

Morphodynamics and habitat safety in sandy beaches: life-history adaptations in a supralittoral amphipod

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ABSTRACT: Understanding the relationships between beach morphodynamics and descriptors of macrofauna assemblages has been a major step in theoretical development in sandy beach ecology. However, the role of morphodynamics in shaping life-history traits is still uncertain. Here, we test the predictions of the habitat harshness hypothesis (HHH) on the life-history traits of the sandhopper *Atlantorchestoidea brasiliensis*, based on information compiled from 7 Uruguayan sandy beaches spanning a continuum from reflective to dissipative states, over a period of almost 2 yr. *A. brasiliensis* showed clear population responses to physical variables in a trend opposite to that predicted by the HHH, including an increase in abundance (total, ovigerous females and juveniles) and individual sizes from dissipative to reflective beaches. A generalized additive model explained 46.1% of the deviance in sandhopper abundance and retained all 4 physical descriptors in the model as significant. Sandhopper abundance increased with grain size and beach face slope, and decreased with low values of water content and compaction of the sand. Per capita rate of recruitment increased linearly with adult abundance, i.e. there was a positive density-dependent effect of adults on recruitment rates, which exponentially decreased from reflective to dissipative beaches. Only the proportion of ovigerous females increased towards the dissipative domain. We conclude that the HHH did not accurately predict spatio-temporal fluctuations in population features of *A. brasiliensis*, particularly because of a limited appreciation of the role played by life-history strategies in explaining population responses to the environment. Our results have important implications for sandy beach macrofauna, particularly supralittoral organisms, and suggest a novel hypothesis (termed here the 'hypothesis of habitat safety'), which states that the combination of narrow swashes and steep slopes makes reflective beaches a more stable and safer environment for supralittoral species.

KEY WORDS: Sandhopper · *Atlantorchestoidea brasiliensis* · Life history · Sandy beaches · Morphodynamics · Habitat safety

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INTRODUCTION

The morphology and dynamics of microtidal sandy beaches (tidal range <2 m) are a function of sand particle size, breaker height and period, and major topographic features (Short 1996). Interactions between these variables produce a continuum of beach morphodynamic types ranging from reflective to dissipative beaches. The former are narrow and have coarse sedi-

ments and steep slopes, whereas dissipative beaches are wide and present fine sands and flat slopes. These interrelated variations in morphodynamic properties have been used to develop ecological theory aiming to explain patterns in macrofauna composition of sandy beaches, as well as to understand the role of morphodynamics in shaping life-history traits in a habitat regarded as one of the harshest of all marine environments.

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Three main non-exclusive hypotheses have been developed to predict how sandy beach communities are structured, as well as how individual species respond to variations in morphodynamics: (1) The 'autoecological hypothesis' (AH), adapted for sandy beaches (McLachlan 1990), states that communities are structured by independent responses of individual species to the physical environment, biological interactions being minimal. (2) In agreement with the AH, but restricted to the intertidal fringe, the 'swash exclusion hypothesis' (SEH) predicts a consistent increase in species richness, abundance and biomass from reflective to dissipative beaches (McArdle & McLachlan 1991, 1992). The harsher swash climate towards reflective conditions determines the progressive exclusion of species until, in the extreme reflective situation, no intertidal species occur and only supralittoral forms remain (McLachlan et al. 1995). (3) Recently, Gómez & Defeo (1999) and Defeo et al. (2001, 2003) formulated new additions to the original SEH and AH (both postulated on the community level), to account for predictions on the population level. To this end, the AH and SEH were merged in the 'habitat harshness hypothesis' (HHH: Defeo et al. 2003). The HHH predicts that not only community characteristics such as species richness, but also various population features (abundance, fecundity, growth and survival), increase from reflective to dissipative conditions for species living in the swash zone as well as those immediately landwards of this zone. It is argued that harsh reflective environments force organisms to divert more energy towards maintenance and their populations, therefore have lower abundance, mean individual sizes and weights, growth rates, longevity, fecundity, reproductive output and survival.

Despite the demonstrated importance of morphodynamics in explaining patterns in attributes of sandy beach macrofaunal assemblages, tests of the main predictions of SEH and HHH have so far provided dissimilar results: (1) Community analyses primarily show a consistent reduction in species richness and/or abundance towards reflective beaches (McLachlan 1990, Defeo et al. 1992, 2003, Jaramillo & McLachlan 1993, McLachlan et al. 1993, Brazeiro 1999a, Veloso & Cardoso 2001, Soares 2003), as a result of increasing environmental severity caused by high swash frequency and velocity, and an increase in erosion–accretion dynamics (Brazeiro 2001). (2) In contrast, population responses to beach morphodynamics have not been as clear. Recent tests of the HHH showed that species that co-occur at beaches with contrasting morphodynamics do not always behave as predicted by the theory. In a multi-scale analysis, Defeo et al. (1997) showed that the abundance and body size of the cirrolanid *Excirolana brasiliensis* throughout thousands of km could not be

explained by a simple animal–morphodynamics relationship. Other studies conducted at smaller spatial scales found contradictory results when the HHH was tested at the population level (Defeo et al. 1997, 2001, 2003, Gómez & Defeo 1999, Nel et al. 1999, 2001, de la Huz et al. 2002, Cardoso et al. 2003, Contreras et al. 2003). One of the most relevant results is that neither the SEH nor the HHH reliably predicted variations in population dynamics and life-history traits of supralittoral forms, which are less influenced by the swash climate and generally have 'autonomous active movement' (sensu Giménez & Yannicelli 1997) on upper beach levels (Defeo et al. 2003, McLachlan & Dorvlo 2005).

