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Author(s): Sandra M. Fiori and M. Cecilia Carcedo

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INFLUENCE OF GRAIN SIZE ON BURROWING AND ALONGSHORE DISTRIBUTION OF THE YELLOW CLAM (*AMARILLADESMA MACTROIDES*)

SANDRA M. FIORI[1,2]* AND M. CECILIA CARCEDO[1]
[1]*Instituto Argentino de Oceanografía, Camino La Carrindanga km 7.5 (8000), Bahía Blanca, Argentina;*
[2]*Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670 (8000), Bahía Blanca, Argentina*

ABSTRACT The yellow clam *Amarilladesma mactroides* (Reeve, 1854), is an intertidal species that prospers mainly on dissipative sandy beaches along the temperate Atlantic coast of South America, from Brazil to Argentina (24–41° S). This large clam is considered a fast burrower, which lives buried in the sediment, migrating seasonally into the intertidal zone. The present study explores the effect of sediment grain size on the burrowing performance of this species, to elucidate the influence of granulometry on the alongshore distribution of the *A. mactroides* population. Laboratory trials were performed with clams of different sizes, to study the influence of grain size on the burial rate. Clam distribution was analyzed along a 32 km coastal fringe whose granulometric composition varies from very fine to coarse sand. The values of the mean burrowing rate index, a measurement of clam mobility, suggest that burrowing is fast to very fast in fine and medium sand and becomes slower toward areas with extreme particle size (very fine and coarse sand). The burial time of *A. mactroides* was positively correlated with shell length: small animals can burrow into substrates that may exclude larger animals. Adults clams burrowed in a very limited range of sand grain sizes. They displayed fastest burial times in grain sizes typical of dissipative beaches, i.e., fine to medium sand. Patchy distribution and density variation of *A. mactroides* alongshore reflect the relation between grain size and burrowing performance: the population is absent in sites with the highest proportion of coarse sands, its density increases in patches with the highest proportion of fine and medium sand and peaks at a site with the highest proportion of fine sand. Results indicate that the discontinuous distribution of *A. mactroides* along its range could be due to a postsettlement process. Clams can potentially recruit on a wide morphodynamic range, but only may thrive in beaches which sand grain size allows them a rapid reburial during migratory and local movements.

KEY WORDS: Mesodesmatidae, clam, burrowing, distribution, grain size, sandy beaches, *Amarilladesma mactroides*

INTRODUCTION

Many of the characteristics of the macroinfauna of exposed sandy beaches are adaptations to an environment dominated by sediment instability and wave action (de la Huz et al. 2002). On intertidal sandy beaches there are no truly sessile animals, and locomotion plays a much larger part in the lives of the animals than it does on other types of shore. A number of different forms of locomotion are in evidence; the one type all sandy beach animals have in common is burrowing (Yannicelli et al. 2002, McLachlan & Brown 2006, Vanagt et al. 2008). Characteristics of the sediment, particularly grain size, have been shown to strongly affect burial time of infauna and in consequence their survival on exposed beaches (Trueman et al. 1966, Trueman & Ansell 1969, McLachlan & Young 1982, Donn & Els 1990, Brown & Trueman 1991, Alexander et al. 1993, Henderson & Richardson 1994).

On sandy beaches the interaction between sediment grain size, beach slope, and wave energy give a continuum of morphodynamic beach types from dissipative to reflective. In general, reflective beaches have harsher conditions—coarser sediments, steeper slopes and shorter swash periods—than dissipative beaches (Short 1996, McLachlan & Dorvlo 2005). Some species are capable of maintaining populations across the whole morphodynamic spectrum; however, harsh conditions of reflective sandy beaches may exclude very sensitive species (Nel et al. 2001, Defeo & McLachlan 2005). Several studies have focused on the direct importance of grain size on the burrowing behavior of bivalve habitat generalists, which live in a broad spectrum of morphodynamic beaches (Alexander et al. 1993, Nel et al. 2001, de la Huz et al. 2002, Lastra et al. 2004). The influence of granulometric features on selective habitat species, restricted to dissipative beaches, is little explored.

