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PRIMARY RESEARCH PAPER

Response of the meiofaunal annelid *Saccocirrus pussicus* (Saccocirridae) to sandy beach morphodynamics

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Abstract Interstitial annelids in the family Saccocirridae live in the extremely turbulent and dynamic swash zone of exposed sandy beaches. We examine herein the relationship between distribution patterns of *Saccocirrus pussicus* du Bois-Reymond Marcus 1948 and morphodynamics, hydrodynamic zones, and environmental variables at beaches sampled along the Brazilian Atlantic coast. The occurrence and the abundance of *S. pussicus* at regional scale were positively correlated with the presence of a steep slope, large waves and coarse sand, which are characteristic of reflective beaches. On a local scale, *S. pussicus* occurred at the swash zone and breaking surf zone of reflective beaches. On a microscale, it preferred the upper 20 cm of the swash zone sediment. *Saccocirrus pussicus* prefers hydrodynamic zones, which change temporally, suggesting dependence with the dynamics of the surging and plunging waves. The coupling of morphological and behavioral adaptations of *S. pussicus* to beach morphodynamics is crucial for understanding its surfing life strategies within turbulent environments.

Keywords Interstitial annelids · Grain size · Surf-scaling parameter · Beach morpho- and hydrodynamics

Introduction

Few interstitial animals are adapted to the harsh hydrodynamic conditions in the surf-swash zones of

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exposed beaches. The high turbulence constantly threatens to resuspend these microscopic animals into the water column where they can be swept away to unfavorable areas, or become exposed to predators (Palmer, 1988; Rodriguez, 2004). Most interstitial groups avoid such risks by occupying deeper layers (Meineke & Westheide, 1979; Foy & Thistle, 1991). However, *Turbanella hyalina* Schultze 1853 can be occasionally dislodged from the sediment into the water column and return to the bottom by adhering to relatively heavy mobile sand grains after short periods in suspension (Boaden, 1968). Adhesion to individual sand grains occurs in several interstitial annelids genera including *Saccocirrus*, *Hesionides*, and *Protodrilus* (Giere, 2009; Di Domenico et al., 2013; Martínez et al., 2013c). Among macrofauna, such drifting in the sediment–water interface at the mercy of the waves is called “surfing” (McLachlan & Brown, 2006). Examples of macrofauna that exhibit this behavior include species of molluscs belonging to the genera *Donax* (Ellers, 1995), *Bullia* (Brown et al., 1989) and *Olivella* (Vanagt et al., 2008), and the mole crab *Emerita* (Dugan et al., 2000). This surfing behavior within the swash zone and among the waves is synchronized with the tide (see McLachlan & Brown, 2006; Vanagt et al., 2008). This allows the animals to access resources in the uppermost sediment layer and water column (Jumars & Self, 1986; Kihslinger & Woodin, 2000). Comparatively, little information is available for sandy beach meiofauna (Boaden, 1968; Rodriguez, 2004).

The morphodynamic state of a beach essentially reflects the relationship between the size of the sediment particles, the wave action, and the tides (Short, 1999; Defeo & McLachlan, 2005; McLachlan & Brown, 2006). The relationships among these factors produce a range of beach states, which span a continuum from reflective to dissipative beach systems (Short, 1999). Overall, wave-breaking zones become gradually more energetic from reflective to dissipative (Short, 1999; McLachlan & Brown, 2006), and these differences in energy relate to wave exposure. Accordingly, the morphodynamic state of a beach depends primarily on the geological origin of the sediments (Jackson et al., 2005) and oceanographic conditions (Short, 1999). Wide and flat beaches are often protected by submersed sandbars, which offer wide breaker zones with a larger amount of wave energy dissipation. In these dissipative systems, wave-breaking zones are divided into surf and swash zones, respectively (Hoefel & Elgar, 2003). Conversely, in steep and narrow beaches, the waves break directly on the beach face, whereby transferring high energy into the swash zone and leads to reflective states (Short & Hesp, 1999). Seasonal or temporary variations in these conditions often change the morphodynamic state of a given locality. This happens in regard to waves, which are larger during storm and swells events (Komar, 1998). When these conditions are present, beaches become more turbulent and variable, with intense offshore-directed currents and high rates of cross-shore sediment transport (Masselink & Puleo, 2006; Butt et al., 2001). Since the surfing behavior in the swash-surf zone depends on the resuspension of the sediment by waves, the prevalence of surfing in meiofauna species may be related to beach morphodynamic state and hydrodynamic zones.