Methodological weaknesses have also precluded powerful testing of the predictions of these hypotheses at the population level: (1) some studies were based only on 1 or few sampling dates, and thus the effects of morphodynamics on life-history traits could have been biased by instantaneous sampling; (2) others provided a single comparison of only 2 beaches, one reflective and the other dissipative (but see Defeo et al. 1997), and thus the observed population trends cannot be attributed incontestably to morphodynamics, but only to location. Recently, an intensive study (16 beaches sampled bimonthly over a 2 yr period) showed that abundance of the mole crab *Emerita brasiliensis* significantly increased from reflective to dissipative Uruguayan beaches, lending support to the HHH (Defeo et al. 2002). Thus, despite years of research effort, remarkably few species have been studied well enough to establish why the existing hypotheses fail to predict population trends on sandy beaches with contrasting morphodynamics.

Talitrid amphipods are usually numerically dominant on exposed sandy beaches (Croker 1967, Brown & McLachlan 1990, Scapini et al. 1995). The sandhopper *Atlantorchestoidea brasiliensis* (Dana 1853)¹ is capable of maintaining populations in the supralittoral to upper midlittoral across the whole morphodynamic spectrum on exposed beaches of Uruguay and Brazil (Defeo et al. 1992, Cardoso & Veloso 1996). Thus, the species is well suited to evaluate population responses to distinct environmental physical features. Following predictions of the HHH, we investigated whether *A. brasiliensis* shows an increase in abundance, body size and indices of reproduction, and recruitment from reflective to dissipative beaches. To this end, we compare the abundance and life-history traits of *A. brasiliensis* from 7 Uruguayan sandy beaches with contrasting morphodynamics, over almost 2 yr.

¹We follow the recent generic re-allocation of this species by Serejo (2004)

MATERIALS AND METHODS

Seven oceanic exposed microtidal sandy beaches (tidal range = 0.5 m) along 200 km of the Uruguayan coast were sampled (Table 1). Biological samples and environmental data were collected every 2 mo from July 1999 to April 2001. Three transects were set up perpendicular to the shoreline and spaced 8 m apart, with sampling units (SUs) on each transect beginning at the base of the dunes and continuing at 4 m intervals in both seaward and landward directions until at least 2 consecutive SUs yielded no sandhoppers. At each SU, a sheet metal cylinder, 27 cm in diameter, was used to remove the sediment up to a depth of 40 cm. Each SU was sieved through a 0.5 mm mesh, and the organisms retained were sexed and measured to the nearest 0.05 mm from the tip of the cephalon to the end of the telson. Samples with coarse sands were carefully sorted in the laboratory in order to retain all organisms. Sandhoppers were classified into 2 groups: juveniles (non-adults) and adults (males and females). Juveniles presented neither a well-developed second gnathopod (males) nor oostegites (females). Abundance was estimated by the number of individuals per strip transect (IST; ind. m⁻¹) (Brazeiro & Defeo 1996) as either the total or by the population component; ovigerous females, which were defined by the presence of eggs or embryos in the brood pouch, were included.

In each SU, sediment samples were taken for determination of granulometric parameters, sand moisture (water content) and organic matter content. In the latter, macrofauna was first removed from the sediment. Sand compaction (resistance to penetration) was measured in the field using a static piston pocket penetrometer (Herrick & Jones 2002). The beach face slope (BFS) and beach slope (*S*) were determined by Emery's profiling technique (Emery 1961). The BFS,

located immediately landward of the surf zone, was quantified from the elevation of low tide to the upper limit of swash action (Hughes & Turner 1999), whereas *S* was estimated for the entire beach, i.e. from the base of the dunes to the lower limit of the swash zone. After completion of the matrix of physical parameters, the compound indices (dimensionless) of beach state, Dean's parameter Ω (Short 1996) and beach deposit index (BDI) (Soares 2003), were calculated as follows:

$$\Omega = \frac{Hb \times 100}{Ws \times T}$$

$$BDI = \frac{1}{S} \times \frac{a}{Mz}$$

where *Hb* is breaker height (m), *Ws* is sand fall velocity (m s⁻¹), *T* is wave period (s), *S* is the beach slope, *a* = 1.03125 mm is the median estimate of the sand particle size classification and *Mz* is the mean sand particle size (mm). Tables from Gibbs et al. (1971) were used to calculate settling velocities based on particle size. Ω values < 2 characterize reflective beaches, whereas $\Omega > 5$ define dissipative ones and $2 < \Omega < 5$ characterize intermediate beach states. Finally, the beach index (BI) formulated by McLachlan & Dorvlo (2005) was calculated as follows:

$$BI = \log_{10} \left(\frac{Mz \times TR}{S} \right)$$

where TR is the tidal range. *Mz* was expressed in (phi units + 1), to avoid negative values (McLachlan & Dorvlo 2005). As in this study TR = 0.5 m for all beaches, the BI was driven by variations in the logarithm of the ratio between *Mz* and *S*.

Single relationships between population and physical variables (averaged over the 22 mo) were modeled by linear or nonlinear fitting, which are more appropri-

Table 1. Full characterization of the main physical variables and the compound indices of beach state (upper and lower levels of 95% confidence intervals) of the 7 Uruguayan oceanic sandy beaches analyzed in this study. Abbreviations for each beach are subsequently used in the figures. Beach states: Ω = Dean's parameter, BDI = beach deposit index, BI = beach index

