

# Life history of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda) in sandy beaches with contrasting morphodynamics

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**ABSTRACT:** Exposed marine beaches are physically rigorous habitats in which macrofauna community patterns are related to physical factors such as sedimentary parameters and wave/swash processes. In this context, a consistent increase in species richness, abundance and biomass from reflective to dissipative conditions has been widely reported, and proposed as a paradigm of sandy beach ecology. Here, we examine this hypothesis on the demography and life history characteristics of the sandhopper *Pseudorchestoidea brasiliensis* of Uruguay. Abundance, population structure by sex and size, individual growth, natural mortality, fecundity, female maturity and size at maturity, and the length-weight relationship were compared between populations of 2 microtidal exposed sandy beaches that differed widely in physical characteristics (i.e. grain size, slope, penetrability and water content), during 20 consecutive months. Contrasting with the predictions of 'the sandy beach ecological paradigm', the population of *P. brasiliensis* at the reflective beach presented (1) higher abundance both for males and females; (2) higher egg production potential and recruitment levels; (3) lower natural mortality; and (4) no major differences in individual growth and estimated life span to those of the dissipative beach population. On the contrary, growth in weight, individual fecundity and average size at maturity were higher for the dissipative beach population. We conclude that population level responses to variation in sandy beach morphodynamics may markedly differ from community level responses, and thus macroscale, world-wide community patterns could not necessarily characterise life history and demographic variations of individual species in a similar manner. We suggest that the paradigm of the forces generating patterns in sandy beach communities has underestimated the importance of population regulation mechanisms in these communities.

**KEY WORDS:** Sandhopper · Amphipoda · Population demography · Life history · Sandy beaches · Beach morphodynamics

## INTRODUCTION

The structure of sandy beach communities has been well correlated with morphodynamic characteristics: species diversity, total abundance and total biomass of benthic communities show a dramatic increase from reflective to dissipative beaches (McLachlan 1988 1990, 1996, Defeo et al. 1992a, McLachlan et al. 1993, 1996, Borzone et al. 1996). Coarse sediments, steep

slopes, high substrate penetrability, low organic matter and low sediment water content have been mentioned as physical attributes that make reflective beaches harsh and inhospitable habitats for macrofauna. In contrast, fine sands, flat slopes, low substrate penetrability, and high water content are important characteristics of dissipative beaches (see review in Short 1996), in which high biomass and high abundance of macrofauna usually occur.

The consistent higher levels of species richness, abundance and biomass of macrobenthos in dissipative beaches seems to be valid world-wide and has become a paradigm in sandy beach ecology (McLach-

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lan et al. 1993 and references therein). However, correlational evidence between community descriptors and physical variables showed that the proportion of variance accounted for is usually very low or even non-significant. McLachlan et al. (1993) looked for patterns in sandy beach fauna communities across different geographic regions around the world. They correlated the beach morphodynamic state, estimated by the Dean parameter (Short & Wright 1983), and the number of species, abundance and biomass previously documented in snapshot studies. Results accounted for, respectively, 52, 25 and 17 % of the total variance. This suggests that other environmental factors or population level responses could also contribute to the observed community patterns.

In the above context, despite significant work examining community level responses to sandy beach morphodynamics, we lack information on the demographic effects of different morphodynamic types on sandy beach populations. McLachlan (1990) suggested a decrease of mean individual size from reflective to dissipative beaches. Jaramillo & McLachlan (1993) suggested that some physical processes associated with beach morphodynamics might affect abundance, biomass and mean individual sizes and thus contribute to explaining variations in community structure and the described community patterns. Increasing sand particle size can also limit body size or burrowing ability in the harshest reflective beaches (McLachlan et al. 1995). A review of 15 species of clam from exposed ocean beaches around the world showed that species with larger individual sizes and biomass dominate dissipative beaches of temperate zones, whereas generally smaller species are found on tropical reflective beaches (McLachlan et al. 1996). Dugan & Hubbard (1996) showed that coastal distance, water temperature, beach slope and sediment diversity influence some life history characteristics of *Emerita analoga*. However, with the exception of the beach clam review, these papers are based only on one sampling date covering as many beaches as possible, and thus the effects of beach morphodynamics on population demography and life history traits could be seriously biased by such an instantaneous sampling scheme (see Brazeiro & Defeo 1996). Thus, there are no detailed studies that investigate how the species respond to the environment in demographic terms, i.e. whether the abundance, individual growth, mortality, fecundity and other population dynamic features undergo changes according to sandy beach characteristics.

Peracarids (isopods, amphipods) are usually numerically dominant members of the macrofauna of exposed sandy beaches (Dahl 1952, Croker 1967, Defeo et al. 1992a, 1997). In this setting, the sandhopper *Pseudorchestoidea brasiliensis* (Dana, 1853), classified

in this genus according to Bousfield (1982), inhabits both reflective and dissipative sandy beaches in Uruguay (Defeo et al. 1992a). The common occurrence of this species in contrasting morphodynamic types, from the supralittoral to upper levels of the midlittoral (Cardoso & Veloso 1996, Defeo & Gómez unpubl.), provides a unique opportunity to contrast the response of population demography and life history traits of an individual species with distinct physical characteristics of the environment.

In this paper we try to determine whether the morphodynamic type affects the main demographic characteristics of sandy beach populations, in order to test the recurrence of the above-mentioned community patterns at the population level. For this purpose, we compared the abundance, structure, dynamics and life history characteristics of 2 sandhopper *Pseudorchestoidea brasiliensis* populations that inhabit 2 Uruguayan exposed sandy beaches with contrasting morphodynamics.