Despite the high turbulence and environmental instability, members of Saccocirridae are present among swash and wave-breaking zones of reflective beaches (Di Domenico et al., 2009). Saccocirrids are grouped into two genera, *Saccocirrus* Bobretzky, 1872 and *Pharyngocirrus* (Di Domenico et al., 2014b), well delineated by morphology, habitat preferences, and feeding guilds (Brown, 1981; Jouin & Gambi, 2007; Di Domenico et al., 2014a, b). *Saccocirrus* species such as *Saccocirrus papillocercus* Bobretzky, 1872, *S. major* Pierantoni, 1907, *S. minor* Aiyar & Alikunhi, 1944, and *Saccocirrus pussicus* du Bois-Reymond Marcus, 1948 are indeed mostly recorded in the intertidal zone of sandy beaches (Martin, 1977; Brown, 1981; Sasaki, 1981; Sasaki & Brown, 1983; Di Domenico et al., 2014a), where they are reported in high densities (Jouin & Gambi, 2007; Di Domenico et al., 2009).

We assess herein the horizontal and vertical distribution patterns of *S. pussicus* using a multi-scale spatial analysis (at regional, local, and microscales) to test its preference for reflective or dissipative beaches and swash or surf zones. Sandy beaches with different morphodynamic states along the Southern Brazilian coast were sampled several times between 2005 and 2009. At the regional scale (tens to hundreds of kilometers) we tested distribution and abundances throughout dissipative and reflective beach environments; at the local scale (dozens of meters) we investigated preferences among swash and surf zones; at the microscale (centimeters) we examined superficial sediment layer preferences of *S. pussicus* using

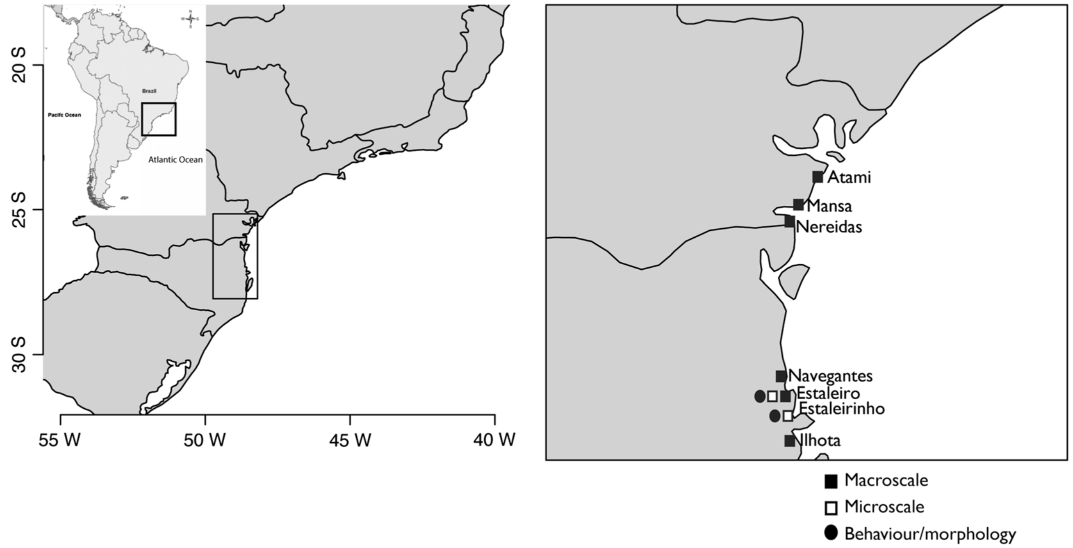

Fig. 1 Map of study area showing sandy beaches sampled in Southwestern Atlantic (Southern Brazil) used in the regional- and local-scale analyses: Ilhota, Estaleiro, Navegantes, Nereidas, Mansa, and Atami. Samples used in the microscale analysis and behavior/morphology studies: Estaleiro and Estaleirinho

vertical distribution analyses. These results are coupled with laboratory behavioral observations on *S. pussicus*, and secondary data from the available literature on *Saccocirrus* morphology and ecology.