The yellow clam *Amarilladesma mactroides* (Reeve, 1854) is a sensitive species that thrives mainly on dissipative sandy beaches along the warm temperate Atlantic coast of South America, form Brazil to Argentina (24–41° S). Although before the mid 90s this species was the dominant suspension feeder of intertidal macrofaunal assemblages on dissipative sandy beaches, at present it is critically endangered as a consequence of recurrent mass mortality events (Fiori & Cazzaniga 1999, Fiori et al. 2004a). This large clam is considered a fast burrower, which lives buried into the sediment and seasonally migrates into the intertidal zone. In winter, adults can be found near low tide, whereas in spring they start migrating to the high tide zone where they will remain during the summer. During fall clams begin the migration to their overwinter position (Coscarón 1959, Fiori et al. 2004b). Clams can also engage in local movement throughout the year into the swash zone, without change their seasonal position (Olivier et al. 1971).

Thompson and Sanchez De Bock (2009) carried out a study to analyze the influence of individual environmental variables and composite indices (values that integrate the effect of several physical factors related to coastal processes like energy, texture, sediment, morphology, etc.) on the density and distribution variations of *Amarilladesma mactroides*. They conclude that individual physical variables such as sediment grain size appear to be better predictors of spatial and

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*Corresponding author. E-mail: sfiori@criba.edu.ar

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temporal fluctuations of clam density, than composite indices. There is no experimental evidence to confirm a cause–effect relationship between sand grain size and alongshore distribution of the yellow clam. This study examines the effect of grain size, under laboratory conditions, on the burrowing performance of *A. mactroides* and on its distribution alongshore to establish whether the variability of clam density on dissipative beaches is related to the granulometric composition of the sand.

MATERIALS AND METHODS

Burrowing Performance

During December 2009 and April 2010, individuals of *Amarilladesma mactroides* (9–75 mm) were collected by hand digging in the intertidal fringe of a dissipative sandy beach (Monte Hermoso, Argentina: 38° S 61° W) (Fig. 1). Beach sands were obtained from the area were clams were collected. This native sediment was sorted with sieves into three grades, following the Wentworth scale: very fine (fraction retained between sieves 0.062–0.125 mm), fine (0.125–0.250 mm), medium (0.25–0.50 mm), coarse (0.5–1.0 mm), and mix sediment (similar to native sediments).

Specimens were maintained in tanks with native sediment and water, and under constant aeration until they were used in the tests. Burrowing times of clams were measured in the laboratory in a 10 l bucket (22 cm in diameter) with 15 cm of sand and 15 cm of water column. Seawater temperature during the burrowing trials varied between 19°C and 22°C. Individual clams were timed in seconds with a stopwatch; from the initiation of burrowing (the effective penetration of the foot into the substrate) until the posterior end of the valves was level with the sand surface. A prerequisite for the valid measurement of burial time was continuous burial by the individual without resting. In each trial 60 clams were used to cover a broad range of sizes (9–75 mm). When individuals become sluggish during experiments, burrowing was induced by means of stirring the water. Burrowing test were done within 24 h of clam collected, clams were removed from the sorted sands immediately after the burrowing test. Only one burrowing test was performed with each individual to avoid the effect of previous treatments (Zar 1996).

For each specimen used, the maximum length of the valves to the nearest 0.01 mm was measured with a digital caliper and the weight wet mass was measured to the nearest 0.001 g and was used to construct a burrowing rate index (BRI) (Stanley 1970), which is considered independent of size:

$$\mathrm{BRI} = \frac{\text{wet mass (g)}^{0.33}}{\text{burrowing time (s)}} \times 100.$$

Size differentiation into adults and juvenils for BRI was based on a shell length larger and less than 25 mm, respectively.

Estimation of the relationships between burrowing time and shell length of bivalves, in the five kind of sand tested, were performed by linear regression analysis (least squares method). Normality of the data and variance equality were tested using a Kolmogorov–Smirnov analysis and Levene test, respectively. The regressions were compared using an analysis of covariance and *a posteriori* Tukey test.