## METHODS

**The habitat.** Two exposed microtidal sandy beaches were considered in this paper (Table 1): Barra del Chuy (33° 45' S, 53° 27' W) and Arachania (34° 36' S, 53° 44' W). Barra del Chuy is an exposed beach (score = 13 according to McLachlan's 1980 rating system: Table 1) with fine to very fine, well-sorted sands, a

Table 1. Full characterization of physical and biological attributes of Arachania and Barra del Chuy beaches, in Uruguay. Values after Defeo (1993, unpubl.), Defeo & de Alava (in press) and Defeo et al. (1992a, 1997)

Beach feature	Arachania Mean $\pm$ SD	Barra del Chuy Mean $\pm$ SD
Beach width (m)	39.75 $\pm$ 6.45	67.75 $\pm$ 11.17
Grain size (mm)	0.56	0.20
Sorting (mm)	0.30	0.70
Textural group	Coarse	Fine
Penetrability (cm) <sup>a</sup>	6.30 $\pm$ 0.48	3.74 $\pm$ 0.34
Penetrability (kg cm <sup>-2</sup> )	3.02 $\pm$ 0.19	4.01 $\pm$ 0.13
Water content (%)	7.70 $\pm$ 1.67	12.23 $\pm$ 2.78
Beach face slope (%)	7.80	3.53
Organic matter (%)	0.23 $\pm$ 0.10	0.30 $\pm$ 0.10
Exposure <sup>b</sup>	16 (very exposed)	13 (exposed)
Dean parameter ( $\Omega$ ) <sup>c</sup>	0.5 < $\Omega$ < 1.5	$\Omega$ > 5
Macrofauna species	5	24
Overall density (ind m <sup>-2</sup> )	65 $\pm$ 16	536 $\pm$ 137
Dry biomass (g m <sup>-2</sup> )	11.59 $\pm$ 6.26	20.32 $\pm$ 8.24

<sup>a</sup>Methodology in Defeo et al. (1997)

<sup>b</sup>After McLachlan (1980)

<sup>c</sup> $\Omega$  = breaker height / sand fall velocity · wave period (Short & Wright 1983)

gentle slope, heavy wave action, a wide surf zone and large aeolian tide ranges. This stretch of beach has the highest values of benthic macrofauna richness (24 species, mesh size = 0.5 mm) in Uruguay (Defeo et al. 1992a). Arachania is a very exposed beach (score = 16) with coarse sediments, a steep slope and relatively low macrofauna richness (5 species) (Defeo et al. 1992a, 1997). A full characterization of the properties of both exposed beaches is detailed in Table 1, in order to illustrate the extreme physical differences between them. According to the evidence provided in Table 1 and to Short's (1996) classification, Barra del Chuy could be defined as dissipative and Arachania as reflective. Details on the methodology employed to estimate the physical parameters described in Table 1 were according to Defeo (1993) and Defeo et al. (1992a, 1997).

**Sampling procedures and data analysis.** Samples of sandhoppers were collected during 20 consecutive months, from May 1996 through December 1997, according to a systematic design. Five transects were set up perpendicular to the shoreline and spaced 8 m apart, with sampling stations on each transect beginning at the base of the dunes and continuing at 4 m intervals in a seaward direction, until at least 2 consecutive stations yielded no sandhoppers. Some 75 samples were taken during each sample period, depending on beach profile and species distribution across the beach. At each station, a sheet metal cylinder 27 cm in diameter was used to remove the sediment up to a depth of 40 cm. Each sample 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. Afterwards, sandhoppers were dried at 50°C for 24 h and weighted to the nearest 0.0001 g.

Sandhoppers were classified into 2 size groups: juveniles (non-adults) and adults. Juveniles presented neither a well-developed second gnathopod (males) nor oostegites (females). Adults were categorised as males, females without eggs (hereafter females) and ovigerous females. The monthly proportion of males to females was tested by a  $\chi^2$  test with the Yates correction for continuity (Zar 1996). Species abundance was estimated by the number per strip transect ( $IST$ , ind.  $m^{-1}$ ), by averaging the density  $q$  (ind.  $m^{-2}$  or  $g\ m^{-2}$ ) in each sampling station  $i$  of all  $m$  samples pertaining to transect  $r$  ( $q_m$ ) and multiplying by the corresponding width of the surveyed area ( $w$ ):

$$IST = \frac{\sum_{i=1}^m q_i}{n} w \quad (1)$$

Eq. (1) was employed in order to avoid biased results as a consequence of changing beach profile during

rough and calm conditions (McLachlan 1983, Defeo 1993). Data were analysed by population component (i.e. juveniles, males, females and ovigerous females), using the Kruskal-Wallis test to make comparisons between beaches.

Eggs of ovigerous females were counted and measured, and the length ( $L$ )-fecundity ( $F$ ) relationship was estimated as follows:

$$F = c \cdot L^d \quad (2)$$

where  $c$  and  $d$  are parameters. An analysis of covariance (ANCOVA) was employed to compare the length-fecundity relationship fitted for sandhopper females of Arachania and Barra del Chuy. The individual length was used as the covariate.

A maturity-size relationship was built taking into account information achieved during the reproductive season (see 'Results' for details). Estimates of the fraction of ovigerous females as a function of size were used to model a logistic maturity function and to estimate the average size at maturity, as follows (Restrepo & Watson 1991):

$$B_L = \frac{\beta}{1 + e^{(\alpha_1 - \alpha_2 L)}} \quad (3)$$

where  $B_L$  is the fraction of females bearing eggs in each size class  $L$  and  $\alpha_1$ ,  $\alpha_2$  and  $\beta$  are parameters. The parameter  $\beta$  allows for the maximum fraction of berried females to be  $\leq 1$  and, as such, the non-linear fitting procedure included a penalty function in the minimisation algorithm by which  $\beta$  was constrained to values  $\leq 1$ . The 3-parameter model was preferred over the 2-parameter logistic function with  $\beta$  fixed to 1, for reasons detailed in Restrepo & Watson (1991). The average size at sexual maturity ( $L_{50\%}$ ) was obtained by:

$$L_{50\%} = -\frac{\alpha_1}{\alpha_2} \quad (4)$$

where  $\alpha_1$  and  $\alpha_2$  were defined in Eq. (3) for the egg production ogive. The function was fitted by non-linear least squares, using the quasi-Newton algorithm. The bootstrap method (Efron 1982) was also employed to estimate confidence limits for the model parameters and for  $L_{50\%}$ . Three hundred bootstrap simulations yielded 300 data sets of the maturity-size function, which allowed us to obtain 300 estimates of the median and 95% confidence intervals for the parameters. Given the skewed nature of the parameter distribution functions, we determined the median and used the 2.5th and 97.5th percentile values to define our 95% empirical confidence interval.