Beach features	Sta. Mónica (SM)	José Ignacio (JI)	Arachania (Ara)	Sta. Isabel (SI)	Pta. del Diablo (PD)	Achiras (Ach)	Barra del Chuy (Bar)
Latitude south	34° 51'	34° 49'	34° 37'	34° 33'	34° 02'	33° 56'	33° 49'
Grain size (mm)	0.57–0.61	0.25–0.33	0.40–0.48	0.44–0.60	0.39–0.47	0.24–0.28	0.19–0.23
Compaction (kg cm ⁻²)	2.08–2.56	3.29–3.65	2.43–2.93	2.29–2.53	2.25–2.87	3.08–3.74	3.83–4.19
Water content (%)	5.02–7.18	7.00–10.60	6.48–8.88	5.70–7.86	6.39–9.25	7.51–11.93	13.64–14.78
Organic matter (%)	0.11–0.15	0.16–0.28	0.16–0.28	0.31–0.39	0.35–0.47	0.20–0.36	0.17–0.29
Slope (cm m ⁻¹)	4.00–4.92	3.95–4.90	5.21–6.89	5.99–9.08	4.31–7.12	3.65–5.09	2.39–3.19
Beach face slope (cm m ⁻¹)	11.39–16.84	4.30–7.24	7.52–11.70	9.87–14.82	9.08–13.81	4.54–7.84	5.22–12.96
Compound indices							
Ω	1.73–3.03	3.10–4.36	1.50–2.56	1.48–2.96	2.20–3.30	3.63–6.17	4.94–7.64
BDI	34.23–44.81	72.88–114.24	31.39–49.23	21.15–34.51	32.38–52.06	74.08–146.40	146.60–257.18
BI	1.23–1.35	1.45–1.53	1.17–1.33	0.99–1.19	1.16–1.36	1.48–1.56	1.67–1.79

ate than multiple comparison procedures that use discrete categorization of continuous variables to depict patterns (Defeo & Cardoso 2004). For both *S* and BFS, the reciprocal of the indices (also termed 'beach gradient') were used for modeling purposes because these perform better statistically (in terms of well-distributed residuals) than raw values. Linear and nonlinear models were fitted, and the model that best explained the relationship between biological and physical variables was selected according to the coefficient of determination (r^2).

The relationship between abundance of *Atlantorchestoidea brasiliensis* and several physical variables used simultaneously was modeled through a Generalized Additive Model (GAM) (Hastie & Tibshirani 1990), because of the nonlinear nature of most relationships (see 'Results'). The following physical variables were selected on the basis of their performance as suitable indicators of species abundance: grain size, beach face slope, sand compaction and sand water content. Based on the rationale provided by Schoeman & Richardson (2002), abundance estimates (ind. m^{-1}) and physical variables from all months were used in order to explicitly account for within-beach variation, and also because the main goal of this analysis was not to detect statistically significant differences among time periods but rather overall relationships between sandhopper abundance and physical variables. A Poisson error distribution was assumed to explain variations in abundance estimates, because the deviance residuals of the

model indicated that this was a more appropriate error structure than a Gaussian distribution. This was also found by Schoeman & Richardson (2002). To avoid including truly redundant variables, yet retaining all important environmental information, the Akaike information criterion (AIC) (McCullagh & Nelder 1989) was used in a bidirectional stepwise procedure to select the most parsimonious model and to assess the significance of each model term. All predictors were included as smoothed terms, and a spline function of the *j*th smoothed component (splines) was used to estimate the nonparametric functions. The procedure was implemented through the S-Plus 'step.gam' function (Venables & Ripley 1999), which enabled the objective selection of significant variables and avoided multicollinearity problems in model development.

RESULTS

The habitat

A full characterization of physical variables and indices of the 7 Uruguayan sandy beaches analyzed is shown in Table 1. The steepest beaches (Santa Isabel, Arachania and Santa Mónica) had coarsest sediments and lowest sand compaction and organic matter content, and vice versa. The mean particle size ranged from 0.21 (Barra del Chuy) to 0.59 mm (Santa Mónica); slope *S* ranged between 2.79 (Barra del Chuy) and 7.54 cm m^{-1} (Santa Mónica); and sand compaction ranged from 2.32 (Santa Mónica) to 4.01 kg cm^{-2} (Barra del Chuy). Concerning the mean values of composite indices, Ω varied between 2.03 (Arachania) and 6.29 (Barra del Chuy); BDI between 27.83 (Santa Isabel) and 201.89 (Barra del Chuy); and BI from 1.09 (Santa Isabel) to 1.73 (Barra del Chuy). Relationships between physical variables (Fig. 1) were statistically significant, but the strongest ones were found between sand compaction and (1) 1/BFS ($r^2 = 0.99$; $p < 0.001$) and (2) sand grain size ($r^2 = 0.98$; $p < 0.001$). Most relationships were linear, but several nonlinear models best explained these relationships (Fig. 1). According to Short's (1996) classification based on Ω and the estimated 95% confidence intervals (CI) of Ω provided in Table 1 for each beach, Barra del Chuy and Achiras tended to be dissipative ($\Omega > 5$); José Ignacio and Punta del Diablo

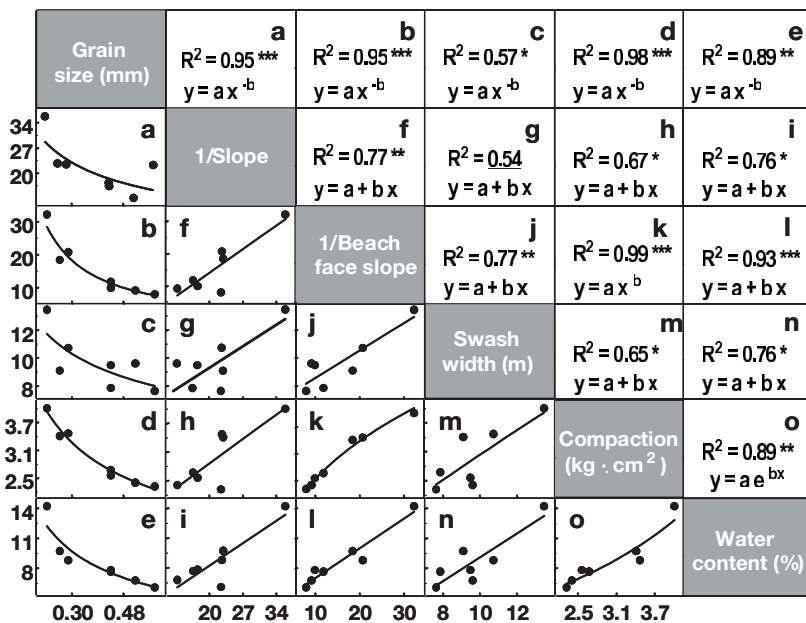


Fig. 1. Scatter plots of relationships between physical parameters on 7 Uruguayan beaches. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Underlined value indicates trend that approached significance ($0.10 < p < 0.05$)