Methods

Study area

The sampled beaches were located between 25°S 47°W and 27°S 49°W in the Southwestern Atlantic. Estaleiro, Estaleirinho, Ilhota, Mansa, Navegantes, Nereidas, and Atami (Fig. 1) beaches were chosen based on their a priori morphodynamic states, previously assessed by Borzone et al. (1996), Barros et al. (2001), and Klein & Menezes (2001). The local tidal regime consists of micro-tides of discontinuous semi-diurnal periods with mean amplitude of 0.8 m (Schettini et al., 1999), but up to 1.2 m during meteorological tides (Carvalho et al., 1996; Schettini et al., 1999). The investigated beaches are shaped by four major sea states: (i) sea winds from East-Northeast (ENE), predominant throughout the year; (ii) sea winds from South-Southeast (SSE); (iii) swells from Southwest (SW); and (iv) swells from East (E). Southwest swells and waves from the E are more frequent during the winter and spring due to increased frequency and intensity of frontal systems. More energetic incident waves occur from SSE (Alves & Melo, 2001).

Patterns in *S. pussicus* density were compared among three reflective beaches (Estaleiro, Ilhota, and Mansa), and three intermediate to dissipative beaches (Navegantes, Nereidas, and Atami) at both regional and local scales. Microscale (centimeters) analysis of vertical distribution patterns of *S. pussicus* density and behavioral analyses were carried out only at the Estaleiro and Estaleirinho beaches, the latter not sampled at the regional and local scales. Both localities are exposed to swells from SSE and E. They display coarse grain sizes, steep slopes, embayment between headlands, absence of redox layers, and high hydraulic flux in the swash zone.

Sampling design

Macroscale: regional and local

Samples for regional- and local-scale analyses were taken along three transects (separated between 50 and 100 m), at the six studied beaches, on two sampling periods (several days in September 2005 and several days in March 2006). Seven haphazard samples were collected at two 3 × 3 m sampling areas established along each transect, one in the swash zone and one in the surf zone. The swash zone was defined as the zone where surging or just-breaking waves move up the foreshore (uprush) and flow back down over the foreshore slope infiltrating the sediment (backwash). The surf zone was characterized by oscillatory shoaling waves (Bauer & Allen, 1995). Samples in the swash zone where collected at 0–0.1 m depth, whereas samples in the surf zone were collected during low-water spring tides at a standard depth of 1.2 m. Samples were taken using a core made with PVC tubing (4.6 cm in diameter and 10 cm high). Six samples were used for faunal analysis and one for the determination of sediment variables (see below).

Microscale: vertical distribution in centimetres

For the microscale analysis, six samples (i.e., five for fauna and one for sediment variables) were collected haphazardly at each of three sampling plots (same size as area in macroscale analyses, see above), 50–100 m apart in the swash zones (distributed as transects in macroscale analyses) of Estaleiro and Estaleirinho beaches. Sampling occurred once in July 2008. Each sample was then stratified into four layers of 10 cm increments (0–10 cm, 10–20 cm, 20–30 cm, and 30–40 cm) using the above mentioned corer.

Laboratory studies

Samples for faunistic analyses (whole cores and core layers) were fixed in 4% formalin after ice relaxation (Westheide, 2008), and those for sediment variables were frozen at −4°C. Animals were extracted by a flotation method using colloidal silica Ludox TM 50 (specific gravity adjusted to 1.15 mg/l; Higgins & Thiel, 1988; Somerfield et al., 2005). The solution was decanted through a 63 µm mesh and the animals were transferred to 70% ethanol. Individuals of *S. pussicus* were identified and counted.

