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Attachment features of mytilids in ecosystems with mobile substrate: *Brachidontes rodriguezii* in San Antonio Bay (Patagonia, Argentina)

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The force required to dislodge mussels from the substrate is known as attachment strength. This feature has been mostly studied in mytilids inhabiting the intertidal of consolidated rocky substrates, whereas it has been less studied in sedimentary substrates. The aim of this study was to evaluate the attachment strength and the number of byssal threads of Brachidontes rodriguezii *in two sites with mobile substrates in San Antonio Bay, Argentina [Punta Verde (PV) and Punta Delgado (PD)]. PV has relatively higher current velocities and coarser grain size than PD. Along coastal line transects at two different levels of the mid-intertidal of each site, the attachment strength was measured. The number of byssal threads in collected mytilids and the weight of the sediment adhered to them were recorded in the lab. The attachment strength, the number of byssal threads and the sediment adhered to the byssus differed significantly between levels and sites. Mytilids from the mid-level of both sites where the density was relatively lower, had a significantly greater number of byssal threads and higher weight of sediment adhered. This study reveals that a high amount of coarse sediment adhered to the byssus affects the attachment strength of* B. rodriguezii *in ecosystems relative to unstable substrates. We underline the importance of mobile substrates in understanding attachment features (attachment strength and byssal threads) of mytilids in this unstable ecosystem.*

Keywords: *Brachidontes rodriguezii*, attachment strength, byssal threads, mobile substrate

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INTRODUCTION

The persistence of mussels in intertidal environments is, primarily, the result of their ability to adhere byssus to the surrounding substrate. The byssus is composed of several extracellular, collagenous threads secreted by pedal glands (Price, 1983; Bell & Gosline, 1996, 1997). The bond between the byssus and the substrate is known as attachment strength (Stephens & Bertness, 1991; Bertness *et al*., 2006; Caro *et al*., 2008; Babarro & Abad, 2013; Seguin-Heine *et al*., 2014), or tenacity (Denny, 1987; Bell & Gosline, 1997; Carrington, 2002a; Moeser *et al*., 2006). Tenacity has been better defined as the force required to dislodge a mussel from the substrate divided by the shell planform area of the individual (N m^{-2}) (Bell & Gosline, 1997), while attachment strength is the force required to dislodge a mussel without correction for a size effect. Tenacity and attachment strength, as well as the environmental and biological factors affecting them, have been mostly studied in mytilids inhabiting stable substrates, such as rocky intertidal environments, but not for sessile species living in sedimentary, less stable substrates (wa Kangeri *et al*., 2014).

Among the environmental factors affecting tenacity and attachment strength in rocky shores, hydrodynamic stress has been the most studied effect not only for mytilids in natural beds but also in suspended culture (Lahance *et al*., 2008). In rocky shores, under hydrodynamic stress, mytilids increase the number of their byssal threads to enhance their tenacity (Bell & Gosline, 1997; Carrington, 2002a) or their attachment strength (Zardi *et al*., 2007). However, in laboratory flume experiments, thread production per individual of *Mytilus* declined with increased flow speed in the flume (Moeser *et al*., 2006; Carrington *et al*., 2008; Babarro & Carrington, 2013). On the other hand, it is unclear whether byssal production is related to hydrodynamic stress in environments with sedimentary substrates. For example, wa Kangeri *et al*. (2014) evidenced that the number of byssal threads in mussels is not related to the hydrodynamic gradient (i.e. increasing shear stress) of sedimentary coasts of the Western Dutch Wadden Sea. However, these authors also showed that, under mechanical perturbation produced in laboratory conditions, mussels increased the number of byssus threads, suggesting that additional factors could be interacting with the hydrodynamic stress. Sea surface temperature (Young, 1985; Zardi *et al*., 2007), salinity (Young, 1985), sediment weight (reviewed by wa Kangeri *et al*., 2014), food availability

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(Clarke, 1999; Zardi *et al.*, 2007), seasonality (Carrington, 2002a; Moeser *et al.*, 2006) and ocean acidification (Carrington *et al.*, 2015) also affect the byssogenesis and therefore may influence the attachment strength (Zardi *et al.*, 2007) and tenacity (Carrington, 2002a; Moeser *et al.*, 2006).