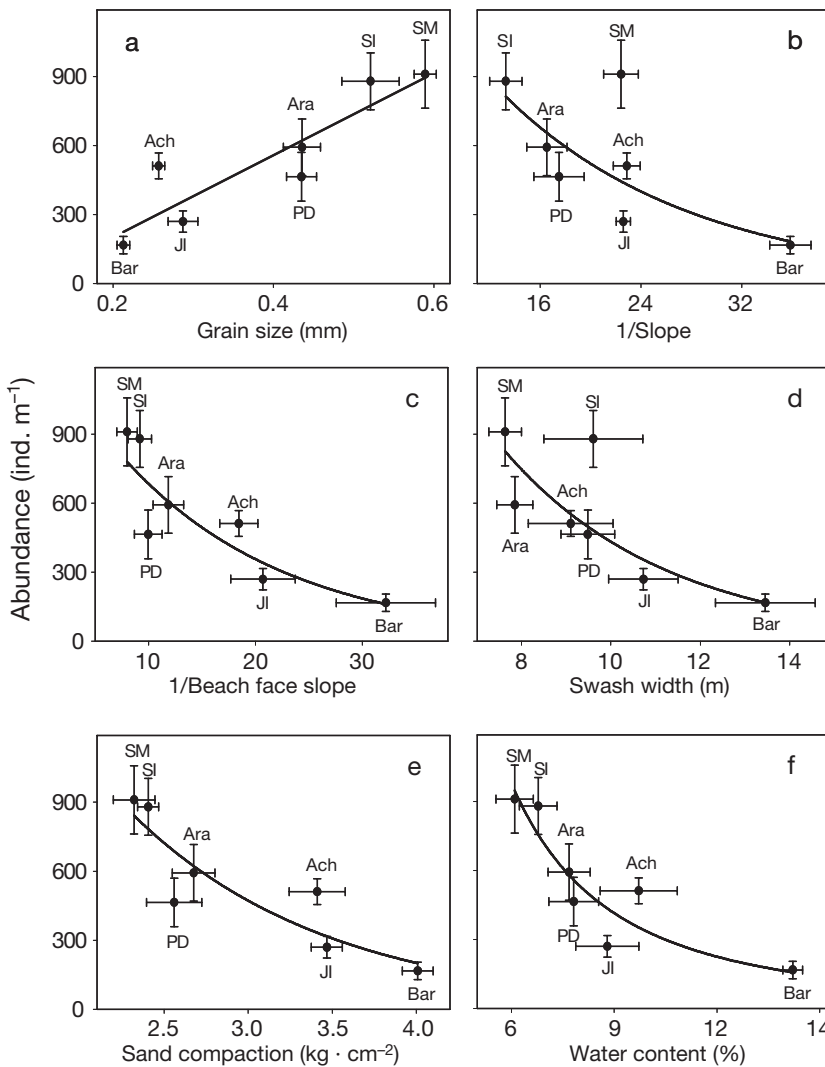


Fig. 2. *Atlantorchestoidea brasiliensis*. Mean (●) ± SE of sandhopper abundance (vertical lines) and physical variables (horizontal lines), together with the models that best fitted the relationship between these variables: (a) grain size; (b) 1/slope; (c) 1/beach face slope; (d) swash width; (e) sand compaction; and (f) sand water content. Abbreviations beside each point refer to the corresponding beaches as in Table 1

were intermediate during the whole period ($2 < \Omega < 5$); and *Arachania*, Santa Isabel and Santa Mónica had the lower CI bound included within truly reflective states (i.e. $\Omega < 2$).

Abundance

Contrary to the main predictions of the HHH, the abundance of *Atlantorchestoidea brasiliensis* increased from dissipative to reflective beaches (Fig. 2), and this was reflected by significant relationships between abundance and several individual physical variables (Table 2, Fig. 2). The best model was the monotonically decreasing exponential function $IST_T = ae^{-b(1/BFS)}$ ($r^2 = 0.85$; $p < 0.003$), where IST_T is total abundance per strip transect and BFS is the beach face slope (Fig. 2). This remained true for the total population, and for adult males and females separately. Following the same pattern, amphipod abundance was significantly related to the compound indices of beach states Ω , BDI and BI (Table 2, Fig. 3) through nonlinear decreasing functions ($0.65 < r^2 < 0.75$; $p < 0.05$). In summary: (1) The abundance of *A. brasiliensis* markedly increased towards reflective beaches. (2) Most relationships were nonlinear. (3) Individual physical variables tended to be more useful predictors of abundance than compound indices.

The GAM explained 46.1% of the deviance in sandhopper abundance. All physical variables considered in the analysis were significant, as revealed by the AIC stepwise approach, which retained all predictors in the model. The importance of