Environmental and sediment variables

Beach profiles, breaking wave height (H_b), wave period (T_w), and swash period (T_s) were measured in situ for each transect. The subaerial beach volume (V) [m^3] was calculated for each profile using a sum of consecutive rectangles predicted by the equation $V = \sum y_i \cdot dx_{(j-i)} \cdot z$, where y_i is the height (m) above mean sea level at point i, dx is distance (m) between successive points ($dx_i - dx_j$) and z is the thickness (1 m). Temperature and salinity were measured in situ at each sampling point with a multi-analyzing HORIBA-^{TM} placed in each layer of the sediment. Permeability (i.e., hydraulic conductivity, cm s^{-1}) was measured at swash zone performing geotechnical tests in open PVC tubes (Caputo, 1980). The sediment variable sample was divided in three subsamples for each of the subsequent analyses. For granulometric analysis, a 100 g of sediment was dried for 24 h at 60°C (Buchanan, 1984). Samples were sieved through eight stacked sieves in an Octagon D200 test sieve shaker for 1 h. Granulometric parameters were calculated with the RYSGRAN package for R (Camargo, 2006; Gilbert et al., 2012), following the method of McCammon (1962). Textural classification of the sediment is based on Wentworth tables (Wentworth, 1922). Calcareous carbonate concentrations were determined by acidic digestion with hydrochloric acid (HCl 10%) in a 10 g total sample of sediment collected for the estimation of sediment parameters. Concentration of organic matter (OM) was determined after burning 5 g of sediment in a muffle furnace for 8 h at 800°C (Buchanan, 1984). Microphytobenthic pigments (chlorophyll *a* (Chl-*a*) and phaeopigments) were extracted from 15 cm^3 of sediment. After 24 h, the sediment was then filtered through cotton. Concentrations were determined before and after acidification with HCl_2 from absorbance readings at 665 and 759 nm in a spectrophotometer using Lorenzen's (1967) equation.

Morphodynamic state of beaches

The morphodynamic state of the sampled beaches was estimated from three geomorphodynamic indexes: (i) dimensionless fall velocity or Dean's parameter (Dean, 1973) adapted for natural beaches by Wright & Short (1984); (ii) the surf-scaling parameter (Guza & Inman, 1975; from Battjes, 1974), which is related to the wave breaking type and dissipation energy; and (iii) relative tidal influence to the incident wave.

Dean's parameter was calculated using $\Omega = H_b/(W_s T_w)$, where H_b is the significant breaking wave height (m), W_s is the sediment fall velocity (m s^{-1}), and T_w is the wave period (s), which were measured in situ for each transect. When $\Omega < 2$, beaches were defined as reflective (steep, without subtidal bar), becoming dissipative when $\Omega > 5$ (flat, multibarred), and considered intermediate for $2 < \Omega < 5$ (often, with one or two bars).

The surf-scaling parameter (ε) was calculated as $\varepsilon = a_b \cdot \omega^2 / g \cdot \tan^2 \beta$, where a_b is the breaking wave amplitude (m), ω is the wave radiation frequency (π / T_w), g is the gravitational acceleration (9.81 m s^{-2}), and β is the beach angularity (°). Guza & Inman (1975) and Aagaard & Masselink (1999) classified four types of breaking waves using the surf-scaling parameter (ε) including spilling breakers (which occur for $\varepsilon > 20$), plunging breakers (which occur for $\varepsilon = 2.5$–20), and collapsing and surging waves (which occur for $\varepsilon < 2.5$).

The tidal influence in relation to the incident wave was calculated by the relative tide range (RTR) (Masselink & Short, 1993), where $RTR = TR/H_b$ and TR is the tidal amplitude (m). We used three beach classifications in regards to RTR; (i) $RTR < 3$, the beach is classified as a wave dominated; (ii) $3 < RTR < 7$, is classified as a mixed wave-tide beach; and (iii) $RTR > 15$, for tidal dominated beaches (sand flat).