Individual growth patterns of sandhoppers were determined by analysing the monthly length frequency composition. To this end, we proceeded as follows: (1) For each month, we separated normally distributed



components of size-frequencies by maximum likelihood, through the application of the routine NORMSEP (Gayanilo et al. 1996). (2) As we followed each cohort through its entire life span, we were able to assign absolute ages to relative ones (lengths) and thus to build an age-length key. Time 0 (birthday) was defined on the basis of the size at recruitment of a sandhopper to the beach (3 mm length). Subsequent ages were assigned from time 0, taking into account the date of the  $i$ th sample, measured as a portion of the year. (3) The age-length key obtained in (2) was used to fit the generalised von Bertalanffy growth function (VBGF) proposed by Pauly & Gaschütz (1979) and modified by Somers (1988). The function allows for the estimation of growth seasonality as follows (Gayanilo et al. 1996):

$$L_t = L_\infty [1 - e^{-(K(t-t_0) + (KC/2\pi) \sin 2\pi(t-WP) - (KC/2\pi) \sin 2\pi(t_0-WP))}] \quad (5)$$

where  $L_t$  is the length at age  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is the curvature parameter,  $t_0$  is the computed age at length zero,  $C$  is the parameter reflecting the intensity of seasonal growth oscillation, and  $WP$  is the time (expressed as a decimal fraction of the year) where growth is slowest (Pauly 1984). The VBGF was fitted by non-linear optimisation methods, and the quasi-Newton approach was used to estimate mean and standard errors for the parameters. Longevity was estimated on the basis of the maximum observed length and the relative age-length key obtained from length frequency analyses.

To compare the VBGF obtained for sandhopper populations at Arachania and Barra del Chuy, we followed an analysis of the residual sum of squares (ARSS) detailed by Chen et al. (1992). We compared (1) the summed residual sum of squares (RSS) and an associated degree of freedom (df) of each VBGF fitted for both sandhopper populations; with (2) the RSS and df resulting from a total VBGF (samples from both populations pooled). The  $F$ -statistic was calculated as (Chen et al. 1992):

$$F = \frac{\frac{RSS_p - RSS_s}{3 \cdot (J-1)}}{\frac{RSS_s}{N-3 \cdot J}} \quad (6)$$

where  $RSS_p$  is the RSS of the VBGF fitted by pooled data,  $RSS_s$  is the sum of the RSS of each VBGF fitted to each population,  $N$  is the total sample size, and  $J$  is the number of samples in the comparison. The difference in VBGF between sandhopper populations was calculated by the comparison between the observed  $F$  and the critical  $F$ , with  $[3 \cdot (J-1)]$  and  $[N-3 \cdot J]$  DF for the numerator and denominator, respectively.

The standard growth index  $\phi'$  (phi prime: Pauly & Munro 1984) was used as a measure of overall growth performance:

$$\phi' = 2 \log_{10}(L_\infty) + \log_{10} K \quad (7)$$

Phi prime has been used successfully as a growth index in sandy beach populations (Defeo et al. 1992b, McLachlan et al. 1996).

The instantaneous rate of natural mortality ( $M$ ) was calculated by length-converted catch curves (LCCC: Pauly et al. 1995). The ELEFAN II routine of the FISAT program (Gayanilo et al. 1996) was used for this purpose, using the growth parameters estimated above as inputs. The equation employed allows for the estimation of total mortality  $Z$  (in this case  $Z = M$ ) where growth exhibits annual oscillations (i.e.  $C > 0$ ):

$$\ln(N) = g - M \cdot t' \quad (8)$$

$N$  being the number of sandhoppers in cohorts 'sliced' by means of successive growth curves,  $g$  the regression intercept,  $t'$  the relative age in that pseudo-cohort, and  $M$ , with sign changed, the unbiased mortality estimate (Pauly et al. 1995).

The length-dry weight was estimated separately by sex by a power function of the form:

$$W = a \cdot L^b \quad (9)$$

where  $L$  is the individual length,  $W$  the individual weight, and  $a$  and  $b$  are parameters. An ANCOVA was employed to compare the length-weight relationship fitted for each sex between beaches, using length as the covariate to remove the effect of individual sizes on weight.

## RESULTS

### Abundance and population structure

Abundance of *Pseudorchestoidea brasiliensis* was significantly higher in the reflective Arachania than in the dissipative Barra del Chuy (Fig. 1). This remained true for the total population (Kruskal-Wallis test  $H_{1,40} = 10.03$ :  $p < 0.01$ ), and for adult males ( $H_{1,40} = 6.08$ :  $p = 0.01$ ) and females ( $H_{1,40} = 11.37$ :  $p < 0.01$ ) separately. Concerning the total population (both sexes pooled), Arachania presented a higher abundance in 17 of the 20 months analysed, whereas females and males had a higher abundance than in Barra del Chuy in 15 and 14 months, respectively. In all cases, monthly variations in abundance per running meter (ISTs) showed 2 clear peaks: May 1996 and June 1997. During most of the time, the ratio of males to females (ovigerous + non-ovigerous) was 1:1 ( $\chi^2$  test:  $p > 0.05$ ), with the exception of February (0.2:1) at Barra del Chuy, and June (0.7:1) and July (0.3:1) 1997 at Arachania.

The reproductive period, as highlighted by the abundance of ovigerous females, presented a similar bimodal, intraannual pattern, in both sandhopper pop-

ulations (Fig. 2): they peaked in October 1996 (austral spring), February–March 1997 (austral summer), the spring peak being recurrent in 1997. Ovigerous females were almost absent from May to September of 1996 and from May to August of 1997. However, ovigerous females were significantly more abundant in the reflective beach ( $H_{1,24} = 8.31$ ;  $p < 0.01$ ). This prevalence was consistent in 10 of the 12 months in which gravid females were registered (Fig. 2).

Juvenile sandhoppers showed the same bimodal pattern as ovigerous females, with an average time delay of 2 mo between the peaks of massive maturation and recruitment to the beach (Fig. 2). Juveniles peaked in December 1996, May–June 1997 and October to December 1997. Consistent with the trend observed in ovigerous females, juveniles at Arachania were significantly more abundant than in Barra del Chuy ( $H_{1,36} = 4.12$ ;  $p = 0.04$ ).

### Fecundity and maturity functions

The minimum size of an ovigerous female was 7.3 mm for Barra del Chuy and 7.8 mm for Arachania, whereas the maximum observed size was 12.2 and 12.1 mm, respectively. The relationship between the number of eggs per brood and female body length (Eq. 2) was statistically significant for both sandhopper