Distribution Alongshore

Sampling was made in July 2009 along intertidal transects perpendicular to the shoreline. Twenty six transects were located at intervals of 1.5 km to cover the whole beach length. The material contained in a quadrat of 50 × 50 cm was dug out up to 40 cm depth every 10 m along each transect, from low tidal until at least two consecutive sampling units yielded no clam. All clams retained after sieving through a 0.50 cm mesh were measured (total shell length) with a digital caliper (0.01 mm). Quantitative data are expressed in abundance as individuals per meter strip transect (IST; ind/m), which is a good measure of the

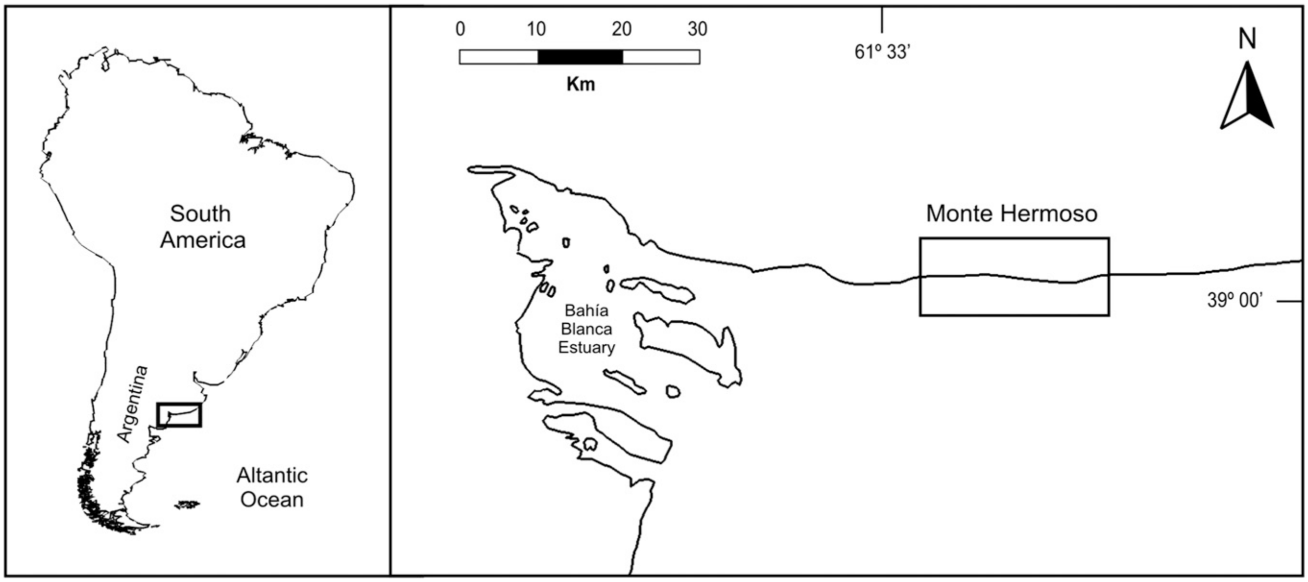

Figure 1. Map of the study area showing the location of Monte Hermoso beach (Buenos Aires, Argentina).

TABLE 1.

Burial time (BT) in seconds and burrowing rate index (BRI) of *Amarilladesma mactroides* for the five kind of sand selected.

	Very fine sand	Fine sand	Medium sand	Coarse sand	Native sediments
N	50	60	60	30	60
Mean BT (s)	62.10 ± 17.99	36.66 ± 18.28	39.92 ± 18.32	150.22 ± 211.89	42.10 ± 17.99
Minimum (s)	23.03	6.31	11.53	29.65	13.03
Maximum (s)	98.06	68.03	77.55	761.41	78.06
Mean BRI	2.85 ± 1.23	7.36 ± 2.08	5.69 ± 0.98	2.02 ± 0.98	4.02 ± 2.51

N, number of individuals.

total population size independent of the beach type (Defeo 1996). A sediment sample was taken near the site of field data collection. Sand samples were washed, dried in an oven at 100°C, homogenized manually, weighed, and sieved using traditional techniques of mechanical agitation. A series of standard Tyler sieves of decreasing mesh size was used to obtain the proportion of the main sand fractions in the Wentworth scale (coarse, medium, fine, and very fine sand).

RESULTS

Burrowing Performance

Under laboratory conditions, burrowing by large clam (greater than 40 mm) had to be induced by aerating/stirring water, whereas in all small clams (less than 40 mm) burrowing start in calm conditions.