Motility and feeding strategies

Motility and feeding strategies were examined in living *S. pussicus* collected from Estaleiro and Estaleirinho beaches from February 2008 to December 2009. Specimens of *S. pussicus* were extracted using the $MgCl_2$ decantation technique (Higgins & Thiel, 1988) and revitalized immediately with seawater. Individuals of *S. pussicus* were sorted and incubated in Petri dishes (at 16°C under a standard light cycle, 12 h light/12 h dark, over 14 days) with seawater and a shallow layer of sediment. *Saccocirrus pussicus* cultures were fed with *Skeletonema* sp. from lab cultures or with phytoplankton directly collected at the sampled beaches using a 0.01 mm plankton net. The specimens were removed and placed in two distinct treatments: a Petri dish with few grains of sand; and a Petri dish with a shallow layer of sediment. Motility and feeding strategies were observed and video recorded on ca. 20 individuals (2–3 h per day) using a Canon PowerShot S45 video camera mounted on an Olympus SZH-ILLD stereomicroscope. Motility strategies were typified as (1a) sedentary, (1b) ciliary glider, or (1c) muscular crawler according to the observed motility patterns in two conditions: (i) still water and (ii) water slightly agitated by hand. Feeding strategies were classified as (2a) deposit feeder, (2b) active collecting of particles (similar to suspension feeding strategy).

Data analysis

Sandy beaches characterization

Geomorphodynamic indexes, environmental and sediment variation across localities on regional, local and microscale (see below) were assessed using two principal component analyses (PCA). The first PCA focused on the environmental patterns at regional and local scales and included the following variables: average grain size (AGS), percentage of carbonate (carbonate), OM content, hydraulic conductivity (cm s^{-1}), temperature (T°C), slope of the beach (slope), H_b, RTR, relation between wave and swash periods (T_w/T_s) and the Ω. The following variables, salinity, ε, beach angularity, kurtosis (KUR), skewness (SKW), sorting (SOR), Chl-*a*, T_w, and T_s showed collinearity with variables left in the PCA and were removed. The first PCA for regional and local scales was run in MVSP 3.0 (Kovach, 1998) with centralized data.

The second PCA was focused on the environmental patterns on a vertical scale and included the following variables: AGS, OM, carbonate, percentage of shelly gravels, and Chl-*a*. The following variables, KUR, percentage of sand, salinity, air T°C, hydraulic conductivity, SKW, SOR, sediment T°C, T_w, H_b, Ω showed collinearity with variables left in the second PCA and were removed. The second PCA was performed using bpca function (bpca package, Faria & Demétrio, 2013).

Macroscale: regional and local

The regional-scale analyses were designed to test the preferences of *S. pussicus* for reflective or dissipative beaches, whereas local-scale analyses were designed to test the preference of *S. pussicus* for hydrodynamic zones (surf versus swash). Four factors were considered in this model: (i) time (two levels, fixed: first and second sampling); (ii) beach (six levels, random, crossed with time: Ilhota, Estaleiro, Navegantes, Nereidas, Mansa, and Atami); (iii) transect (three levels, random, nested in beach: one, two and three); and (iv) hydrodynamic zone (two levels, fixed, crossed with time and beach: swash and surf zone). The null hypothesis predicts no significant difference of *S. pussicus* density (number of