The degree of aggregation of mussels also affects tenacity: individuals of *Mytilus californianus* and *Mytilus trossulus* within beds have a lower tenacity than solitary individuals (Bell & Gosline, 1997). Thus, the condition of living in beds may reduce flow velocities (Carrington *et al.*, 2008), and the degree of aggregation may promote the production of lower numbers of byssal threads (Bell & Gosline, 1997). Other biological factors that may affect the tenacity (or attachment strength) are the thickness of the byssal threads (Bell & Gosline, 1997; Zardi *et al.*, 2007; Babarro & Fernández Reiriz, 2010; Babarro & Carrington, 2013), material properties of the byssal threads (Moeser *et al.*, 2006), the reproductive condition (Carrington, 2002a; Zardi *et al.*, 2007), which also affects the byssogenesis (Babarro & Fernández Reiriz, 2010; Hennebicq *et al.*, 2013), individual size (Bertness *et al.*, 2006; Babarro *et al.*, 2008), predation pressure (Nicastro *et al.*, 2007; Caro *et al.*, 2008; Garner & Litvaitis, 2013b) and the presence of conspecifics (Bell & Gosline, 1997).

In sedimentary environments, mytilids prefer to adhere to big shell debris (>5 mm), conspecific shells (wa Kangeri *et al.*, 2014) and gravel material (Young, 1983a). The adhesive strategy is a selective process driven by physical perturbation and mediated by bed densities across a hydrodynamic gradient (wa Kangeri *et al.*, 2014). Although interest in gravel and mixed sand and gravel beaches has increased in recent years, processes on coarse-grained beaches are less well understood than on fine sand beaches (Horn & Walton, 2007) or soft-bottom coasts. Therefore, the aim of this study is to evaluate the attachment strength in environments with less stability to provide additional insights into mytilid responses to stressful environmental conditions. To this end, we assessed the attachment strength and the number of byssal threads of the mytilid *Brachidontes rodriguezii* (d'Orbigny 1846) in relation to mussel density, water flow, grain size and weight of the sediment adhered to the byssus in two areas of mobile sedimentary substrate in Patagonia, Argentina.

MATERIALS AND METHODS

Study sites

The study was carried out in San Antonio Bay (40°45′S 64°56′W) located at the NW of San Matías Gulf (northern Patagonia, Argentina: Figure 1). The region presents a semidiurnal tidal regime with maximum amplitude of 9 m. The tidal currents are weak in the inner sector of the bay (<0.5 m s^{-1}), whereas the turbulence increases and currents reach 2 m s^{-1} in the outer zone near the mouth of the bay (Aliotta *et al.*, 2000). Mean seawater temperatures vary between 7°C in winter and 24°C in summer and salinity within the bay is higher than in the adjacent areas (up to 36 ppt, Ocampo & Storero, 2007) due to its high evaporation rate (Piola & Scasso, 1988). The San Antonio Bay is characterized by sediments with a wide range of grain sizes (silt, sand, gravel-including granule, pebble and cobble) that cover the tidal channel sides. In this area we selected two mussel beds of the mytilid *Brachidontes rodriguezii*, Punta Verde (PV) and Punta Delgado (PD) (Figure 1), separated 2.3 km between each other. PV is located on the entrance of a main channel of the bay and has relatively higher current velocities and coarser grain size than PD, which is located on a secondary channel. This mytilid, which is of the epibyssate morph, occurs in the mid-intertidal as a mono-layer assemblage with variable density between vertical levels, being relatively lower on the mid-level (ML, 145 and 440 ind. m^{-2} on average, in PD and PV respectively) than on the lower one (LL, 2480 and 4352 ind. m^{-2} on average, in PD and PV respectively) (Salas *et al.*, 2013).

Attachment strength, byssal threads and sediment adhered to byssus

In October 2011, sampling transects to collect mussel samples and measure the attachment strength were established parallel

