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Effects of wave exposure on morphological variation in *Mytilus edulis platensis* (Mollusca, Bivalvia) of the Atlantic Uruguayan coast

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Abstract. Wave action is a severe physical stress for many organisms of rocky intertidal ecosystems. We analyzed the effects of wave exposure on morphological variation in the blue mussel (*Mytilus edulis platensis*), a dominant species of rocky intertidal zones along the Atlantic Uruguayan coast. We analyzed the effects of wave exposure on 1036 individuals, by comparing morphological traits of mussels in zones exposed to wave action *vs*. protected zones in three sites. We found that wave exposure affected the size distribution of mussels such that mussels in wave protected zones were larger in size and body weight. Although an increase in the mass of byssus threads was expected under wave exposure to reduce the likelihood of dislodgement, we found no difference in byssus mass between protected and exposed zones. While our results confirm the importance of wave exposure for spatial variation in blue mussel morphology, they suggest that the effects of wave exposure may be more complex than expected.

Key words: blue mussel, byssus, morphology, Rio de la Plata, rocky shores, wave exposure

Resumen. Efectos de la exposición a las olas en la morfología de *Mytilus edulis platensis* (Mollusca, Bivalvia) en la costa uruguaya. En ecosistemas intermareales rocosos, la acción del oleaje puede constituir un severo estrés físico. En este trabajo se analizó el efecto de la exposición al oleaje en la morfología del mejillón azul (*Mytilus edulis platensis*), especie dominante del intermareal rocoso de la costa atlántica uruguaya. Se analizaron los efectos de la exposición al oleaje en 1036 individuos, seleccionadas para contrastar zonas expuestas al oleaje *vs* zonas protegidas, en tres localidades: Punta Ballena, Punta del Chileno y José Ignacio. Se encontró que la exposición al oleaje influye en la distribución de tamaños de los mejillones. En las zonas protegidas los mejillones alcanzaron mayor tamaño y peso corporal. Se espera que bajo condiciones de exposición al oleaje los mejillones generen mayores filamentos bisales, para reducir la probabilidad de ser desprendidos del sustrato. Contrariamente a lo esperado, el peso del biso no presentó diferencias entre zonas protegidas y expuestas. Al mismo tiempo que nuestros resultados confirman la importancia de la exposición a las olas en la morfología del mejillón azul, sugieren que los efectos del oleaje podrían ser más complejos de lo esperado.

Palabras clave: mejillón azul, biso, puntas rocosas, morfología, Río de la Plata

Introduction

Mussels are an important component of rocky intertidal communities around the world (McQuaid & Lindsay 2000 a,b). They are often dominant competitors for space in such environments due in part to their adhesive strength on rocky surfaces (Bell & Gosline 1996, Carrington & Gosline 2004, Moeser *et al.* 2006). Mussels attach to one another or to the substrate by producing a byssal complex composed of multiple extracellular collagenous byssal threads (Moeser *et al.* 2006). *Mytilus edulis platensis*, the blue mussel, inhabits the intertidal and subtidal rocky zone of the Atlantic coast of Uruguay (Riestra & Defeo 2000). It is the dominant species in this system, forming extensive mussel beds. Blue mussel populations in Uruguay have been exploited for over 40 years by artisanal fishing and currently constitute the second most important molluscan resource in the country.

Wave action has been traditionally viewed as a key factor in the ecology of rocky intertidal systems (Raffaelli & Hawkins 1996). Rocky intertidal environments are characterized by a land-sea transition zone gradient, across which resident organisms are affected by a series of varying physical factors such as, heat stress and wave action as well as substrate availability (Raffaelli & Hawkins 1996). Among them, wave action is a potentially severe physical stress with important implications/effects on organism biology (Denny *et al.* 1985). Wave action influences the abundance and distribution of intertidal organisms (Ferreira Silva *et al.* 2009). The effects of wave action are particularly relevant to sessile species such as mussels that must withstand continual wave shock (Raffaelli & Hawkins 1996).