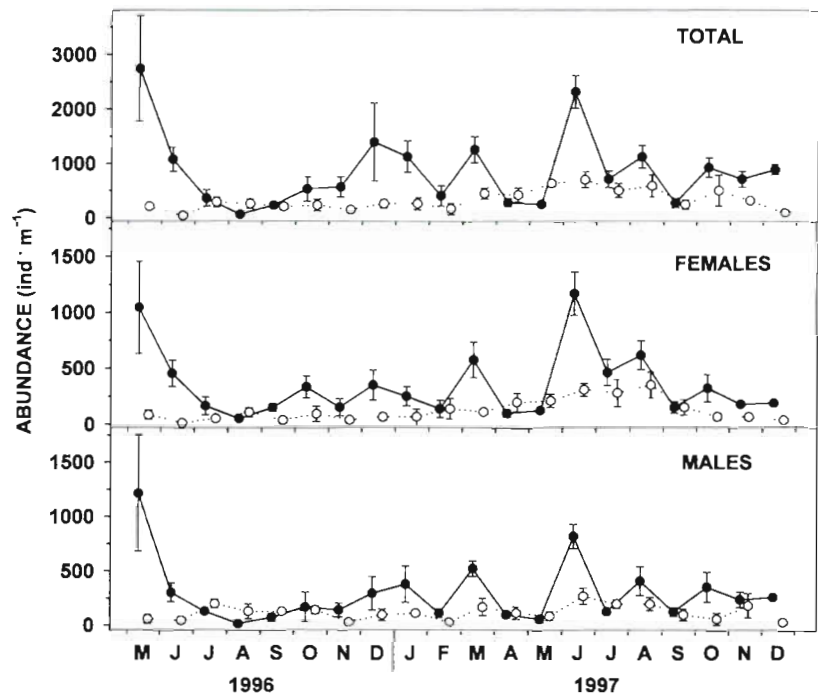


Fig. 1. *Pseudorchestoidea brasiliensis*. Monthly variations in abundance (ind.  $m^{-1}$ : mean  $\pm$  SE) of the total population, females and males in Barra del Chuy (---○---) and Arachania (—●—)

populations (Table 2). Female sandhoppers at Barra del Chuy had higher fecundity than those of Arachania (ANCOVA  $F_{1,276} = 20.66$ ;  $p < 0.01$ ) (Fig. 3a). However, the expected number of eggs per running meter, estimated by the product of mean number of ovigerous females and mean individual fecundity, was more than 2 times higher for females at Arachania (e.g. 806 eggs  $m^{-1}$  in October) than for Barra del Chuy (300 eggs  $m^{-1}$

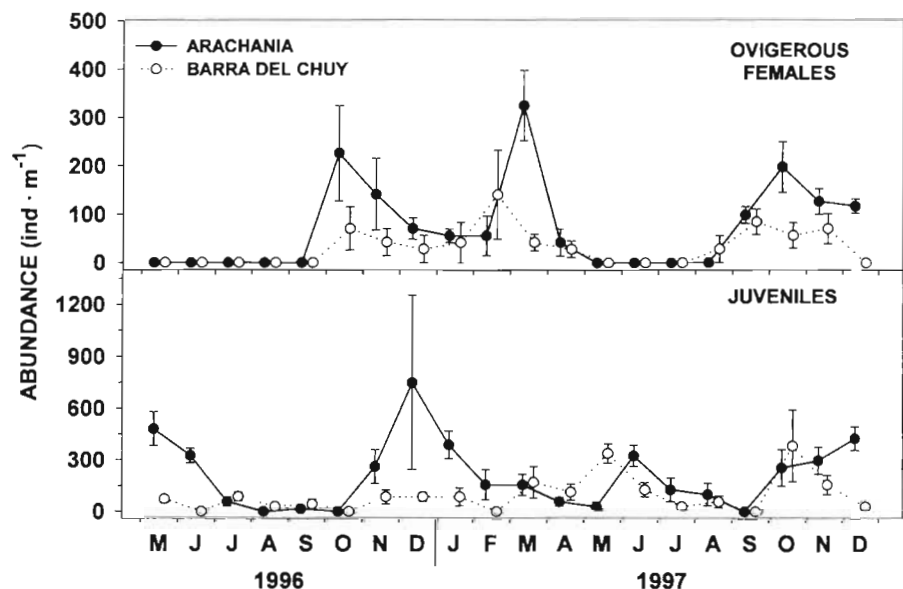


Fig. 2. *Pseudorchestoidea brasiliensis*. Monthly variations in abundance (ind.  $m^{-1}$ : mean  $\pm$  SE) of ovigerous females and juveniles in Arachania and Barra del Chuy

Table 2. *Pseudorchestoidea brasiliensis*. Parameters of the fecundity function (Eq. 2) fitted for Barra del Chuy and Arachania populations by non-linear regression. Results of ANCOVA are also shown

Parameter	Arachania		Barra del Chuy	
	Mean (SE)	p	Mean (SE)	p
c	0.03 (0.03)	0.3191	0.02 (0.01)	0.1496
d	2.21 (0.39)	0.0001	2.40 (0.29)	0.0001
R <sup>2</sup>	0.18	0.0001	0.38	0.0001
ANCOVA: $F_{1, 276} = 20.66$ ; $p = 0.00008$				

in October). This was consistent with the higher number of juveniles per running meter in the reflective beach.

The progression from immaturity to maturation showed a successive increase in the proportion of mature female sandhoppers with size, and thus the matu-

Table 3. *Pseudorchestoidea brasiliensis*. Parameters of the maturity function (Eq. 3) and average size at maturity  $L_{50\%}$  (Eq. 4) estimated from (a) non-linear regression (all data); and (b) bootstrap analysis. In this case, the median and 95% asymmetric confidence interval (CI: percentile approach) resulting from 300 bootstrap runs are presented

Parameter	Arachania		Barra del Chuy	
	Mean (SE)	p	Mean (SE)	p
<b>(a) Non-linear regression</b>				
$\beta$	0.86 (0.02)	0.0001	1.00 (0.00)	0.0000
$\alpha_1$	17.55 (2.54)	0.0062	8.22 (1.89)	0.0224
$\alpha_2$	-2.01 (0.30)	0.0066	-0.92 (0.21)	0.0216
$L_{50\%}$ (mm)	8.74		8.92	
R <sup>2</sup>	0.995		0.949	
<b>(b) Bootstrap</b>				
$\beta$	0.86	0.79; 0.93	1.00	0.82; 1.00
$\alpha_1$	18.63	7.91; 28.75	9.11	0.68; 44.57
$\alpha_2$	-2.13	-0.93; -3.26	-1.02	-0.16; -6.12
$L_{50\%}$ (mm)	8.72	8.43; 9.22	8.90	4.29; 9.30
R <sup>2</sup>	0.998	0.99; 1.00	0.953	0.25; 1.00