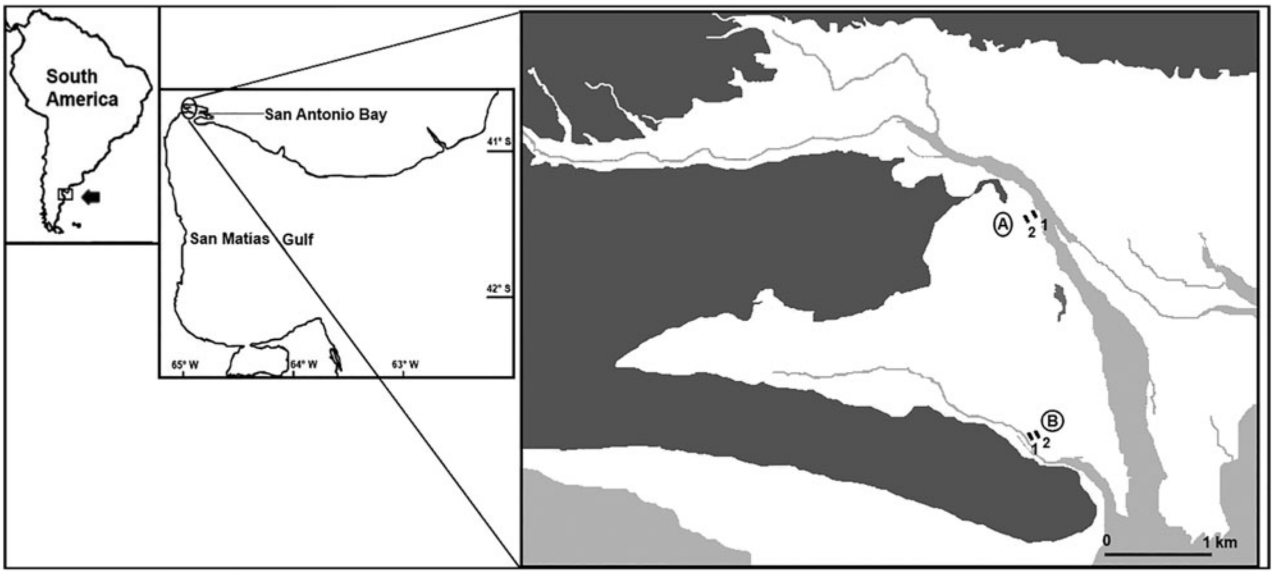

Fig. 1. Location of the two study sites in San Antonio Bay: Punta Verde (A) and Punta Delgado (B). Right: Image of the main channels (light grey) at low tide, showing the transects used to measure the attachment strength in the low level (1) and mid-level (2) of the mid-intertidal (white) of both sites.

to the water line (100 m) at two tidal levels, Mid-Level (ML) and Lower-Level (LL). This was done at both study sites (PD and PV). In this study we defined the attachment strength as the maximum force required to dislodge each mussel with their byssus and attached sediment from the substrate. In our case, the substrate consists of a mix of mussels, shells and other faunal debris, and sediments with a wide range of grain sizes (silt, sand and gravel material). Along each transect, the attachment strength (in N) of 70 randomly selected individuals was recorded. Representative individuals of the individual size range (8.93–32.35 mm) in natural beds of *B. rodriguezii* were sampled. Following a method similar to that proposed by Denny (1987), we recorded the perpendicular force required to dislodge each mussel from the substrate with a Pesola® spring scale (precision ± 0.3%). The spring scale was tied to the metal clamp by a fine rope and each mussel was surrounded by the metal clamp (Appendix 1). The mussels which recorded attachment strength were collected by hand (including the sediments adhered to their byssus) and then stored at −20°C until analysis. In order to establish any relationship between the attachment strength and the shell planform mussel area, the shell height (dorsal-ventral), and width (lateral) were measured with vernier calipers to the nearest 0.1 mm. Shell height and width were used to calculate the shell planform area (cm^2), which was approximated to an ellipse (with shell height and width as major and minor axes, respectively; Bell & Gosline, 1997). From each stored mussel all byssal threads were counted under a binocular microscope and the total dry weight of sediments adhered to the byssal threads weighed to the nearest 0.001 g.

Environmental data

To characterize the substrate granulometry at the two levels of the mid-intertidal in both sites, independent 100 m-transects (within the same mussel patch) were followed parallel to the previous ones used to collect sediment samples. Along each transect, core samples were collected (5 cm depth, 10 cm diameter) each 10 m. Sediment subsamples of 100 g from the core samples were dried (70°C, 72 h) and then sieved to estimate granulometric fractions and mean grain size using the software GRADISTAT version 6.0 (http://www.kpal.co.uk/gradistat.html).