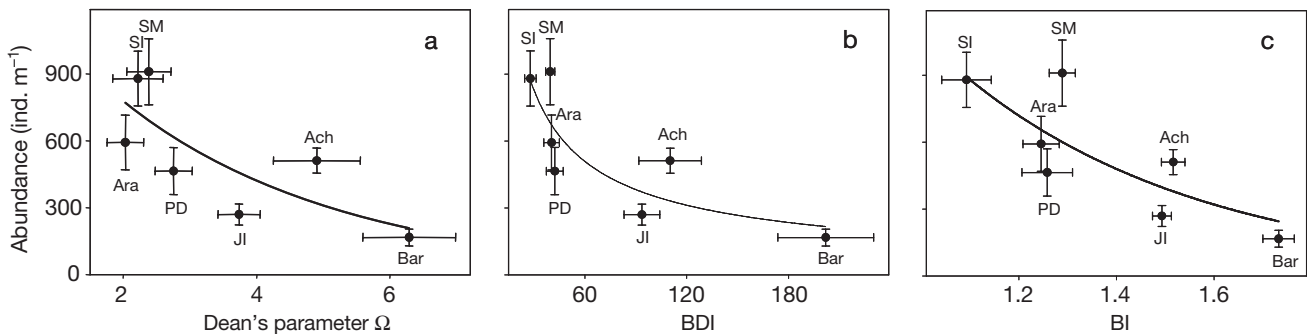


Fig. 3. *Atlantorchestoidea brasiliensis*. Mean (●) ± SE of sandhopper abundance (vertical lines) and compound indices of beach state (horizontal lines). In all cases, the best model (solid line) that related a beach index with abundance (highest r^2) is shown. Regression details are in Table 2. Abbreviations beside each point refer to the corresponding beaches as in Table 1

the predictors in explaining *Atlantorchestoidea brasiliensis* abundance, inferred from the AIC statistics in the stepwise model, was, in decreasing order: grain size, beach face slope, water content, and compaction

of the sand. The analysis showed that sandhopper abundance increased as grain size increased, reaching a peak at 0.63 mm (Fig. 4a). The highest abundance was also found at the steepest (>20 cm m⁻¹) beach face

Table 2. *Atlantorchestoidea brasiliensis*. Best linear and nonlinear models estimated between population features and physical variables and compound indices (Ω, BDI and BI, see Table 1). *p < 0.05; **p < 0.01; ***p < 0.001; Mz: mean grain size; S: slope; BFS: beach face slope; SC: sand compaction; SWC: sediment water content; SW: swash width

Biological descriptor	Physical variable					
	Mz (mm)	1/S	1/BFS	SW (m)	SC (kg cm ⁻²)	SWC (%)
Total abundance (ind. m ⁻¹)	$y = -a + bx^{**}$	$y = ae^{-bx^*}$	$y = ae^{-bx^{**}}$	$y = ae^{bx^{**}}$	$y = ae^{-bx^{**}}$	$y = ax^{-b^{**}}$
Ovigerous females (ind. m ⁻¹)	$y = a + bx^*$		$y = ae^{-bx^{**}}$	$y = ae^{-bx^*}$	$y = ae^{-bx^*}$	$y = ax^{-b^{**}}$
Juveniles (ind. m ⁻¹)	$y = -a + bx^{**}$	$y = ae^{-b^*}$	$y = ax^{-b^{**}}$	$y = ae^{-bx^*}$	$y = ae^{-bx^{**}}$	$y = ax^{-b^{**}}$
Fertility (juveniles/ovigerous)	$y = a + bx^{**}$		$y = ax^{-b^{**}}$		$y = ax^{-b^{***}}$	$y = ax^{-b^*}$
Proportion ovigerous (%)	$y = ax^{-b^*}$		$y = ax^{-b^{**}}$	$y = -a + bx^*$	$y = -a + bx^{**}$	$y = ax^{-b^*}$
Mean ovigerous size (mm)		$y = ae^{-bx^*}$				$y = ae^{-bx^*}$
Largest male (mm)		$y = ae^{-bx^*}$				$y = ae^{-bx^*}$
Largest female (mm)		$y = ae^{-bx^*}$				$y = ae^{-bx^*}$
		Ω	Compound index			
			BDI	BI		
Abundance (ind. m ⁻¹)		$y = ae^{-bx^*}$	$y = ax^{-b^*}$	$y = ae^{-bx^*}$		
Ovigerous females (ind. m ⁻¹)			$y = ae^{-bx^*}$	$y = ae^{-bx^*}$		
Juveniles (ind. m ⁻¹)		$y = ae^{-bx^{**}}$	$y = ax^{-b^{**}}$	$y = ae^{-bx^{**}}$		
Fertility (juveniles/ovigerous)		$y = ax^{-b^*}$	$y = ax^{-b^*}$	$y = ae^{-bx^*}$		
Proportion ovigerous (%)			$y = a + bx^*$	$y = -a + bx^*$		
Mean ovigerous size (mm)		$y = ae^{-bx^*}$	$y = ae^{-bx^*}$	$y = ae^{-bx^*}$		
Largest male (mm)						
Largest female (mm)		$y = ae^{-bx^*}$	$y = ae^{-bx^*}$			