Organisms inhabiting rocky substrates support flow rates of considerable velocity, which imposes certain physical limitations on body size and morphology. Among the many predictions as to how morphology varies with wave action, Denny *et a*l. (1985) proposed that flat forms and small sizes should be most common in zones with high wave action, whereby the maximum potential size of an organism is function of the most extreme wave action to which that organism may be submitted. According to this hypothesis of physical limitations imposed by wave action, it is predicted that mussels in wave exposed zones are smaller in size and weight and present enhanced attachment structure (i.e., byssus) in comparison to those in protected zones (e.g., Harger 1970, Jørgensen 1976, Alvarado & Castilla 1996).

The aim of this study is to analyze the effects of wave exposure on morphological variation of the blue mussel (*Mytilus edulis platensis*), using morphometric measurements (length, width and thickness) and body mass (valve, body and byssus weight) of *Mytilus edulis platensis.*

Methods

Study sites

The Uruguayan coast extends 660 km, including approximately 440 km of estuarine coast along the Río de la Plata Estuary and ~220 km of oceanic waters along the Atlantic Ocean. The study area was located in the external zone of the Río de la Plata Estuary (Figure 1), a coastal fringe dominated by sandy beaches sparsely interrupted by rocky points.

The main energy pulse shaping this coastal fringe is the joint action of waves, currents and tides (Giordano & Lasta 2004b). Winds along the Río de la Plata are usually mild, reaching a mean of ~5 ms^{-1} on the coast. Higher wind speeds have been recorded at exposed sections of the Uruguayan Atlantic coast (Giordano & Lasta 2004a). The most intense winds in the region originate in the South (SE, S y SW) while more mild winds blow from the NW. The Río de la Plata is located in an area of greatest cyclogenesis in Southern Hemisphere. During extreme weather events there are strong southeasterly winds over 30 ms^{-1} and storms persist in the area for several days, a phenomenon known locally as *sudestada*.

Sampling Design

We used a stratified random sampling design at three rocky points (i.e., sites), in order of location from West to East: Punta Ballena (34°54’48" S - 55°3’8" O), Punta del Chileno (34°54’44" S - 55°0’54" O), and José Ignacio (34°50’52" S - 54°38’6" O) (Figure 1). At each rocky point, wave exposed and wave protected zones were identified according to the orientation of the most prevalent storm wind direction. Southeast-facing zones were classified as exposed and Southwest-facing zones as protected. Depending on the spatial extent of blue mussel banks at each rocky point (no point exceeds 1 km), between 5 and 7 replicates of the blue mussel population in the lower intertidal zone (Z = 1.5 m) were sampled per treatment (exposed and protected).

Samples were collected within quadrants of 0.33 m^2 and using hand nets all mussels were removed. Collected organisms were fixed in 10% formalin. In the laboratory each sample was manually sieved (mesh = 2 mm) and all mussels were identified and counted quantified. We randomly selected N = 30 individuals of *Mytilus edulis platensis* within each sample to measure maximum length, maximum width, maximum thickness and dried weight of valves, soft body, byssus and total weight. To obtain dried weights organism were placed for 48 h in dried oven at 60°C.