To quantify relative differences of water flow between mid-intertidal levels in both sites, we measured the dissolution rate of block plasters (clod cards of calcium sulphate). The block plasters dissolve at a rate proportional to water velocity, and thus represent an integrated measure of flow (dissolution block technique; Thompson & Glenn, 1994). Each block plaster was 2.5 cm in height, 4.0 × 3.5 cm in the bottom surface and 3.3 × 2.7 cm in top surface, and their sides were coated with polyurethane so that only the top surface could erode. Each block plaster (initial weight = 37.16 ± 3.05 mg) was glued with epoxy putty to a piece of plastic mesh (18 × 7 cm^2) and fixed to the substrate in each level (N = 10 units per level) for 48 h. The total mass loss dissolved per hour (in percentage) was calculated by weighting the block before and after exposing it on the intertidal.

Statistical analysis

The relationship between the attachment strength and the shell planform area was fitted to linear and non-linear models, and the best one was selected according to the coefficient of determination (r^2). Two-way ANOVAs were used to assess variations in attachment strength, number of byssal threads, total dry weight of sediment adhered to byssal threads, the total mass loss (%) of the block plaster and grain size, using levels and sites as main factors. To meet model assumptions, data of attachment strength and number of byssal threads were square-root transformed, and sediment data (both mean grain size and weight of sediment adhered to byssal threads) were $\log_{10}$-transformed. When significant differences were detected, multiple comparisons were conducted with Tukey tests. All the statistical analyses were performed with InfoStat software (Di Rienzo *et al.*, 2014).

RESULTS

Environmental effects

The two-way ANOVA revealed a site–level interaction on grain size ($F_{1,\ 36} = 21.15$; $P = 0.0001$; Table 1). While the mean grain size did not differ between the low levels of PD and PV ($P > 0.05$), mid-levels of PV and PD showed the highest and the lowest mean grain sizes, respectively (Table 1, Tukey test, $P \leq 0.05$; Figure 3D).

The total mass loss of block plasters was significantly different between levels ($F_{1,\ 36} = 141.61$; $P < 0.0001$) but not between sites ($F_{1,\ 36} = 0.06$; $P = 0.8059$) (two-way ANOVA; Table 1). An interaction effect of sites and levels on the total mass loss of block plasters was found ($F_{1,\ 36} = 23.24$; $P < 0.0001$; Table 1). Low levels showed the highest percentage of total mass loss, whereas mid-levels showed the lowest percentage of total mass loss (Table 1; Tukey test, $P < 0.05$; Figure 4).

Attachment strength, byssal threads and sediment adhered to byssus

The relationship between the attachment strength and the shell planform area of *Brachidontes rodriguezii* in the San Antonio Bay showed a weak linear relationship, explaining only 16% of the variance ($y = 1.05 + 0.15x$) (Figure 2).

The mean (±SE) attachment strength varied between 1.92 ± 0.92 N (LL) and 2.52 ± 0.98 N (ML) in PV, and between 2.10 ± 0.94 N (ML) and 2.24 ± 0.97 N (LL) in PD. There was a site–level interaction effect on the mean attachment strength ($F_{1,\ 276} = 10.81$; $P = 0.0011$; Table 1). This means no independence of the effect of the factor 'site' on the factor 'level', so the interaction itself is the most important effect to interpret. The attachment strength of *B. rodriguezii* from the low level of PV and the two levels of PD did not show significant differences [$P > 0.05$, PV = 1.92 ± 0.92 N (LL); PD = 2.10 ± 0.94 N (ML) and 2.24 ± 0.97 N (LL)], and was significantly higher in the mytilids from the mid-level of PV (Table 1, Tukey test, $P \leq 0.05$; Figure 3A).

The effect of the vertical level on the number of byssal threads also differed between sites (two-way ANOVA interaction effect, $F_{1,\ 276} = 18.69$; $P < 0.0001$; Table 1). The number of byssal threads significantly differed between the low levels of both PD and PV ($P \leq 0.05$, PV = 75.70 ± 48.91; PD = 148.20 ± 98.84) but not in the mid-level of both sites (Table 1, Tukey test, $P > 0.05$; Figure 3B).

Table 1. *Brachidontes rodriguezii*: Two-way ANOVAs showing the effect of site, intertidal level and their interaction on the attachment strength, number of byssal threads, weight of sediments adhered to mytilid byssus, grain size and total mass loss (indicative or the water low (see text for details). Data of attachment strength and number of byssal threads were square-root-transformed, and data of weight of sediment adhered were grain size $\log_{10}$ transformed to meet ANOVA assumptions.