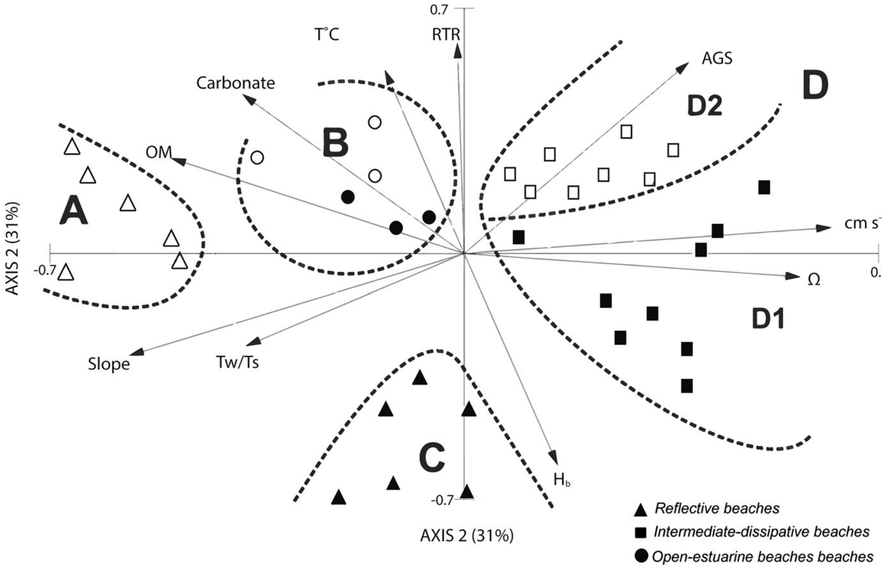

Fig. 2 Principal component analysis (PCA) of the horizontal distribution patterns analyses (regional and local) of *S. pussicus*. Axes 1 and 2 explained 38 and 31% of the variance in the data, respectively. Vectors represent environmental variables: with average grain size (AGS), organic matter (OM), carbonate percentage (carbonate), slope, ratio between wave and swash period (T_w/T_s), hydraulic conductivity (1/cm s^{-1}), temperature (T°C), wave height (H_b), Omega index (Ω), relative tide range (RTR), and symbols indicate sample sites. *Closed symbols* indicate the first sampling (September 2005) and *open symbols* indicate the second sampling (March 2006). *Letters* and *numbers* represent the time-spatial associations: A—Estaleiro and Ilhota beach in the second sampling time, B—Mansa beach in the second sampling, C—Estaleiro and Ilhota in the first sampling, and D—Navegantes, Atami and Nereidas, in the first sampling (D1) and second sampling (D2)

individuals per core) among the beaches, and zones. The factor time was used in the model for the interpretation of possible temporal variations of *S. pussicus* densities among beaches and zones.

The linear models proposed for the regional and local scales were investigated using generalized linear mixed-effects models (GLMM; Bolker et al., 2009). Our data contains evidence of over dispersion and zero inflation, so zero-inflated negative binomial and zero-inflated Poisson distributions were used as candidates to fit models. Models were fit in the *glmmADMB* package of R and simplified by sequential term removal using likelihood ratio tests and Akaike's information criterion (AIC) scores (Zuur et al., 2009; Skaug et al., 2011; R Development Core Team, 2013). Because the dissipative and intermediated beaches of Atami, Nereidas, and Navegantes contained only zero counts, i.e., no variance, they were removed from analyses (see results, Fig. 4). Only three of the 36 replicates collected in the open-estuarine beach of Mansa (see results) during the first sampling presented *S. pussicus* (five individuals in total). Therefore, the beach was considered an outlier and removed from the analyses (Fig. 2).

Multiple regression analyses were used to test for the significance and nature of relationships between regional and local distribution of *S. pussicus* density ($\log_{10}X + 1$ transformed) and the variables AGS, SKW, SOR, KUR, OM, carbonate, hydraulic conductivity, T°C, slope, H_b, T_s, T_w, RTR, Ω, ε, and Chl-*a*. Step-wise model selection was performed based on AICc (corrected AIC for finite sample size) scores and using backward selection to identify the minimum adequate model (Burnham & Anderson, 2002). The significance of the effects of each of the environmental variables on the distribution patterns of *S. pussicus* at regional and local scales was then quantified by its contribution to model fit determined by AICc.

Microscale: vertical distribution in centimetres

Vertical distribution patterns in cm were analyzed considering three factors: (i) layers (four levels, fixed: 0–10, 10–20, 20–30, and 30–40 cm's into the sediment); (ii) beach (two levels, random and crossed with "layer": Estaleiro and Estaleirinho beaches); and (iii) plot (three levels, random and nested in "beach": point one, two, and three). The null hypothesis predicts no significant differences in *S. pussicus* densities (fourth root transformed) among layers. Student–Newman–Keuls (SNK) tests were used for a posteriori multiple comparisons of *S. pussicus* density means among layers.

To test the linear model for vertical scales, the degrees of freedom, the mean square estimates, the *F* ratios and the *P* values were calculated according to Underwood (1997) using GAD package (Sandrini-Neto & Camargo, 2010) available in software R (R Development Core Team, 2013). Homogeneity of variances was estimated using Cochran test.

The multiple regression analyses (see above) were also used for microscale analyses to test for significance and correlation between vertical distribution of *S. pussicus* density ($\log_{10}X + 1$ transformed) and the variables, AGS, SKW, SOR, KUR, OM, carbonate, hydraulic conductivity, sediment T°C, H_b, T_s, Ω, percentage of gravel, and Chl-*a*.