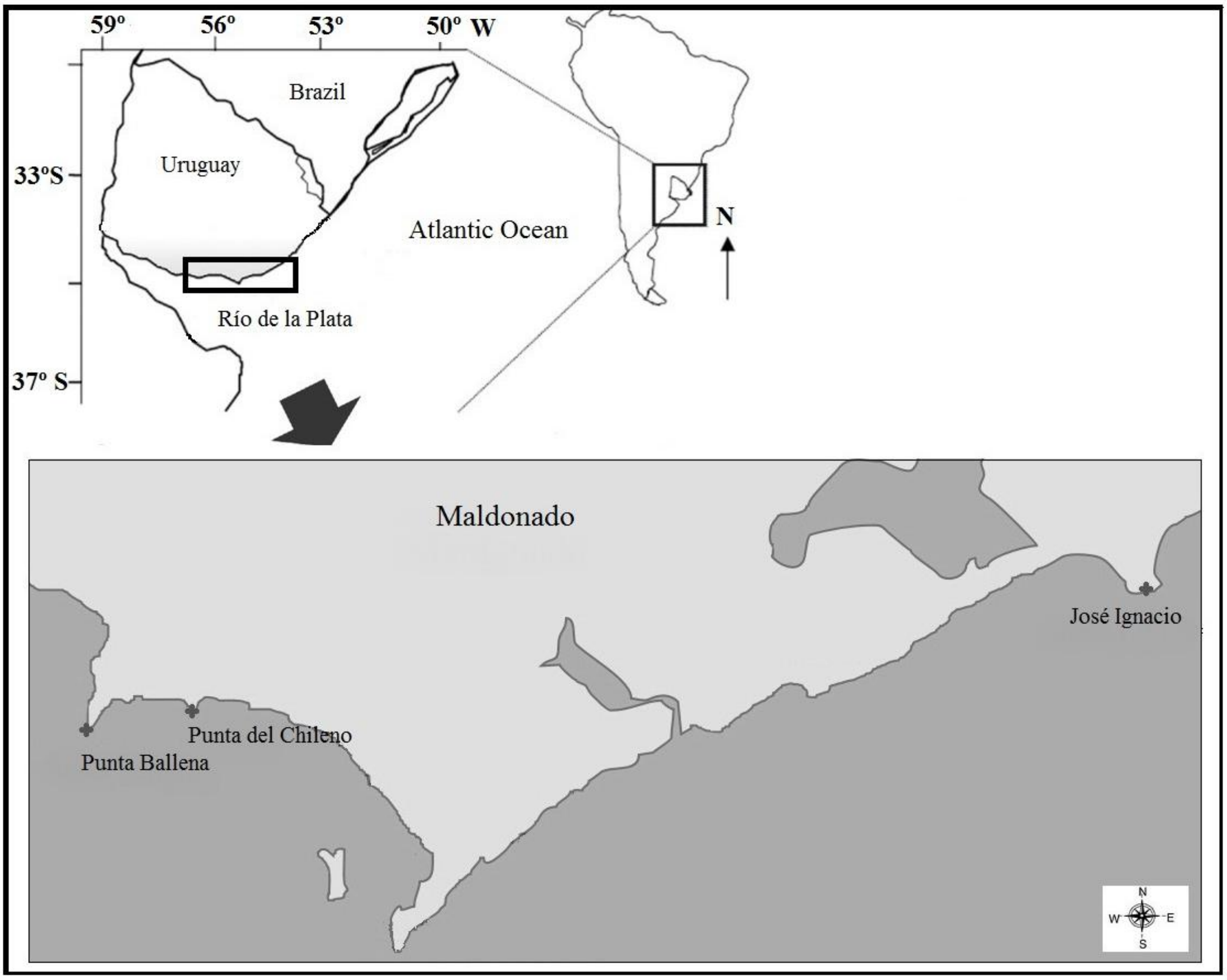

Figure 1. Study area and location of sampling sites: Punta Ballena, Punta del Chileno and José Ignacio, Uruguay.

Statistical analysis

The size (maximum length, L) structure of the *Mytilus edulis platensis* population was compared between exposed and protected zones using a Kolmogorov-Smirnov test. In addition, the 25% percentile (L_{25}) and 75% percentile (L_{75}) were calculated from the cumulated length (L) distribution, to obtain a descriptor of the smallest and largest organisms in each treatment. The variability of L_{25} and L_{75} among sites and wave exposure treatment (exposed vs. protected zones) was analyzed using a two-factor ANOVA, with exposure and sites as factors with density as covariate. The effects of exposure and site on population density were also assessed using a two-factor ANOVA design. Finally the effects of exposure (exposed *vs*. protected) on morphological traits (maximum width, maximum thickness, valves weight, body weight, byssus weight and total weight) were assessed using ANCOVAs, with maximum length and density as covariates, respectively. Log_{10} (body weight, byssus weight and total weight) and square root (valve weight) transformed data were used in analyses due to data heteroscedasticity of all morphological traits except total length. As no suitable transformation was achieved for total length, we used a nonparametric test.