Burrowing performance of *Amarilladesma mactroides* changed with changes in sediment particle size. Burial times (BT) ranged from 6.31 to 761.41 s. The shortest mean BT was obtained in fine and medium sand and there was an increased in BT in both the very fine and coarse sand. Some clams (N = 40) stopped moving few seconds after of initiates burial movements. This behavior was only observed in clams over 40 mm in trials with very fine or coarse sediments (these trials were not included in the analysis). In trials with coarse sediments, 50% of clam were successfully managed to bury (22 juveniles and 8 adults); the remaining clams, although started burying movements, stopped to rest before their bodies were fully covered. In very fine sand, 10 clams (adults) were never able to completely bury (Table 1). The BRI values for all clams, without discrimination between juveniles and adults, ranged from 2.02 ± 0.98 to 7.36 ± 2.08. Table 2 shows that juveniles burrowing faster than adult clams given that BRI values decreased with increasing shell size. In all trials BRI was highest, and thus burrowing fastest, in fine sand followed by medium and native sand.

Burial time was also related with shell length. Linear regressions of burrowing rate against shell length were significant in all cases ($P << 0.001$), increase in burial time with increasing shell indicated that larger animals take more time to achieve complete burial (Table 3; Fig. 2). The burial time–length relationship showed significant differences between all experiment (analysis of covariance $F_{(3,\ 230)} = 10.60$; $P << 0.01$). There were significant differences in the slope of the regressions lines between very fine versus fine, medium, and native sediments. No significant difference were found between slopes of the regressions lines between fine, medium, and native sand, but there were significant difference in the elevations, i.e., clams burrowed significantly faster in fine sand than others sediments. Coarse sand experiment was excluded of this comparison because only juveniles were able of burrowing (Table 4).

Distribution Alongshore

The 26 transects that were sampled have different proportion of very fine to coarse sand. The yellow clam was found on 24 of the 26 transects. The population abundance increased with increasing sediment grain size to peak at 2248 ind/m on the transect 11 (modal grain size 0.250 mm—textural group fine sand) and decreased toward sediment with modal grain size more than 1 mm (coarse sand) or less than 0.125 (very fine sand) (Fig. 3).

DISCUSSION

Most research on locomotory behaviors of macroinfauna has considered reactions to external stimuli as determinants of the timing to emerge from the sediment at the appropriate

TABLE 2.

Mean burrowing rate index (BRI) of *Amarilladesma mactroides* in the five kinds of sand tested.

Sand size	BRI juveniles	BRI adults
Very fine	3.02 ± 0.95	2.51 ± 1.78
Fine	7.87 ± 2.30	6.85 ± 1.78
Medium	5.87 ± 0.64	5.47 ± 1.17
Native	5.16 ± 1.28	4.03 ± 0.64
Coarse	2.67 ± 0.98	1.10 ± 0.40*

* Correspond to eight individuals.

TABLE 3.

Linear regressions of burial time (BT) in terms of shell length (L) in the five kinds of sand tested.

Sand size	BT (s) versus L (mm)	R^2	F	Range (mm)
Very fine	BT = 2.13 L – 3.92	0.48	128.17**	11.02–61.03
Fine	BT = 0.42 L – 0.44	0.62	98.91**	14.09–77.77
Medium	BT = 1.05 L – 3.24	0.85	324.46**	10.92–62.87
Coarse	BT = 2.19 L – 5.75	0.59	65.61**	18.90–30.21
Native	BT = 1.25 L – 2.08	0.78	108.57**	16.96–71.95

** $P < 0.01$.

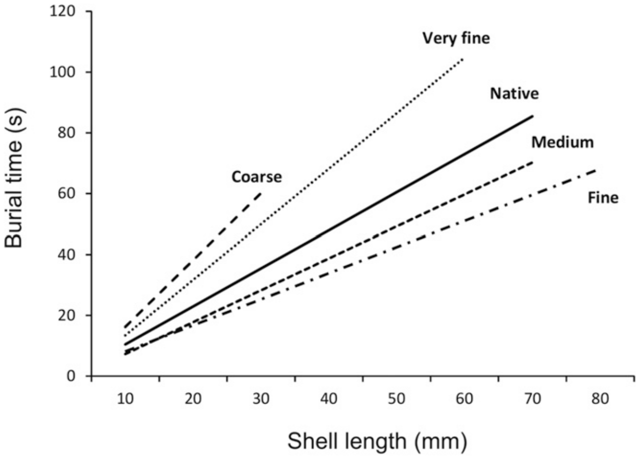

Figure 2. Burial time as a function of shell length of *Amarilladesma mactroides* in the five kinds of sand tested.