Source	df	Attachment strength			Nr. byssal threads			Wt. sediment adhered			df	Grain size			Total mass loss		
		MS	F	P	MS	F	P	MS	F	P		MS	F	P	MS	F	P
Site (A)	1	0.02	0.18	0.6708	143.46	10.72	0.0012	16.04	41.51	<0.0001	1	0.17	7.56	0.0093	1.9×10^{-4}	0.06	0.8059
Level (B)	1	0.44	3.97	0.0474	1123.16	83.89	<0.0001	13.78	35.67	<0.0001	1	3.4×10^{-5}	1.5×10^{-3}	0.9691	0.45	141.61	<0.0001
A × B	1	1.21	10.81	0.011	250.23	18.69	<0.0001	1.87	4.85	0.0284	1	0.48	21.15	0.0001	0.07	23.24	<0.0001
Error	276	0.11			13.39			0.39			36	0.02			3.2×10^{-3}		

Interestingly, there was also a significant site–level interaction in the weight of sediments adhered to the mytilid byssus ($F_{1,\ 276} = 4.85$; $P = 0.0284$; Table 1). Mytilids from the low level of PV and those of the mid-level of PD had, respectively, the lowest and highest total dry weight of sediment adhered ($P \leq 0.05$), while mytilids from the mid-level of PV and the low level of PD did not differ in sediment weight (Table 1, Tukey test, $P > 0.05$; Figure 3C).

DISCUSSION

Our results suggest that mytilids inhabiting unstable sediment substrates respond to habitat heterogeneity in a complex manner that varied according to the vertical level and mussel bed. The key findings from our study were that: (1) the linear relationship between the attachment strength and the shell planform area was weak; (2) the attachment strength differed significantly between sites and levels; (3) an unclear relationship was found between the attachment strength and the number of byssal threads; (4) the number of byssal threads was higher in mytilids from the upper level than in those from the lower one; (5) the amount of sediment adhered to the byssus at each site was larger in mytilids from the upper level than in the lower one.

We found a small effect of size (shell planform area) on attachment strength (Figure 2) and therefore it was unnecessary to correct the adhesion strength for mussel size effects (tenacity). We recommend performing the analysis of the relationship between size and attachment strength in future studies, in order to be sure for applying corrections in strength measurements.

In rocky shores, the mussel attachment strength has been found to be related to hydrodynamic stress (in terms of current velocities) (Zardi *et al.*, 2007). Even though the attachment strength in mytilids from both rocky and mobile substrates cannot be compared, it is likely that mussel attachment in both intertidal types may be affected by hydrodynamic stress. However, the attachment strength of *B. rodriguezii* in San Antonio Bay may not be explained by the flow velocity, since mussels had the highest attachment strength in the mid-level of PV where flow velocities were lowest (see Figures 3A & 4).

Another factor that could explain the tenacity of mytilids in rocky shores is the number of byssal threads (Bell & Gosline *et al.*, 1997; Zardi *et al.*, 2007). In San Antonio Bay the relationship between the number of byssal threads and the attachment strength was not so clear. In both study sites the higher numbers of byssal threads were found in the mid-level (Figure 3B), which could explain the highest attachment strength, but only for PV and not for PD (Figure 3A). Particularly notable in PV was the higher attachment strength in close connection with a high number of byssal threads, together with heavier and coarser sediments. We suggest that attachment strength would be better explained by substrate characteristics, i.e. grain size, its arrangement in space and mobility, which may play a crucial role in the byssal fixation.

The weight of mobile sediments adhered to byssal threads in mytilids was highest in the higher level of both sites analysed (Figure 3C). This result could explain the higher attachment strength of *B. rodriguezii* in the vertical level of PV (Figure 3A), considering that the attachment to a higher amount of sediment will require a greater effort to dislodge