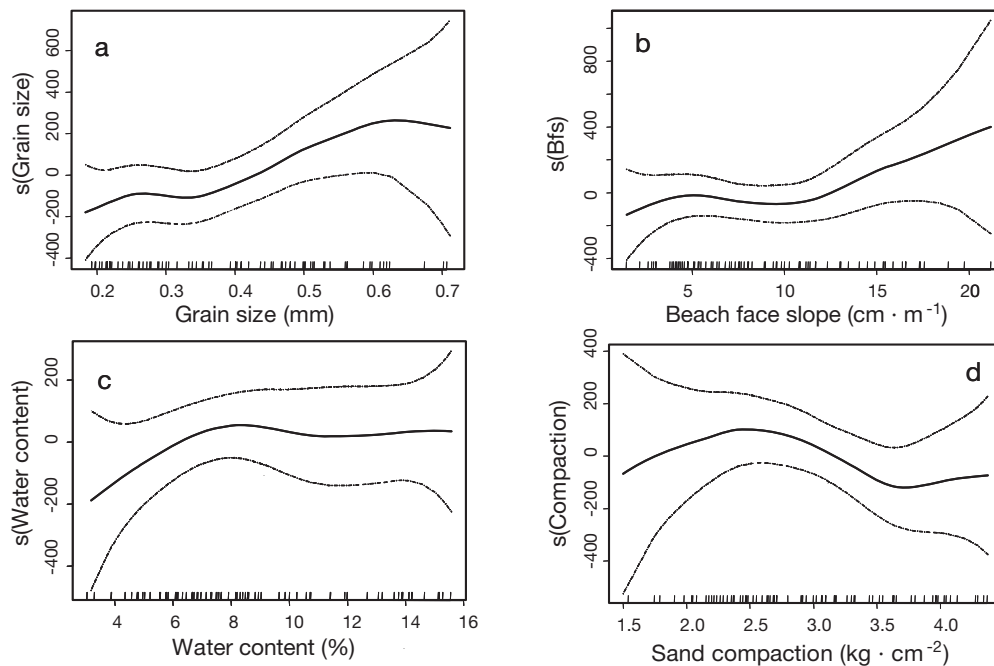


Fig. 4. *Atlantorchestoidea brasiliensis*. Results of the Generalized Additive Model showing the relationship (solid line) between *A. brasiliensis* abundance and each meaningful physical predictor, in order of importance: (a) grain size, (b) beach face slope, (c) water content, and (d) sand compaction. Dashed lines indicate twice the pointwise asymptotic standard errors of the estimated curve, and the 'rug plots' on the x-axis indicate the range of variables over which measurements were taken

slopes (Fig. 4b) and low (8%) water content, after which a plateau of abundance occurred (Fig. 4c). In terms of sand compaction (Fig. 4d), the strong nonlinear effect denoted an abundance peak at ca. 2.5 kg cm⁻², declining towards lower and higher compaction values.

Reproduction, recruitment and body size

Contrary to the main predictions of the HHH, the abundance of ovigerous females increased from dissipative to reflective beaches. The best model was the monotonically decreasing exponential function of the

form $IST_{OV} = ae^{-bSWC}$ (Fig. 5a), where IST_{OV} is the abundance of ovigerous females and SWC is the sand water content ($r^2 = 0.89$; $p < 0.005$). Only the proportion of ovigerous females (P_{OV}) clearly followed HHH predictions, significantly increasing from the reflective to the dissipative domain (Fig. 5b); the best model was a linear function of sand compaction (SC) $P_{OV} = a + (b \times SC)$ ($r^2 = 0.83$; $p < 0.005$). Consequently, P_{OV} was inversely related to total abundance, following the monotonically decreasing exponential function $P_{OV} = a \times e^{-bIST_T}$ ($r^2 = 0.63$; $p < 0.01$), indicating a significant increase in the relative representation of ovigerous females towards dissipative beaches. The mean size of ovigerous females showed a consistent increase from

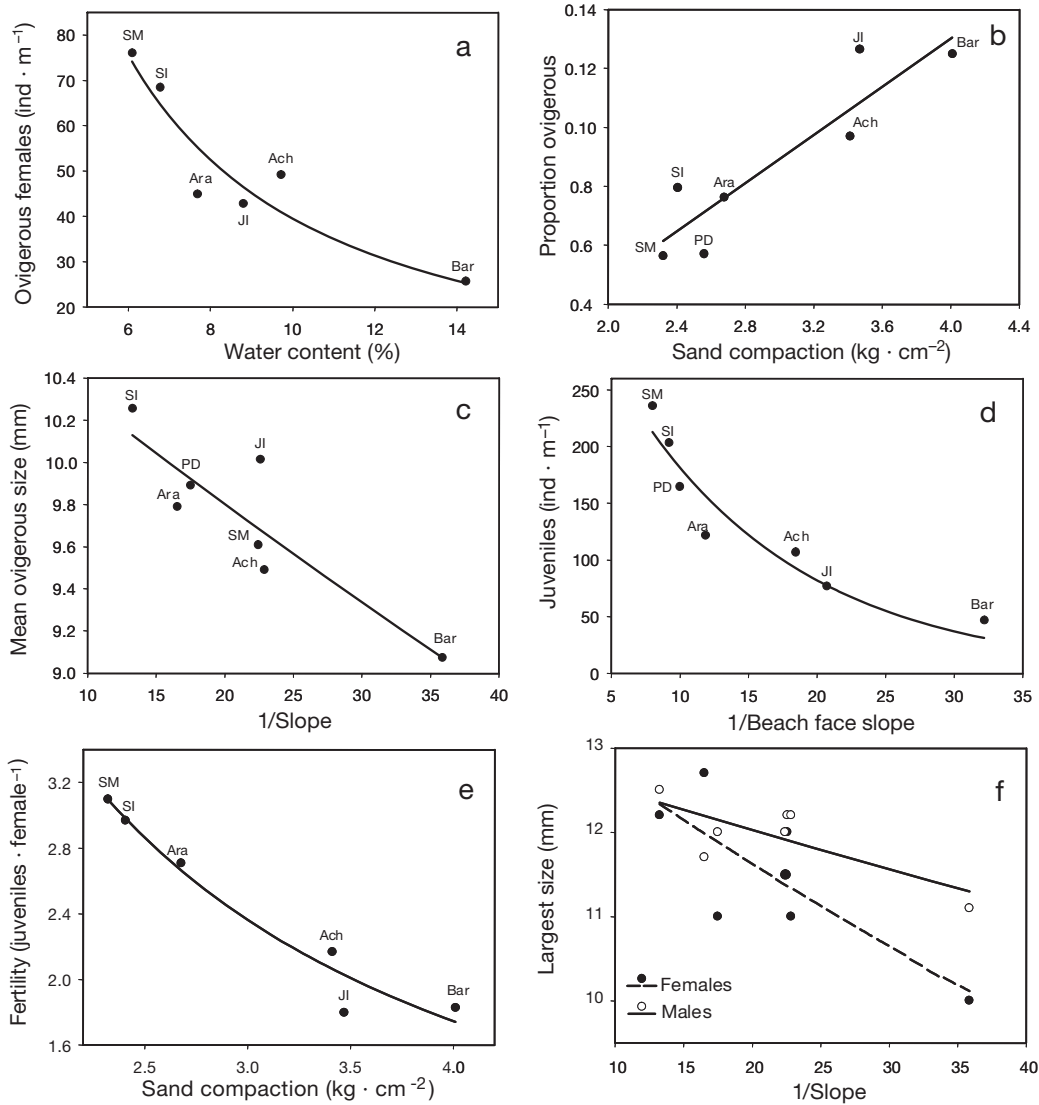


Fig. 5. *Atlantorchestoidea brasiliensis*. Relationship between population descriptors and physical variables: (a) abundance; (b) proportion, and (c) mean individual size of ovigerous females; (d) juvenile abundance; (e) fertility; and (f) largest individual size of (●) females and (○) males. Abbreviations beside each point refer to the corresponding beaches as in Table 1. In all cases, the best model (solid line) that related a physical variable with a biotic one (highest r^2) is shown. Regression details are in Table 2