Results

Size structure

Length-frequency histograms of Punta Ballena and Punta del Chileno (Figure 2) showed two modes, one in the range 5-10 mm (SM: small-size mode) and other at 25-40 mm (LM: large-size mode). Size distribution varied significantly between exposed and protected zones in Punta Ballena ($P<0.001$) and Punta del Chileno ($P<0.001$). In these sites, individuals of the LM tend to be greater at protected zones (Figure 2). The length-frequency histogram of José Ignacio was trimodal with modes at 5-10 mm, 16-20 mm and 30-35 mm ranges (Figure 2). The size distribution varied significantly between exposed and protected zones (P<0.001). Trimodality was evident in the exposed zone, but was not prevalent in the protected zone (Figure 2).

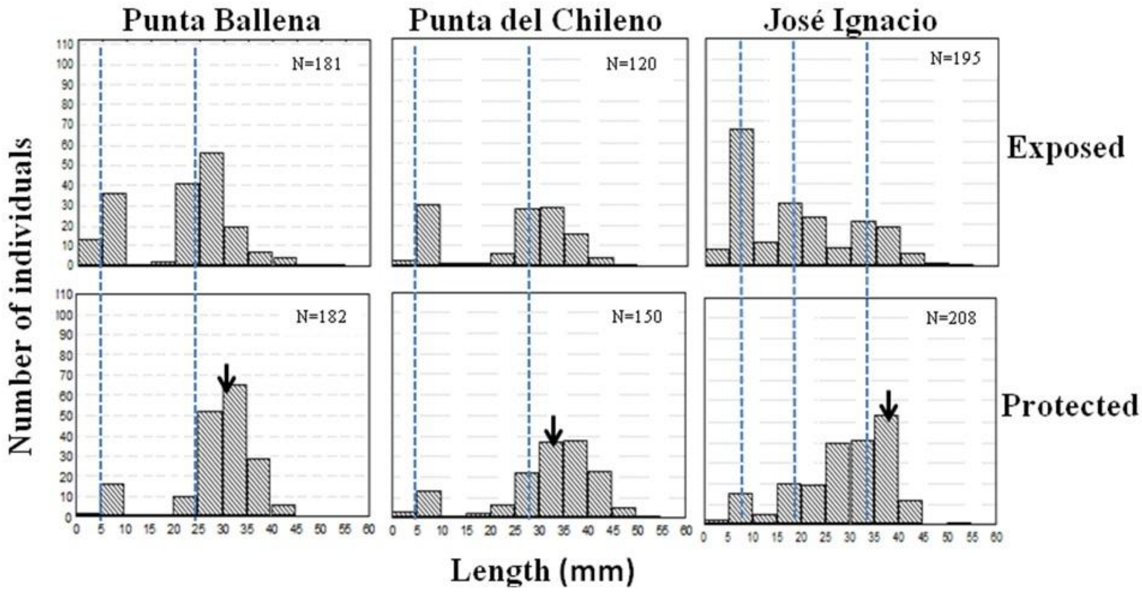

Figure 2. Length frequency histograms of the blue mussel in wave exposed and protected zones, at three rocky points along the Uruguayan coast (Punta Ballena, Punta del Chileno and José Ignacio). Vertical dashed lines indicate the modes at exposed zones, while arrows indicate the modes at protected zones that differed from those of the protected zone.

Significant differences between exposed and protected zones among individuals of the first quartile (L_{25}) were found ($F_{(1,30)} = 9.72$, $p<0.001$), but no effects of site or a site × wave exposure interaction were detected. Mussels from protected zones were larger than those from exposed zones at all three sites (Figure 3).