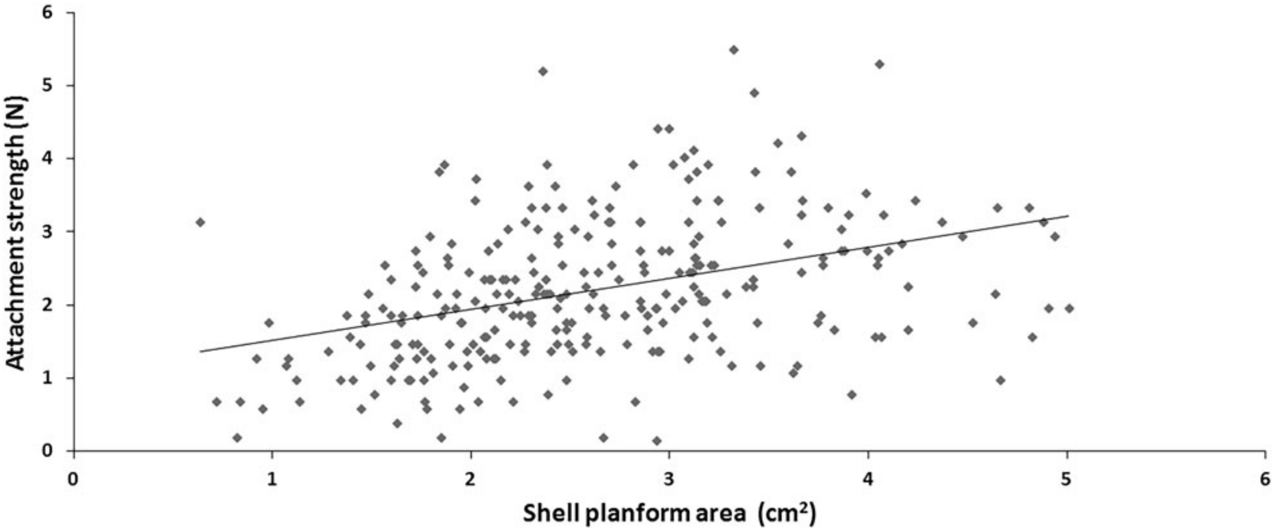

Fig. 2. Shell planform area in relation to attachment strength of *Brachidontes rodriguezii* in San Antonio Bay.

each mytilid from the substrate. Even though this result could not explain the attachment strength of the lower level of PD, which did not differ with respect to the mid-level of PV (Figure 3A), individuals of *B. rodriguezii* found in both levels were found attached themselves to a relatively coarser grain size, which could be seen as a strategy to achieve greater stability (wa Kangeri *et al.*, 2014). Furthermore, it is worth highlighting that the mid-level of PD and low level of PV had the higher attachment strength (Figure 3A) concurrently with the coarsest grain sizes (Figure 3D). Thus, the grain size of the substrate surrounding each individual may play a crucial role in its stabilization, since a smaller grain