dissipative to reflective beaches, ranging from 9.07 mm (Barra del Chuy) to 10.26 mm (Santa Isabel), and the best model was $L_{OV} = a \times e^{-b/S}$ ($r^2 = 0.67$; $p = 0.024$), where L_{OV} is the mean size (mm) of ovigerous females and S the beach slope (Fig. 5c). Following the same trend observed in ovigerous females, juvenile abundance, taken to be a direct measure of recruitment success, decreased exponentially towards dissipative beaches with the reciprocal of BFS as follows: $IST_{JUV} = a(1/BFS)^{-b}$ ($r^2 = 0.96$; $p < 0.0001$; Fig. 5d).

The per capita rate of recruitment or fertility (i.e. juveniles per ovigerous female) increased linearly with adult abundance (IST_{AD}) as follows: $IST_{(JUV/OV)} = a + (b \times IST_{AD})$ ($r^2 = 0.94$; $p < 0.002$); i.e. there was a positive density-dependent effect of adult abundance on reproductive rates. A maximum of 3.1 juveniles per female was estimated for the reflective Santa Mónica, whereas a value 1.7 times lower (ca. 1.8 juveniles female⁻¹) was estimated for José Ignacio and Barra del Chuy. Fertility estimates were strongly correlated with several physical variables, notably as a monotonically decreasing function of sand compaction ($r^2 = 0.95$; $p < 0.001$; Table 2, Fig. 5e). Two clear groups were identified in Fig. 5e: (1) high-fertility sandhoppers on reflective beaches with low sand compaction (ca. 2.5 kg cm⁻²) and (2) low-fertility sandhoppers on intermediate/dissipative beaches with high sand compaction (≥ 3.4 kg cm⁻²).

Largest individual sizes increased significantly from dissipative to reflective beaches, and this was consistent for both sexes (Fig. 5f). Sandhopper sizes were significantly related to physical variables, notably $1/S$, through nonlinear decreasing models (Table 2: $r^2 = 0.59$, $p < 0.05$ for males; $r^2 = 0.65$, $p < 0.05$ for females). An ANCOVA, performed with the reciprocal of slope as the covariate, revealed a statistical lack of significance in a comparison of the largest body size between sexes (homogeneity of slopes: $F_{1,10} = 1.79$, $p = 0.21$; main effect: $F_{1,11} = 3.10$; $p = 0.11$). Despite the consistent trends, males tended to be larger towards dissipative beaches (Fig. 5f).

DISCUSSION

Atlantorchestoidea brasiliensis showed strong patterns in abundance and life-history traits throughout a morphodynamic continuum along 200 km of sandy coast. Results obtained from 7 beaches repeatedly over almost 2 yr demonstrated that *A. brasiliensis* responded systematically to beach morphodynamics in a manner opposite to that predicted by the HHH. Total abundance, body size, and reproduction and recruitment success increased significantly from dissipative to reflective beaches. These trends were explained by

variations in individual physical variables as well as those in compound indices (Ω , BI and BDI) that take into account multiple features of the beach ecosystem. However, the best statistical relationships were found with individual physical factors, as previously shown by Nel (2001) and McLachlan & Dorvlo (2005).

Our results are consistent with the hypothesis that population features associated with fitness in supralittoral peracarids exhibiting direct development are optimized towards reflective beaches (Defeo et al. 1997, Gómez & Defeo 1999), which have been traditionally considered as the harshest sandy beach environment. Contrary to the predictions of the HHH and SEH, the total abundance of *Atlantorchestoidea brasiliensis* significantly increased from dissipative to reflective beaches. This finding was demonstrated both by single relationships and by a model-building approach (i.e. GAM). The GAM showed that sandhopper abundance was clearly related to each environmental predictor after removing the effect of all other predictor variables. The model predicted highest abundances at medium to coarse grain sizes, steep beach face slopes and low values of water content and sediment compaction of the sand, all indicative of beach reflectiveness. Gómez & Defeo (1999) also found higher abundance, growth and survival of *A. brasiliensis* on the reflective beach Arachania than on the dissipative Barra del Chuy (beaches included here but using datasets spaced 3 yr apart). Higher abundances towards reflective beaches were also found by Veloso & Cardoso (2001) for the same species in beaches of Rio de Janeiro (Brazil) and by Contreras et al. (2003) for the amphipod *Orchestoidea tuberculata* in Chile. In South Africa, the supralittoral amphipod *Talorchestia capensis* showed significantly higher abundance on a beach with a pebble berm above the water mark than on an exposed dissipative beach (Schoeman et al. 2003). Abundance of ovigerous females and juveniles, as well as body size (both sexes and ovigerous females) also showed a clear increase from dissipative to reflective domains, following the reverse of the trend predicted by the HHH. This supports previous findings by Gómez & Defeo (1999), who reported greater brood size, egg production potential and recruitment levels among sandhoppers on a reflective beach than those on a dissipative beach. Ovigerous females and juveniles of *O. tuberculata* in Chile were also less abundant on a dissipative beach (Contreras et al. 2003). These consistent trends were also reported for other supralittoral peracarids. The ovoviviparous isopod *Excirrolana brasiliensis* showed greater abundance and larger body sizes on reflective than dissipative beaches all along Atlantic sandy beaches of South America (Cardoso & Defeo 2003, 2004), notably Brazilian (Veloso & Cardoso 2001) and Uruguayan (Defeo et al. 1992, 1997,

Defeo & Martínez 2003) beaches. McLachlan (1990) also found that the individual size of crustaceans increased from dissipative to reflective beaches.