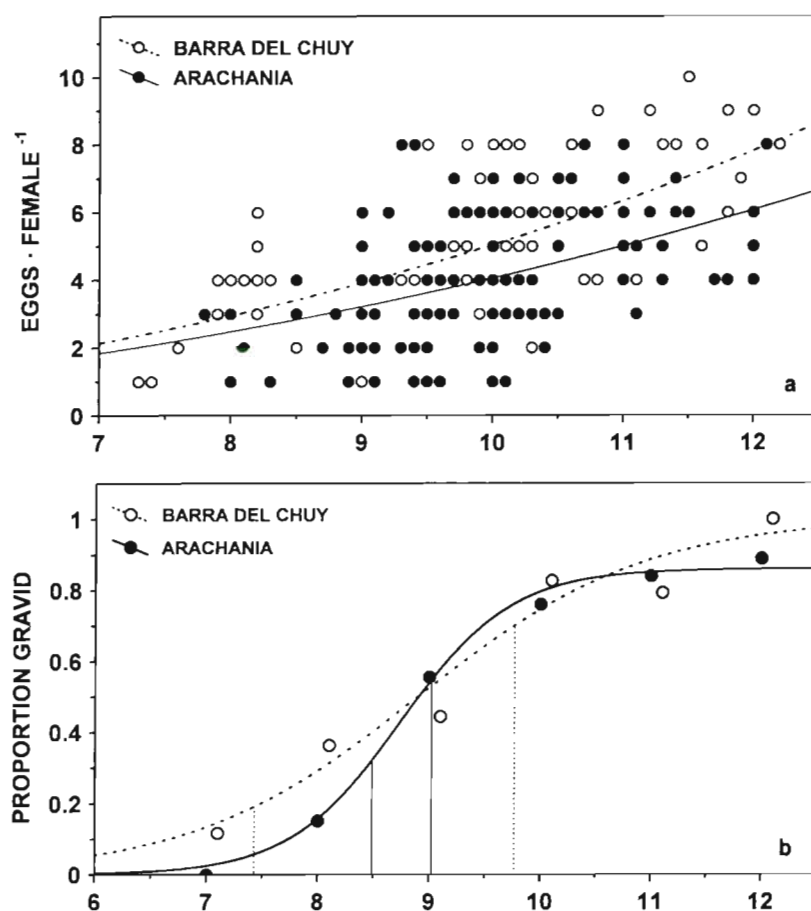


Fig. 3. *Pseudorchestoidea brasiliensis*. (a) Fecundity and (b) maturity functions at the reflective (Arachania) and dissipative (Barra del Chuy) beach, fitted by non-linear regression (details of results are given in Table 2 & 3). Vertical lines in (b) represents the SD estimate for  $L_{50\%}$ , obtained by 300 bootstrap runs of the maturity function

riety-size relationship for both populations was successfully explained by the 3-parameter sigmoid function described by Eq. 3 (Table 3). The average size at maturity  $L_{50\%}$  (Eq. 4) was 8.74 mm for sandhoppers at Arachania and 8.92 mm for Barra del Chuy (Table 3a). In both cases, successive increments in proportion mature at size were observed, but the resulting sigmoid function was steeper for females at Arachania (Fig. 3b), suggesting an abrupt transition to maturity between 8 mm (15%) and 9 mm (56%). We never found 100% of ovigerous females for a given length in Arachania, whereas females at Barra del Chuy were 100% mature in the oldest length class (12 mm: Fig. 3b). This was reflected in the higher asymptote  $\beta$  at Barra del Chuy (Table 3a, Fig. 3a).

The above results were confirmed by bootstrap analysis (Table 3b, Fig. 4). The empirical distribution of  $\beta$  significantly differed between populations (K-S test:  $p < 0.001$ ) (Fig. 4a). In Arachania,  $\beta$  estimates ranged from 0.785 to 0.955, never attaining unity; in contrast,  $\beta$  was equal to 1 in 250 of the 300 bootstrap simulations for the Barra del Chuy data set. The same trend was also found for the  $L_{50\%}$  empirical distribution functions (K-S test:  $p < 0.001$ ). The one at Barra del

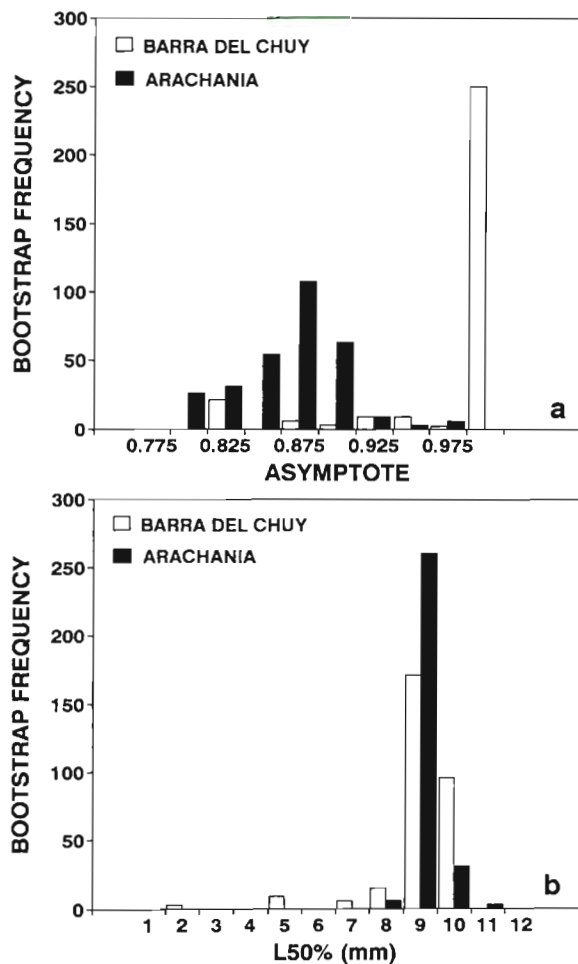


Fig. 4. *Pseudorchestoidea brasiliensis*. Bootstrap distribution functions of: (a) the asymptote  $\beta$  of the maturity function (Eq. 3); and (b) the mean size at maturity  $L_{50\%}$  (Eq. 4), discriminated by beach

Chuy was strongly skewed to the left (skewness = -3.76), whereas Arachania's was skewed to the right (skewness = 1.82) (Fig. 4b). As a result, the empirical confidence interval for the Barra del Chuy population was wider than that of Arachania (Fig. 3b, Table 3b). Median estimate of  $L_{50\%}$ , used instead of the mean as better indicator of the central trend for asymmetric distributions, was significantly higher for Barra del Chuy sandhoppers ( $H_{1,600} = 24.19$ ;  $p \ll 0.01$ , Table 3b).