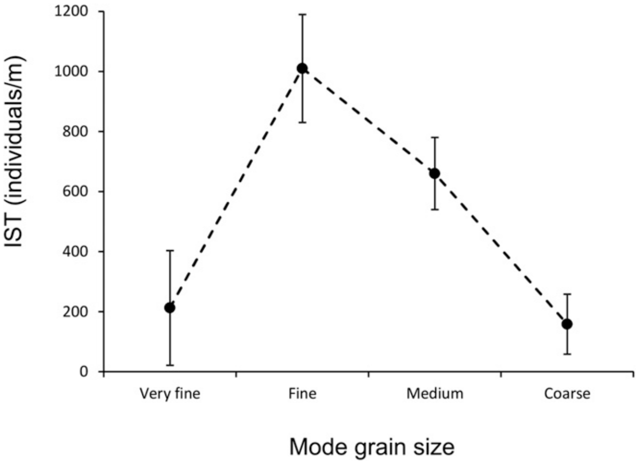

Figure 3. Population abundance of *Amarilladesma mactroides versus* mode grain size in Monte Hermoso beach.

moment (Forward 1986, Warman et al. 1993, Scapini et al. 1997, Yannicelli et al. 2001). In bivalves it has commonly been observed that disturbance acts as a stimulus to initiate burrowing (Trueman & Ansell 1969, Trueman 1971, Ellers 1995). In this study, larger clams (greater than 40 mm) become sluggish during burrowing rate experiments and had to be induced to burrow by aerating/stirring water (simulating swash conditions), whereas small clams (less than 40 mm) burrowed in calm conditions. According to Masello and Defeo (1986), the sexual maturity in this species is reached at age 1, when the mean shell size is near 40 mm. The results of this study show a differential response of each population component to the dynamic conditions experienced in the swash zone. Sexually mature adult clams seasonally migrate into the intertidal fringe; this massive movement is triggered by swash stimulus when water temperature and correlated factors (chlorophyll concentration, gonadal development) are suitable (Olivier et al. 1971). They ride the flow from waves, migrating shoreward during rising tides (reaching their summer location), and seaward during falling tides (winter location). In contrast, small clams do not show seasonal migration and are located near the surface of the sediment (for reasons related to the length of their siphon) and so are unearthed more frequently than adults and appear to be dependent on passive transport (Coscarón 1959, McLachlan et al. 1996, Fiori et al. 2004b). The ability of small clams to burrow even in the absence of a swash stimulus is likely a defense mechanism to avoid predator pressure and desiccation.

TABLE 4.

Significance level (*P* value) of the Tukey's *post hoc* comparison indicating differences in intercept of burial time versus shell length regressions of *Amarilladesma mactroides* individuals between different sands.

	Fine	Medium	Native
Very fine	Different slope	Different slope	Different slope
Fine		0.0033 (*P* value)	0.0007 (*P* value)
Medium			0.0025 (*P* value)

The results of the present study show that the burrowing abilities of the yellow clam are clearly affected by sediment grain size. The mean BRI is a measurement of clam mobility; Stanley (1970) reported BRI values ranging from 0.01 to 20 and classified values of 2–5 as rapid burrowers. In this study, BRI values ranged between 2 and 7, suggesting that burrowing is fast to very fast in fine and medium sand (optimum grain size) and slower toward the extremes (very fine and coarse sand). McLachlan et al. (1995) reported BRI values of *Amarilladesma mactroides* in the natural environment to range between 4 and 6 for adults and juveniles, similar to the results found in the present study in native sediment. The BRI values of this species indicate that the clams can burrow fast in a very limited range of sand grain sizes, like substrate specialist species (*sensu* Alexander et al. 1993) in contrast with other beach clams, called sensitive species, which showed optimal burrowing in a wider range (Dugan et al. 2000, Nel et al. 2001, de la Huz et al. 2002).

The burrowing rate of *Amarilladesma mactroides*, as measured by burial time or BRI, changes through its ontogeny. Under laboratory conditions small clams can burrow into substrates that may exclude larger clams and are expected to be successful in colonizing most beach environments with a wide range of substrates. The patchy distribution of *A. mactroides* along the studied shore appears to reflect the effects of grain size on burrowing performance: the population is absent from coarse sediment, its abundance increases in patches with fine and medium sand and peaks in the patches with a high proportion of fine sediment. The absence of *A. mactroides* on coarse-grained beaches could therefore be due to a postsettlement process, i.e., the clams may establish themselves on intermediate or reflective beaches but subsequently become more vulnerable to predators as their burrowing time increases along their ontogeny.

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