The above patterns are in clear contradiction to those found for truly intertidal species. Indeed, abundance, body size, growth, survival and burrowing performance tend to increase towards dissipative beaches, as documented for the sand crabs *Emerita analoga* (Dugan et al. 1994, Dugan & Hubbard 1996, Brazeiro 1999b) and *E. brasiliensis* (Defeo & Cardoso 2002, Defeo et al. 2002), and clams of the genus *Donax* (McLachlan et al. 1995, 1996, Nel et al. 2001, de la Huz et al. 2002). Thus, we argue that the SEH and HHH have often been accepted almost uncritically wherever (1) community descriptors are related to morphodynamics, and (2) population properties are analyzed in truly intertidal forms directly affected by the swash climate. On the contrary, supralittoral species, notably peracarids capable of maintaining populations across the whole morphodynamic spectrum, exhibit greater fitness indicators (higher abundance, growth and fertility rates) on reflective beaches.

The discrepancy between patterns provided for intertidal suspension feeders and supralittoral forms appears to be related to life-history strategies (see also Defeo et al. 2003): (1) Species that showed relative independence of swash climate effects and no clear responses to beach type mainly occur in the supralittoral and high midlittoral levels of the beach (e.g. the peracarids *Atlantorchestoidea* and *Excirrolana*). These peracarids have direct development (small reproductive effort, a planktonic larval phase and parental care of eggs/embryos). (2) On the other hand, the species that mainly follow predictions of the SEH and HHH are mainly represented by intertidal forms, notably (a) broadcast spawners with external fertilization and planktonic larvae (e.g. clams), and (b) anomuran crabs with brooding females and planktonic larvae. These intertidal species are affected throughout their entire life span by the swash climate. Thus, our results suggest that the theoretical body already developed in sandy beach ecology needs some refinement concerning the explanation of species responses to the physical environment, particularly for supralittoral species.

Only the proportion of ovigerous females (P_{OV}) increased towards the dissipative domain. Concurrent changes in P_{OV} and reproductive characteristics may explain this large-scale pattern, thus depicting interconnected reproductive characteristics. Indeed, the significant increase in the relative representation of ovigerous females towards dissipative beaches could compensate for their lower abundance. Additional analyses with the information provided here showed that the per capita reproductive rates, i.e. the number of juveniles produced per female, was inversely

related to P_{OV} ($r^2 = -0.93$; $p < 0.0017$). This suggests that on reflective beaches, the reduced P_{OV} is successfully counteracted by the increasing fertility of ovigerous females with largest sizes.

The combination of narrow swashes and steep slopes generate accretional states, where wave energy is reflected back to sea from waves breaking directly on the steep beach face (Short 1999), thus making reflective beaches safer environments for species living outside the swash climate. Microtidal sandy beaches are wave-dominated and subject to unpredictable, strong and dramatic short-term increases in tide ranges (i.e. up to the sand dunes) generated by storm surges, barometric tides and wind-driven surf off the ocean (Brazeiro & Defeo 1996). These unpredictable events usually determine high mortality rates common of benthic macrofauna on dissipative beaches (reviewed in Defeo 2003). Higher natural mortality on dissipative beaches, estimated by Gómez & Defeo (1999), was mainly explained by unpredictability in barometric tides and higher predation rates by birds, arachnids, crabs and insects, which are abundant in dissipative beaches (Brown & McLachlan 1990). Lower mortality rates on reflective beaches were explained by coastline stability; intrusion of wave-dominated tides is mitigated by the steep face slope on the lower shore, making incoming waves and backwash collide (Gómez & Defeo 1999). This should imply habitat-driven shifts in sandhopper abundance and behaviour according to beach morphodynamics; substantial variations in sandhopper orientation (Scapini et al. 1995) and in the circadian rhythm of locomotor activity (Nardi et al. 2003) were found as a function of coast stability and dynamics.

Following the mesoscale hypothesis of environmental favourability for sandy beach populations suggested by Caddy & Defeo (2003), we predict that microtidal reflective beaches constitute more stable and safer shores for supralittoral species, because their risk of immersion is substantially lower there than on dissipative beaches. This statement has physical and biological support: concerning the former, Short (1999, p. 195) defined modally reflective beaches as the most stable of the 3 beach types (i.e. dissipative, intermediate and reflective), with stable backshores given by very low backshore mobility (see also his Table 1, p. 178). This is shown in our Fig. 2c; the beach face slope (BFS) variability clearly increased from reflective beaches (with the highest sandhopper abundance) to dissipative ones. Thus, reflective environments appear to favour rather than negatively affect fitness features of supralittoral forms. This constitutes our hypothesis of habitat safety for supralittoral forms inhabiting sandy beaches.

Much work remains before the hypothesis of habitat safety could be tested successfully under several envi-

ronmental conditions and species, but in the end it seems likely that single-factor explanations for why sandy beach populations are regulated will prove unsatisfactory. Given the complexity of life histories and processes that underlie biological responses, we argue against a simple relationship between morphodynamics and population features. In this context, existing hypotheses have limited appreciation of the role played by the variety of life-history strategies in explaining sand beach population responses to the environment. As the large interspecific variation in life-history traits suggests that different species could be controlled by different physical factors, we cannot ignore the fact that variations in life-history traits have great potential for expanding our view of the mechanisms controlling sandy beach population regulation patterns in these physically stressful habitats.

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