#### Growth, mortality and the length-dry weight relationship

The minimum observed length was 3.0 mm and the maximum 12.2 mm for both

Table 4. *Pseudorchestoidea brasiliensis*. Growth parameters (annual basis) determined by non-linear fitting of the von Bertalanffy growth function (VBGF) for Barra del Chuy and Arachania populations.  $t_0$  was fixed for Barra del Chuy prior to fitting (see text)

Parameter	Arachania		Barra del Chuy	
	Mean (SE)	p	Mean (SE)	p
$L_{\infty}$ (mm)	11.64 (1.08)	0.0000	11.27 (1.71)	0.0000
$K$ (yr <sup>-1</sup> )	1.61 (0.59)	0.0237	1.88 (0.36)	0.0005
$C$	0.86 (0.16)	0.0005	0.83 (0.13)	0.0001
$WP$	0.41 (0.03)	0.0000	0.35 (0.04)	0.0000
$t_0$ (yr)	-0.175 (0.07)	0.0273	-0.175 Fixed	
$R^2$	0.98	0.0000	0.95	0.0000
$\phi'$	2.34		2.38	
Max. length (mm)	12.2		12.2	
Est. life span (mo)	14		13	

sandhopper populations. Mean individual sizes in each beach did not differ between sexes during the 20 analysed months (ANOVA test  $F = p > 0.05$ ). Thus, in order to estimate individual growth of the species, we focused on the whole population structure and did not search for differences in growth rates by sex.

Individual growth of the sandhopper *Pseudorchestoidea brasiliensis* did not vary between beaches. The analysis of population structure by means of the NORMSEP-maximum likelihood approach clearly identified one or 2 comparable length modal classes in the frequency distributions for both populations. The progression of modal lengths throughout the entire life span showed a striking similarity between populations (Fig. 5). Consequently, growth population parameters were very similar (Table 4), and the seasonal curves fitted separately for each population reflected almost

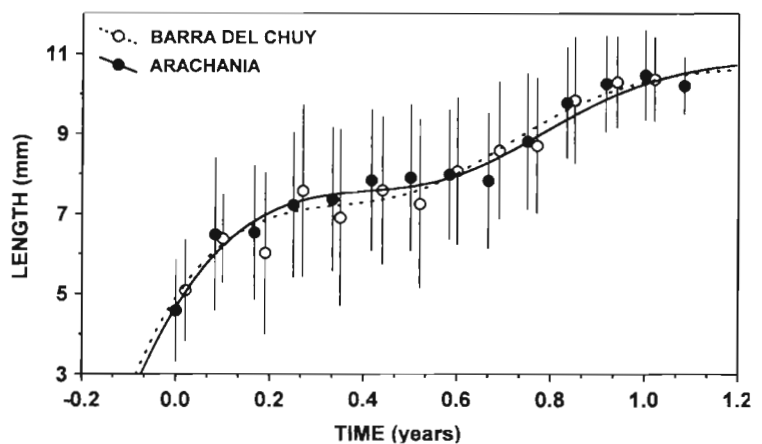


Fig. 5. *Pseudorchestoidea brasiliensis*. Seasonal growth curves fitted for Arachania and Barra del Chuy populations. The vertical lines represent the modal lengths ( $\pm$  SD) determined by maximum likelihood at each age



the same growth rates (Fig. 5). The variance explained by the non-linear fitting procedure of the VBGF was higher than 95% in both cases, and all the regression parameters were always statistically significant ( $p < 0.05$ ; Table 4). Both models easily converged to a global minimum sum of squares (SSQ) value. In the case of Barra del Chuy, the parameter  $t_0$  was fixed in  $-0.175$  yr for 2 reasons: (1) it converged rapidly in the estimation of a global minimum SSQ; and (2) this value was consistent with the above mentioned average time delay of 2 mo between the peaks of massive maturation and recruitment to the beach. The striking similarity between estimates of the VBGF determined that the statistical comparison through the ARSS did not differ between populations ( $F$ -test = 0.77;  $p > 0.50$ ). This similarity determined very close  $\phi'$  values (Table 4).

The parameter  $C$  was close to 1 in both cases, reflecting intense intra-annual oscillations in growth; while the winter point ( $WP$ ) was 0.41 for Arachania and 0.35 for Barra del Chuy, implying a minimal growth in austral fall (April–May). Slow growth persisted until late winter (August), and increased markedly in austral spring, starting in September (Fig. 5). According to the projection of the growth model fitted to each population and to the last mode identified by following the cohort through its entire life span in the benthic environment, a longevity of nearly 13 and 14 mo was estimated for sandhoppers at Barra del Chuy and Arachania, respectively.

The instantaneous natural mortality coefficient  $M$  was higher for the dissipative beach population (Table 5). The LCCC drawn for both sandhopper populations showed that  $M$  (mean  $\pm$  SE) was  $2.47 \pm 0.39$  yr $^{-1}$  ( $r = -0.944$ ;  $p < 0.01$ ) for Barra del Chuy sandhoppers and  $2.35 \pm 0.20$  yr $^{-1}$  ( $r = -0.985$ ;  $p < 0.01$ ) for Arachania's population (Table 5).

The individual dry weight at length of males and females at Barra del Chuy was significantly higher than in Arachania, and thus the corresponding length-dry weight relationship differed significantly between beaches, both for males (ANCOVA  $F_{1,342} = 26.90$ ;  $p < 0.01$ ) and females (ANCOVA  $F_{1,395} = 34.88$ ;  $p < 0.01$ ) (Fig. 6, Table 6).

## DISCUSSION

Most of the life history and population demography features of *Pseudorchestoidea brasiliensis* did not respond to beach morphodynamics as predicted for sandy beach communities. The reflective beach population

Table 5. *Pseudorchestoidea brasiliensis*. Mortality estimates and associated statistics derived from the length-converted catch curve (Eq. 8) fitted for Barra del Chuy and Arachania populations

Parameter	Arachania		Barra del Chuy	
	Mean (SE)	p	Mean (SE)	p
$g$	8.54 (0.31)	0.0001	10.09 (0.55)	0.0001
$M$	2.35 (0.20)	0.0003	2.47 (0.39)	0.0014
$R^2$	0.97	0.0003	0.89	0.0014

presented (1) higher abundance of males, females and ovigerous females; (2) higher egg production potential and recruitment levels; (3) lower natural mortality; and (4) no major differences in individual growth and estimated life span when compared with the dissipative beach population. Thus, even though beach morphodynamics could explain community patterns relatively well, this would not be always true at a population level.