Results

Characterization of the sampling localities at macro- and microscale

The first PCA analysis clearly separated exposed reflective beaches (Estaleiro and Ilhota) from Mansa, and intermediate-dissipative beaches (Navegantes, Nereidas, and Atami). The first two principal components accounted for 69% of the total variance (Fig. 2). The first component (38% of the total variance) accounted for the high hydraulic conductivity (cm s^{-1}), coarse sediments and the steep slope present on reflective beaches versus that of the fine, well-sorted sediments and the high Ω values characteristics on dissipative beaches. The second principal component (31% of total variance) included the larger H_b present on reflective beaches from the first sampling, and higher RTR in the second sampling time on dissipative beaches and Mansa beach.

The second PCA analysis applied in at the microscale yielded two factorial axes explaining 67% of the total variation (Fig. 3). In the first axis, AGS and carbonate in positive direction and OM in negative direction accounted for 50% separation of Estaleiro from Estaleirinho. Estaleiro had coarse sediments with higher OM content than Estaleirinho, which presented also coarse sediments, but with a higher percentage of carbonates. The second axis (17%) weakly separated 10 and 20 cm deep layers from 30 and 40 cm deep layers within each beach, based on the lower amounts of Chl-*a* in the deeper layers (Fig. 3).

Navegantes, Nereidas, and Atami were characterized as dissipative ($\Omega > 5$). They were all exposed, with a wide surf zone and well-sorted fine sediments. Wide swash zones presented low hydraulic conductivity, gentle declivity, and superficial redox layers.

Mansa beach is categorized as reflective in the literature. However, the present results categorize it as low tide, terrace at open-estuarine beach (Masselink & Turner, 1999). Mansa Beach had poorly to moderately sorted sediments, primarily composed of medium sand in the swash zone, and fine sand in the surf zone. Inclination of the beach face was steep with a narrow surf zone controlled by both wave and tide amplitude (RTR = 3–5). Salinity at Mansa Beach was 25–30 psu.

Estaleiro and Ilhota were all characterized as exposed reflective beaches ($\Omega < 2$), having medium and coarse-grained sediments with large interstitial spaces. Salinity was 35 psu, redox layers were absent, and hydraulic conductivity was higher than dissipative beaches. Geomorphologically, the beach faces showed steep slope, and low values for the Ω and ε. Estaleiro and Ilhota showed clear changes in the wave regime, with larger H_b during the first sampling (September 2005), and a change in the wave type from plunging ($\varepsilon = 2.6$–5.8) to surging during the second sampling time (March 2006) ($\varepsilon = 0.1$–0.8). The beach slope of both beaches was steeper at the first sampling. The mean subareal volume of the beaches transects changed from 59 m^3 (SE = 3.5) at Estaleiro and 30 m^3 (SE = 2.05) at Ilhota at the first sampling to 75 m^3 (SE = 5.5) and 75 m^3 (SE = 2.9) at the second sampling, respectively. The steeper slope and small volume of sand during the first sampling were correlated with larger plunging waves breaking on the beach face and the offshore sand migration. The Estaleirinho beach sampled only for microscale analyses and behavior studies (from 2008 to 2009) showed Ω and ε similar to Estaleiro Beach.

Macroscale horizontal distribution patterns of *Saccocirrus pussicus*: regional and local scales

No individuals of *S. pussicus* were recorded at the intermediate-dissipative beaches of Atami, Navegantes