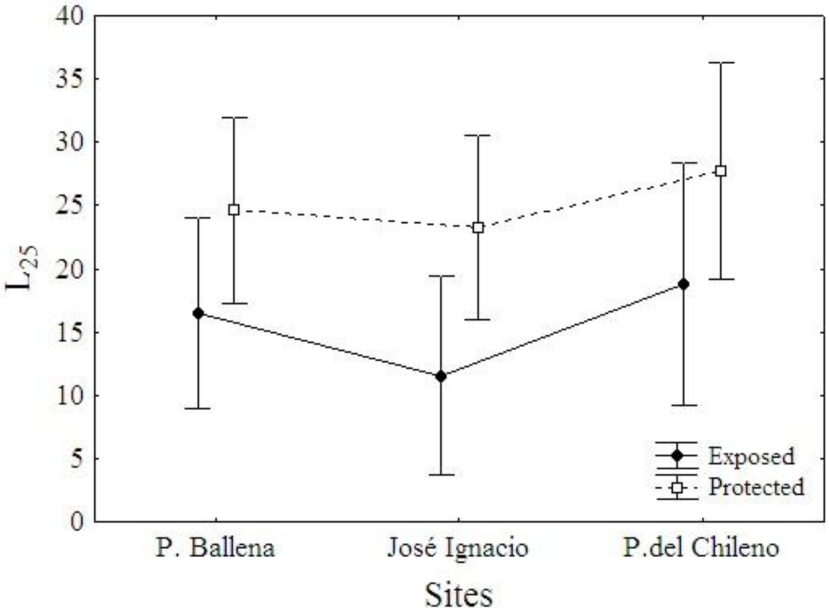

Figure 3. Differences in L_{25} (size of smallest individuals, first quartile) between exposed and protected zones among rocky sites. (Mean ± 1 SD).

We also found significant differences between exposed and protected zones among individuals of the fourth quartile (L_{75}) ($F_{(1,30)}$=16.44, p<0.001). The largest individuals at each site were larger in protected zones than in exposed zones (Figure 4). The effect of site and site × wave exposure interaction were not significant.

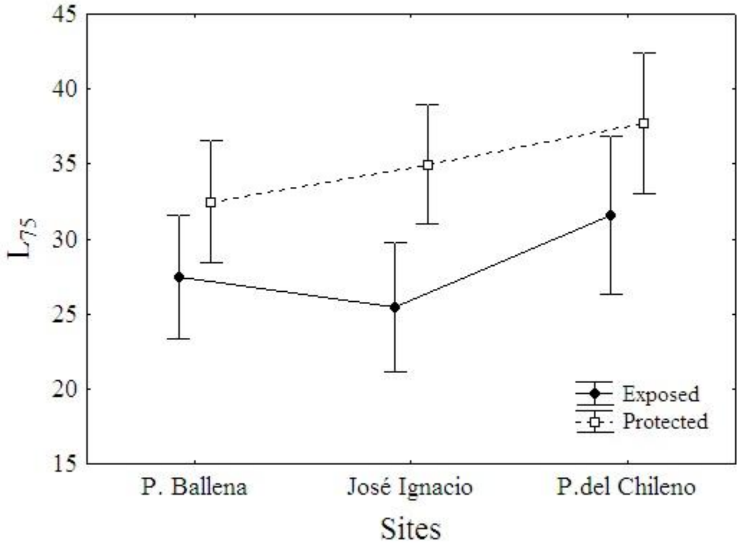

Figure 4. Differences in L_{75} (size of largest individuals, fourth quartile) between exposed and protected zones among rocky sites. (Mean ± 1 SD).

Population density showed substantial variation among sites ($F_{(2,31)}$= 4.15, p <0.05), while the effects of wave exposure and the site × wave exposure interaction were not significant (Figure 5).

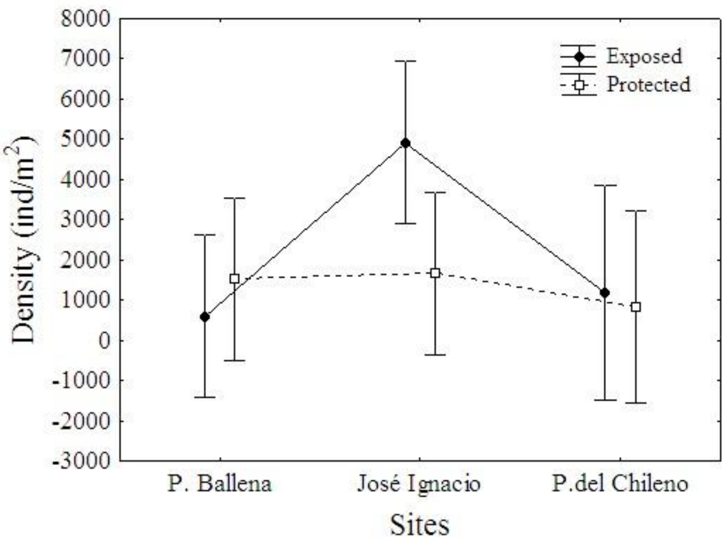

Figure 5. Differences in population density (Mean ± 1 SD) between exposed and protected zones among rocky sites.