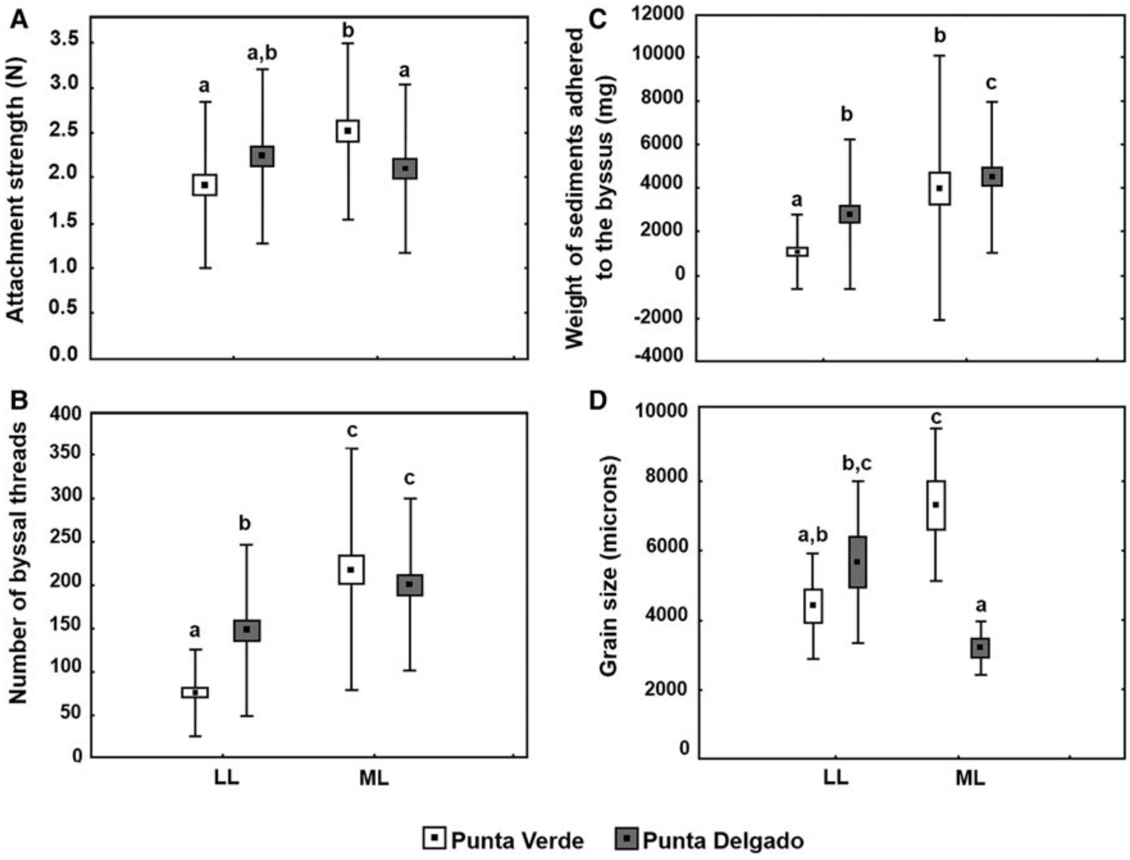

Fig. 3. (A) Attachment strength, (B) number of byssal threads, and (C) total dry weight of sediments adhered to byssal threads by each individual of *Brachidontes rodriguezii* in low (LL) and mid-level (ML) of the mid-intertidal of Punta Delgado and Punta Verde. (D) Variations in grain size (arithmetic mean) at two levels (LL and ML) of mid-intertidal of Punta Delgado and Punta Verde. Box: mean ± SE; whisker: mean ± SD. Letters denote significant differences ($P \leq 0.05$) according to the Tukey test.

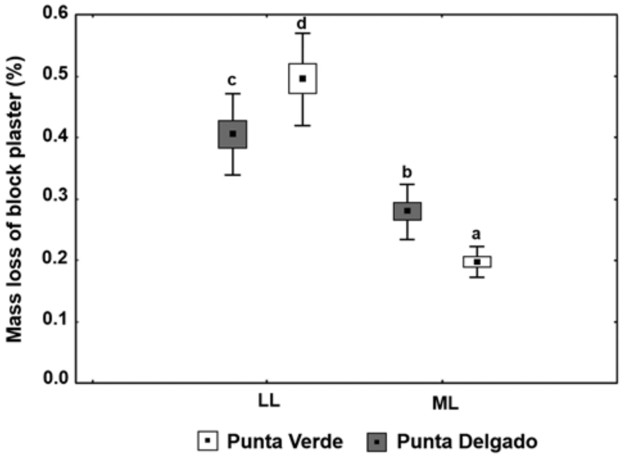

Fig. 4. Total mass loss of block plasters (per hour, in percentage, indicative of the water flow) in low level (LL) and mid-level (ML) of the mid-intertidal of Punta Delgado and Punta Verde. Box: mean ± SE; whisker: mean ± SD. Letters denote significant differences ($P \leq 0.05$) according to the Tukey test.

size would constitute a less stable habitat that could lead to a lower attachment strength. This fact was also observed for rocky shores where accumulation of sand and shell fragments in the mussel bed can weaken the attachment strength of intertidal mussels (Zardi *et al*., 2008). Consequently, the amount and size of sediment particles adhered to the mytilid byssus, together with the grain size of the substrate surrounding the mussels, could determine the attachment strength of *B. rodriguezii* in unstable substrates. It is important to highlight that gametogenesis and spawning influence the attachment strength of other mytilids (*Mytilus*) (Carrington, 2002a; Babarro & Fernández Reiriz, 2010; Hennebicq *et al*., 2013), and therefore variations in gametogenesis or spawning conditions between sites and intertidal levels may also have affected the attachment strength of *B. rodriguezii* documented in this study. This hypothesis will be subject to further testing.