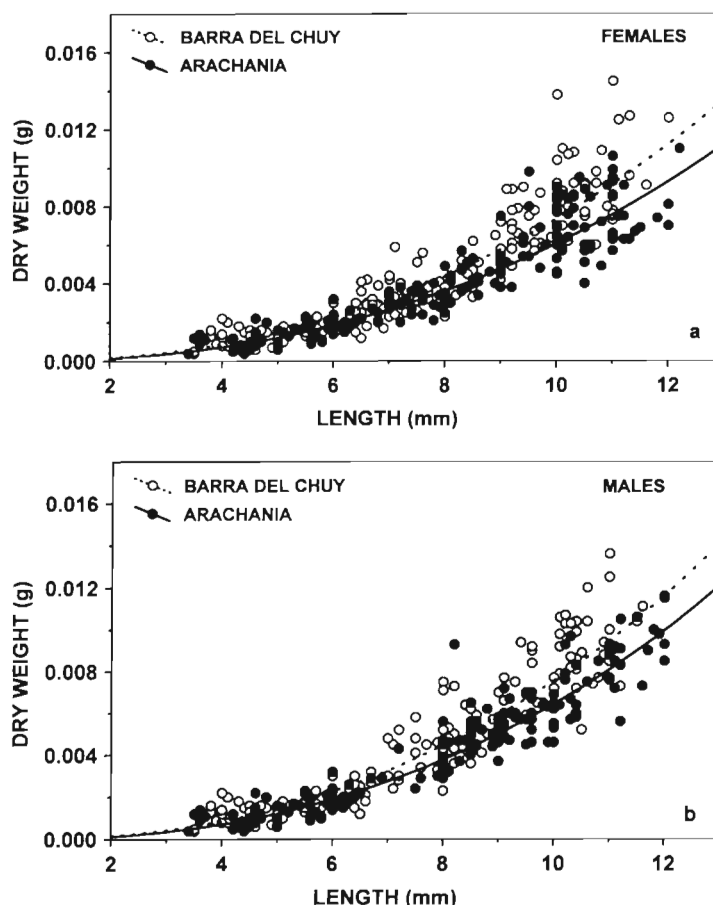


Fig. 6. *Pseudorchestoidea brasiliensis*. Length-dry weight relationship fitted by sex for Arachania and Barra del Chuy populations. Statistical results are detailed in Table 6



Contrary to the predictions of the main hypotheses used to explain sandy beach community patterns, total abundance of *Pseudorchestoidea brasiliensis* was significantly higher in the reflective beach in 17 of the 20 months analysed in this study. This trend was highly consistent for all population components (males, females, ovigerous females and juveniles). Cardoso & Veloso (1996) also characterised *P. brasiliensis* as a typical and abundant species in the midlittoral of reflective beaches of Rio de Janeiro State, Brazil (23° 05' S). However, Gianuca (1983) reports the species as a typical inhabitant of the lower fringe of the supratidal zone at dissipative beaches of southern Brazil (31° S). The co-occurrence of sandhoppers in contrasting morphodynamic environments on a biogeographic scale denotes a high long-term phenotypic plasticity (Brown 1996) that enabled the species to inhabit drastically different sandy beaches.

The higher abundance of sandhoppers at the reflective beach was similar to the pattern found by Defeo et al. (1997) for the cirrolanid isopod *Excirrolana braziliensis*, which co-occurs at dissipative and reflective beaches of Uruguay. The higher abundance of *E. braziliensis* at reflective beaches was attributed to inhibitory competitive effects by the dominant congeneric isopod, *Excirrolana armata*, in dissipative beaches (de Alava & Defeo 1991). On the contrary, Jaramillo & McLachlan (1993) showed increasing abundance towards dissipative conditions for the same cirrolanid isopod (*E. braziliensis*), and also for the talitrid *Orchestoidea tuberculata* and the sand crab *Emerita analoga*. Dugan & Hubbard (1996) did not find any correlation between abundance and biomass of *E. analoga* and beach morphodynamics. However, these papers were based on snapshot studies and thus could not be properly used to address variations in population dynamics and demography.

No differences were found between the 2 sandhopper populations in the number of reproductive and recruitment events (Fig. 2): ovigerous females and juveniles peaked twice within the year, following a distinct bimodal pattern in both beaches. In spite of this agreement, abundance of ovigerous females and juveniles was significantly and consistently higher in Arachania's reflective beach. The number of eggs per brood at size followed the reverse pattern, i.e. it was significantly higher for Barra del Chuy female sandhoppers (Fig. 3a). The higher individual fecundity at size for the dissipative beach population could be explained by (1) evolutionary aspects directed to counteract higher mortality rates occurring at early stages of the life history; and (2) a higher amount of food availability that enhances fecundity. Concerning (1), sandhoppers at Barra del Chuy showed higher mortality rates (see full discussion below). Thus, the higher

Table 6. *Pseudorchestoidea brasiliensis*. Parameters of the linearised length-weight relationship for Barra del Chuy and Arachania populations, discriminated by sex. Regressions and parameter estimates were highly significant in all cases ( $p < 0.001$ ). ANCOVA results are also shown

Parameter	Arachania Mean (SE)	Barra del Chuy Mean (SE)
<b>Males</b>		
lna	-10.5496 (0.1273)	-10.3219 (0.1378)
b	2.3941 (0.0622)	2.3602 (0.0699)
R <sup>2</sup>	0.90	0.87
ANCOVA $F_{1,342} = 26.90$ ; $p < 0.00001$		
<b>Females</b>		
lna	-10.4678 (0.1285)	-10.2712 (0.1288)
b	2.3359 (0.0627)	2.3224 (0.0646)
R <sup>2</sup>	0.88	0.86
ANCOVA $F_{1,265} = 34.88$ ; $p < 0.00001$		

fecundity might be seen as an internal adjustment (*sensu* Stearns & Koella 1986) defined as a compensatory effect linked to other life history traits (mortality in this case). Argument (2) supports the hypothesis of dissipative beaches as more suitable habitats for feeding than reflective beaches (McLachlan 1983, Defeo & Scarabino 1990). Dissipative beaches are defined as self-sustaining ecosystems, in which food availability is provided in high amounts by the beach itself and by a surf zone extremely rich in surf phytoplankton and water-column microbes (Brown & McLachlan 1990). This fact generates a much larger trophic chain, a strong recycling/regeneration of nutrients, intense microbial decomposition and high availability of organic matter and detritus, i.e. high food availability for sandhoppers. On the contrary, reflective beaches without main surf zones such as Arachania, are totally dependent on food imports, mainly as carrion, thus supporting low macrofauna (Table 1; Defeo et al. 1992a).