There were significant effects of wave exposure on both thickness and body weight according to ANOVAs. Individuals in protected zones had thicker ($F_{(1,\ 1026)}$= 21.37 p< 0.001) and heavier ($F_{(1,1020)}$= 4.07 , p< 0.001) shells in comparison to exposed zones (Figure 6). Moreover, there was a significant interactive effect of site and wave exposure on width, thickness and weights (shell, body, total), but without consistent trends between wave exposure zones. Finally, shell width and thickness, as well as soft body, byssal and total weights showed significant differences among sites (Figure 6).

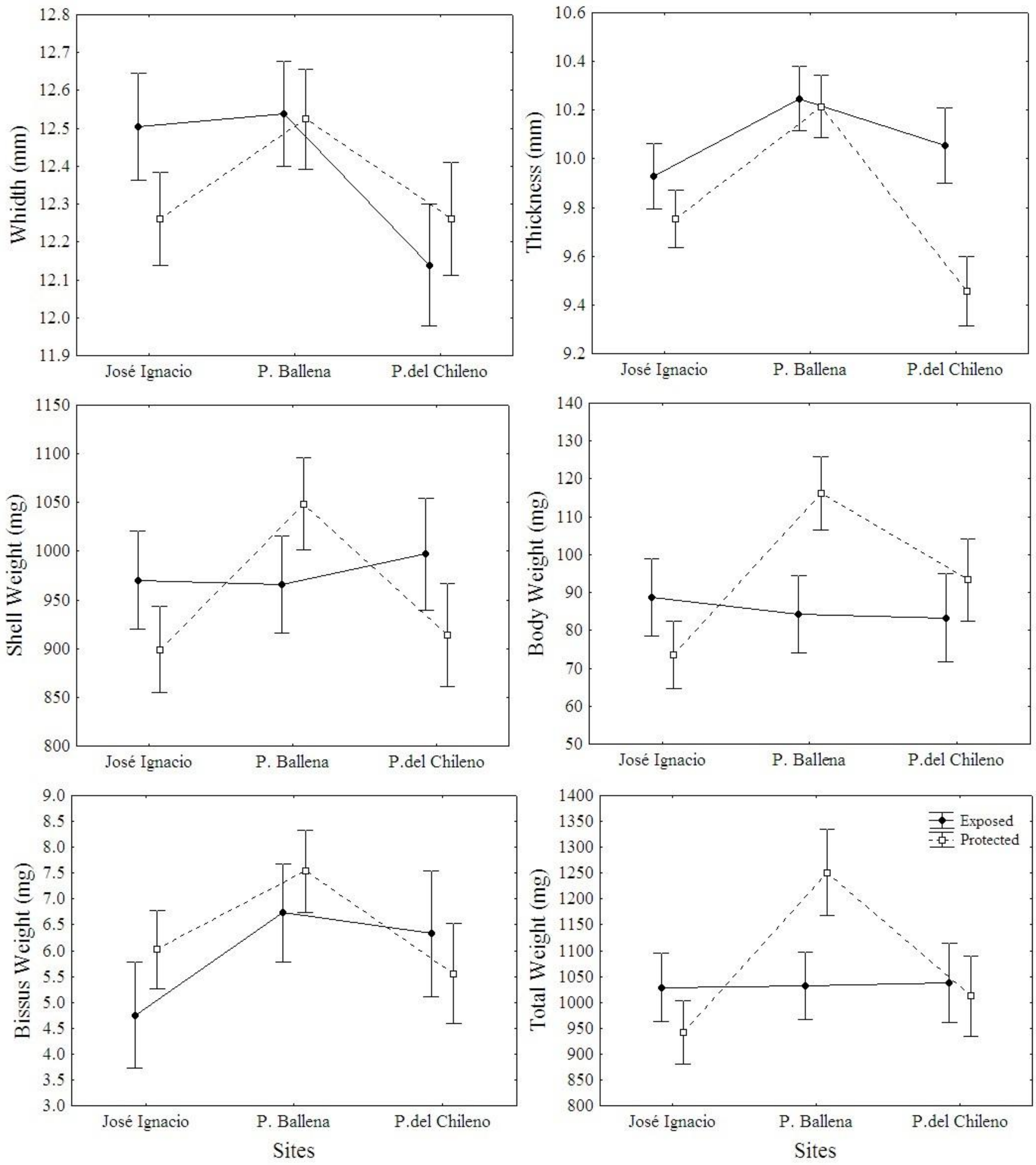

Figure 6. Variability of selected morphological descriptors of blue mussel individuals, between exposed and protected zones and among three rocky points on the Uruguayan coast.

Discussion

Our results confirm the importance of wave exposure in explaining variation in blue mussel morphology within rocky intertidal areas. As predicted by the physical limitation hypothesis, we found smaller mussels in wave exposed zones. Contrary to expectations, no difference in byssus biomass was observed between wave protected and exposed zones.

We found that individuals living in wave exposed zones tended to be smaller in length and have lower body weight, showing an inverse relationship between wave exposure and the size for both the largest (L_{75}) and smallest individuals (L_{25}). Two complementary explanations may describe this pattern. (a) Size-specific mortality: under wave exposed conditions larger individuals are more vulnerable to dislodgement than smaller individuals due to an increase in surface area exposed to waves (Denny *et al.* 1985, Alvarado & Castilla 1996). (b)

Reduced growth: growth rates may be reduced under wave-exposed conditions as the allocation of energy towards survival (*i.e.*, attachment to substrate using byssus) may compromise energy available for growth. Experimental studies are needed to assess the mechanisms behind these trends in the study region, but previous studies of the mussel *Perna perna* in South African coasts support the former explanatory hypothesis (a) and reject the latter (b) (McQuaid *et al.* 2000a). Using density-independent experiments, these authors demonstrated that both mortality and growth rates were higher under wave-exposed conditions. The lack of a difference in byssus biomass between protected and exposed zones observed here on the Uruguayan coast did not support the growth reduction hypothesis (b).