The total number of byssal threads found in *B. rodriguezii* inhabiting both sites and intertidal levels (ranging from 75 to 218; Figure 3B) was higher than that found in mytilids from wave exposed rocky intertidal environments (variable between 20 and 70; Bell & Gosline, 1997; Carrington, 2002a). Interestingly, *M. edulis* inhabiting tidal flats of Western Dutch Wadden Sea had a higher number of byssal threads (from 77 to 140: wa Kangeri *et al*., 2014). Mytilids from our study and those from the tidal flats described by wa Kangeri *et al.* (2014) inhabit unstable substrates, and thus they probably need to increase their contact area for a better attachment. A positive linear relationship between byssal thread production and water flow has been demonstrated in *M. edulis* (Bell & Gosline, 1997; Carrington, 2002a). In San Antonio Bay, the high number of byssal threads of *B. rodriguezii* in the mid-level of both sites (Figure 3B) was found concurrently with the lowest flow velocity (see Figure 4). In this sense, even in the absence of mussel beds replication in PD and PV, our results are in agreement with those found for *Mytilus* in rocky shores, where byssus production is limited by wave action (Moeser *et al*., 2006; Garner & Litvaitis, 2013a). In addition, the high number of byssal threads of *B. rodriguezii* in the mid-level of both sites was found in mussel beds with the lowest mean densities and adhered to a greater mass of mobile sediments (Figure 3C). In this sense, it has been proposed that high intertidal flows are significantly dampened within dense mussel beds, altering the forces experienced by individuals within the structure (Moeser *et al*., 2006). wa Kangeri *et al.* (2014) found a lack of conspecific sheltering (Moeser *et al*., 2006) in the low density Back-edge of the bed. The need of *B. rodriguezii* to face a higher hydrodynamic stress could explain the fact that, in the mid-level of both sites, each individual is found with the highest number of byssal threads and adhered to a greater mass of mobile sediments (Figure 3C), which could be seen as a strategy of each individual to respond to environmental constraints to achieve greater stability.

In summary, the higher weight of adhered sediments and the preference of mussels to attach to coarse grains could explain the higher attachment strength. Also, the hydrodynamic stress would promote higher byssal thread numbers in *B. rodriguezii* living in unstable, mobile substrates. Future studies will be directed to assess the role of the condition index, reproductive condition, food availability, water temperature and sediment cohesion in explaining spatio-temporal variations in the byssal attachment strength of mytilids in these harsh environments with mobile substrates.

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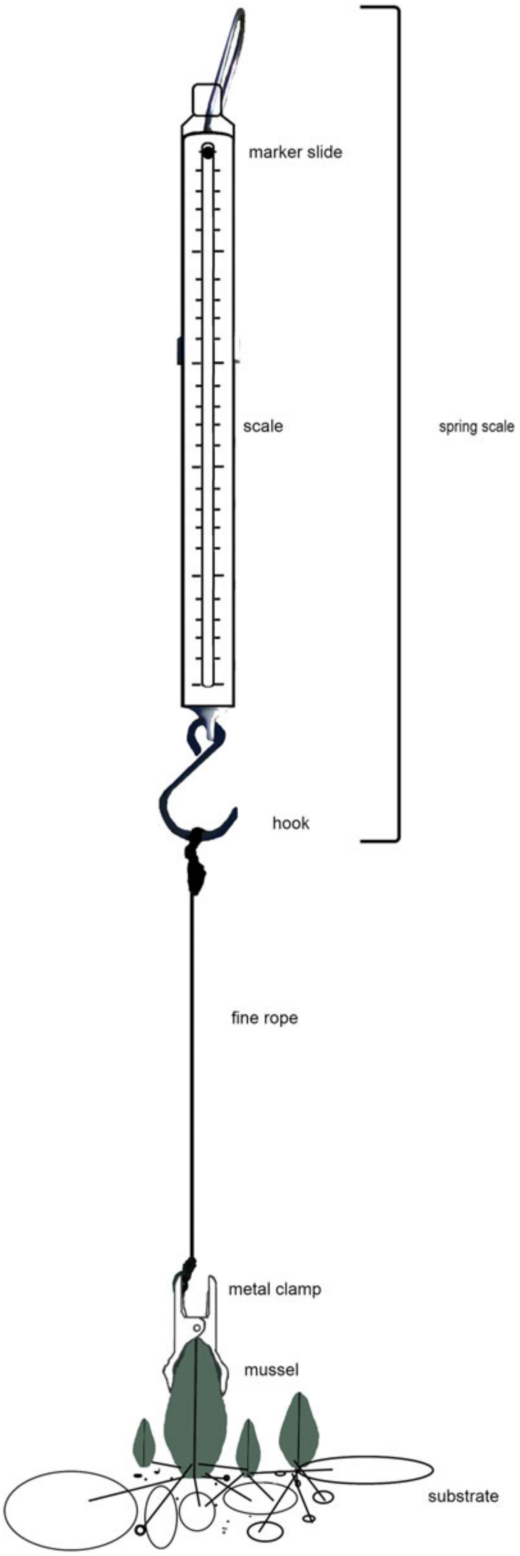
APPENDIX 1

Schematic diagram of the device used to measure the attachment strength in San Antonio Bay.



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