The 3-parameter model accurately explained the observed variability in the proportion of berried females in both sandhopper populations. The maturity at size distribution of both populations corresponded to a type II distribution described by Trippel & Harvey (1991) that characterises stable populations with a gradual transition from immaturity to maturity. Nevertheless, the form of the logistic maturity function differed between sandhopper populations. Arachania's sandhoppers had a steeper maturity function, suggesting a more abrupt transition to maturity; moreover, this population failed to attain 100% maturity at any length class (Fig. 3b), probably as a well-known scarcity of food documented in reflective beach systems. In contrast, female sandhoppers at the dissipative beach showed a gradual increase in the proportion of individ-

uals with length, with 100% reaching maturity at 12 mm. As a result, bootstrap simulations denoted significantly higher values of the asymptote  $\beta$  of this sigmoid model for the dissipative beach population. This agrees with the high fecundity at size found in the dissipative beach population. Thus, the release of larger hatchlings should be a strategy to counteract higher mortality rates and to increase survival probability of juveniles. According to the results obtained, local conditions may exert a strong influence on reproductive characteristics of sandhopper populations.

The length at maturity  $L_{50\%}$  was higher for the dissipative beach population. A late-maturing sandhopper should have a higher initial fecundity than an earlier-maturing organism with the same growth rate (i.e. *Arachania's* sandhoppers). The presence of larger mature female sandhoppers at Barra del Chuy, together with a higher fecundity at size, explain the higher lifetime reproductive output at Barra del Chuy. In this context, delaying maturity, higher fecundity and individual weight at size should be seen as mechanisms directed to generate numerous offspring of higher quality, thereby providing organisms with a higher life span and decreasing the usually higher rates of juvenile mortality (Stearns & Koella 1986; see discussion below). Dugan et al. (1994) also found that the largest sizes of ovigerous *Emerita analoga* sand crabs tended to increase in dissipative beaches. They showed a significant correlation between size at maturity and a combination of grain size and surf water temperatures, attributing this trend to a major amount of food availability (surf zone chlorophyll *a*) in dissipative beaches. These concepts should also be invoked to explain higher individual weight, fecundity at size and average size at maturity for the sandhopper population at Barra del Chuy.

Growth rates of both sandhopper populations were almost identical (Fig. 5 and Table 4), and thus variations in individual sizes and growth rhythms of *Pseudorchestoidea brasiliensis* were not affected by beach morphodynamics. McLachlan (1990) suggested that the individual size and weight of crustaceans increased from dissipative to reflective beaches. Jaramillo & McLachlan (1993) showed that another talitrid amphipod, *Orchestoidea tuberculata*, tended to be larger with increasing grain size and beach face slope (i.e. reflective beach characteristics), but these trends were not significant. They also showed that other crustaceans, the isopod *Excirolana brasiliensis* and the sand crab *Emerita analoga*, have no clear patterns in the relationship between body size and physical beach features. Defeo et al. (1997) documented an increase in individual size for the cirrolanid isopod *E. brasiliensis* in reflective beaches. The limited temporal scale of these studies precludes powerful statements

and thus could be invoked only as circumstantial evidence. Nevertheless, the contradictory trends illustrated above imply that population level responses do not necessarily follow the general trends described for community level responses. Thus, beach morphodynamics could not necessarily explain long-term and mesoscale variations in life history traits, demography and population dynamics for a single species (e.g. the isopod *E. brasiliensis*, see detailed discussion in Defeo et al. 1997). In the specific case of *P. brasiliensis* of Uruguayan sandy shores, similar growth rates in contrasting environmental conditions should mean that the phenotype is locally adjusted in order to optimise fitness (Stearns & Koella 1986, Scapini et al. 1988, 1995, 1996, Scapini 1997 and references therein).

Natural mortality of *Pseudorchestoidea brasiliensis* tended to be higher in Barra del Chuy. The higher mortality at the dissipative beach could be explained by: (1) unpredictability in aeolian tide ranges; (2) higher rates of predation by many birds and arachnids, crabs and insects (Griffiths et al. 1983, Brown & McLachlan 1990, Colimbini & Chelazzi 1996), which are far more abundant in dissipative beaches. Concerning (1), Barra del Chuy is a microtidal beach subject to short-term, unpredictable and strong increases in aeolian tide (i.e. up to the supralittoral) caused by onshore winds, storms, and wind-driven surf off the ocean (Brazeiro & Defeo 1996). These unpredictable events usually determine common mass mortalities of benthic macrofauna (Defeo 1993), including juvenile sandhoppers, which settle at lower beach levels and are restricted to the substratum surface (Mardsen 1991, Cardoso & Veloso 1996). The probability of occurrence of mass mortalities of juvenile sandhoppers at a dissipative beach could be higher than in a reflective beach, in which intrusion of aeolian tides is mitigated by the steep face slope on the lower shore, making incoming waves and backwash collide.

Mortality agents might also be operating during early life history stages, in which predation rates by birds and insects are found to be substantial (Brown & McLachlan 1990). This statement could be supported by the opposite pattern between individual fecundity (higher at the dissipative beach) and abundance of ovigerous females and recruitment (higher at the reflective beach). *Pseudorchestoidea brasiliensis* develops without larval stage, and juveniles are released from the brood-pouch of the female at an adult-like autonomous stage. This implies that variations in recruitment abundance should be explained almost exclusively by variations in fecundity and abundance of gravid females. However, the results of reproductive potential (i.e. the product of *IST* estimates of ovigerous females by mean individual fecundity) for the peak of the reproductive season (i.e. October 1996) clearly pre-

dicted a higher abundance of juveniles for Barra del Chuy than that observed in the field. This suggests high mortality rates during this stage, and thus explains why recruitment was consistently lower in the dissipative beach population, in spite of high values of mean individual fecundity. We suggest that microtidal reflective beaches constitute more stable shores for the sandhopper *P. brasiliensis* in which the risks of immersion, desiccation and predation are reduced. This should be subjected to further analysis and experimentation.

In summary, the results obtained herein showed that beach morphodynamics might not always contribute to explaining patterns in the life history of macrofauna species. Population level responses to variation in beach characteristics may differ markedly from community level responses, and thus macroscale community patterns could not necessarily characterise life history and demographic variations in individual macrofauna species. This might be especially true in species like *Pseudorchestoidea brasiliensis*, with great plasticity in life history traits that enables the species to survive under contrasting environmental conditions. The results detailed in our paper should lead to the conclusion that life histories of sandy beach populations are plastic and have dissimilar responses to physical characteristics of the environment. Future work will be crucial to understand the role of morphodynamics in shaping life history traits and to develop life history evolution theory in a habitat regarded as the most physically harsh of all marine environments.

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