991; Kingsley-Smith *et al.*, 2009; Lomovasky *et al.*, 2014). Shell growth displayed a similar pattern across the intertidal, with faster growth at LIL compared with MIL, but no differences was observed between LIL and HIL. Distribution and growth patterns of bivalve species across tidal flats have been related to the level of physiological stress and to feeding restrictions that increase from low to high tidal levels (Dame, 1972; Marsden & Weatherhead, 1999; Gosling, 2003). In *T. plebeius* which did not show migration across the intertidal (Holland & Dean, 1977b; this study), this hypothesis could explain the density patterns found (higher at LIL than at HIL) in part by differential adult mortality and/or survival of recruits. However, shell growth rate is higher both at HIL and LIL compared with MIL, which leads to the belief that other, yet unknown factors are likely to play a role here.

Biological interactions such as predation (e.g. Bartol *et al.*, 1999; Bologna & Heck, 1999; Nakaoka, 2000), competition (e.g. Peterson & Beal, 1989; Cognie *et al.*, 2006) and/or parasitism (e.g. Lim & Green, 1991; Taskinen, 1998) can also affect bivalve distribution and size. Different biological interactions affect *T. plebeius* shell growth (e.g. with crabs, parasites, predators: Lomovasky *et al.*, 2005, 2006; with salt marsh plants: Addino *et al.*, 2015). In this sense, in the Mar Chiquita coastal lagoon the co-habiting of bivalves with the crab *Neohelice granulata* showed that this crab negatively affects the morphology and growth of *T. plebeius* differentially across the intertidal (Lomovasky *et al.*, 2006). Negative effects become stronger toward the low intertidal, where the burrowing and migrating of crabs may disrupt bivalve

feeding and/or may force bivalves to invest more energy into escape movements and burrow rebuilding, thus leaving less energy for growth (Lomovasky *et al.*, 2006). In areas without crabs, there is a strong effect of intertidal level on morphology and growth showing the typical gradient of intertidal distribution, density and growth (see Lomovasky *et al.*, 2006). Thus, the crabs add an additional effect (although with the opposite gradient to the physiological stress); as we did not discriminate areas with and without crabs looking at the system as a whole this particular process was masked in our results. Additionally, a strong predation pressure by the American oystercatcher *Haematopus palliatus* (Bachmann & Martínez, 1999) was observed in the study site. In this case a strong interaction with parasitism by the gymnophallid metacercariae, which increases the bivalves available for predators, was observed in the medium intertidal zone (see Lomovasky *et al.*, 2005; Addino *et al.*, 2010). Thus, the intertidal differences in growth rate are likely to be mediated by the presence of the crabs, parasitism and strong predation causing the slower growth rate at MIL found in this study. In conclusion, we hypothesize that the distribution pattern and razor clam characteristics reflect a response to the combined effects of the physical tidal stress gradient and strong biological interactions.

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