According to the size-specific mortality hypothesis, under comparable ecological conditions (i.e., recruitment, predation, etc.) population abundance should be higher within protected areas than exposed areas (Akester & Martel 2000). Here we found considerable among-site variability in mussel population density, but no differences in population density between exposed and protected zones. The interpretation of this result is not straightforward as among-site variability in other ecological factors relevant for population density is generally important, thus complicating the ability to isolate single factor effects (Mengue & Sutherland 1987). For example, the among-site variability in the density of small-sized individuals (see small-size mode in Figure 2), suggests that recruitment is higher in the exposed zones of each rocky point.

The patterns in shell morphology observed among Uruguayan mussels also indicate that wave exposure as an important selection factor. Mussels displayed the typical “wave-exposed” shell morphology, i.e., a more compact or cylindrical shell, as a strategy to avoid being dislodged by the force of wave action (Akester & Martel 2000).

Blue mussels withstand substantial hydrodynamic forces of Uruguayan rocky shores by attaching themselves to the substrate with a byssal complex composed of multiple extracellular collagenous byssal threads (Moeser & Carrington 2006). It has been proposed that thread production increases following periods of higher wave action (Gosling 1992), which should be reflected by an increase in byssus weight. Nonetheless, our results as well as recent findings (Moeser & Carrington 2006, Moeser *et al.* 2006, Carrington *et al.* 2008) do not support this hypothesis, thus questioning the role of thread production in enhancing mussel attachment. As such, the dynamics of attachment strength may not be directly related to thread production in terms of weight. Rather, the role of byssus for mussel attachment strength may be more related to byssal thread quality, rather than on total thread quantity or weight (Moeser & Carrington 2006). Future studies are needed to clarify how environmental and physiological conditions contribute to byssal thread mechanics in Uruguayan rocky shores.

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