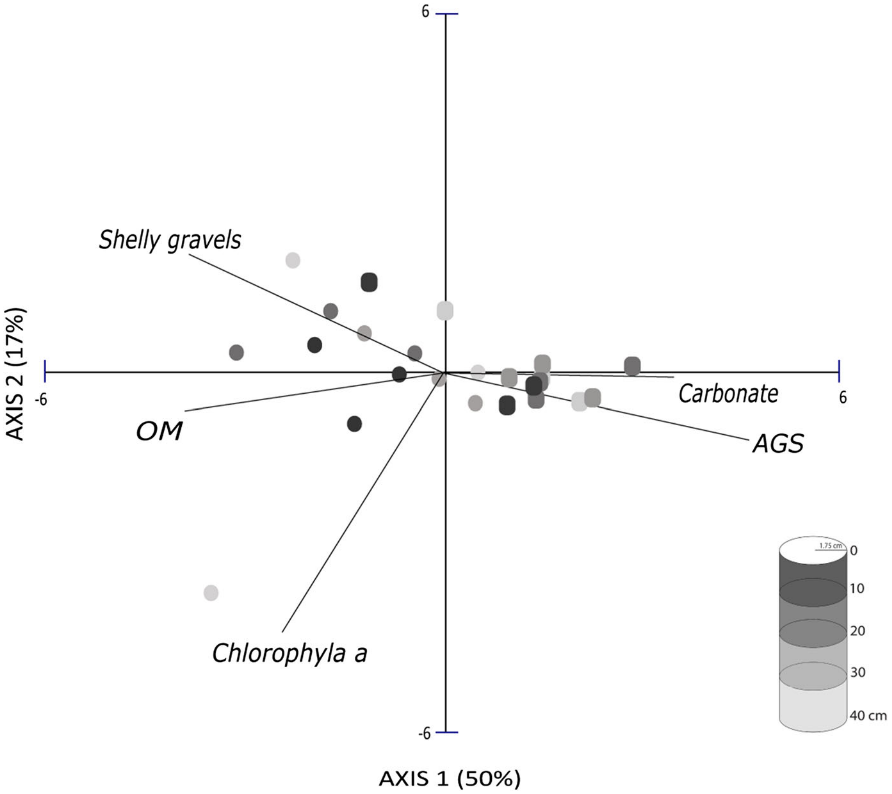

Fig. 3 Principal component analysis (PCA) of the vertical distribution patterns of *S. pussicus*. Axes 1 and 2 explained 50 and 17% of the variation, respectively. Vectors represent environmental variables: average grain size (AGS), organic matter (OM), carbonate percentage (carbonate), percentage of shelly gravels, and symbols indicate the sample. Square = Estaleirinho and Circle = Estaleiro, colors/gray scale representing each sediment layer

and Nereidas, but they were abundant in the reflective beaches of Estaleiro and Ilhota (Fig. 4). The Mansa beach, categorized as a low tide terrace at an open-estuarine beach, had low abundances of *S. pussicus*, with only five specimens recovered in three of the 36 samples collected during the first sampling (September 2005).

Likelihood ratio tests and AIC scores applied over glmmADMB models containing all possible interactions (Table 1A, B), revealed that the models using zero-inflated negative binomial distribution were best fitted to *S. pussicus* densities (Results not shown). The best model includes all fixed variables and interactions among them $(\text{Beach} + \text{Zone} + \text{Time})^2$ (Model 2, Table 1B). No effects were detected for the Time * - Beach * Zone interaction (Model 1, Table 1B). The density of *S. pussicus* changed from beaches and zones depending of the sampling time (Zone * Time and Beach * Time interactions, Table 1C), and the density in the zones depended on the beach (Beach * Zone interaction, Table 1C). Densities at Estaleiro and Ilhota were higher in the breaking wave zone (equivalent to surf zone in dissipative beaches) during the first sampling than during the second sampling. At Ilhota beach, *S. pussicus* could be recorded in the breaking wave zone only during the first sampling. At the same sampling time, at Estaleiro beach, density of *S. pussicus* was higher in the breaking wave zone than in the swash zone. Densities of *S. pussicus* were higher in the swash zone on the Estaleiro and Ilhota beaches during the second sampling (Fig. 5). The calculated variance for the random effect of transects was 0.13 (SE = 0.36) (Table 1D), which introduced a small variance to the model. Within beaches, transects showed a slight difference of *S. pussicus* densities among the hydrodynamic zones (Fig. 5).

The multiple regressions indicated that the model containing H_b, slope, AGS, SKW, and carbonate best explained the data for macroscale distribution of *S. pussicus* among beaches and zones (Table 2). Among these factors, slope and H_b were the significant predictors of *S. pussicus* density.

In summary, S. *pussicus* was restricted to reflective beaches. However, the preference for hydrodynamic zones (swash or surf zone) was time dependent, with slight variation among transects, showing a dynamic pattern correlated to the morphodynamic states, slope,

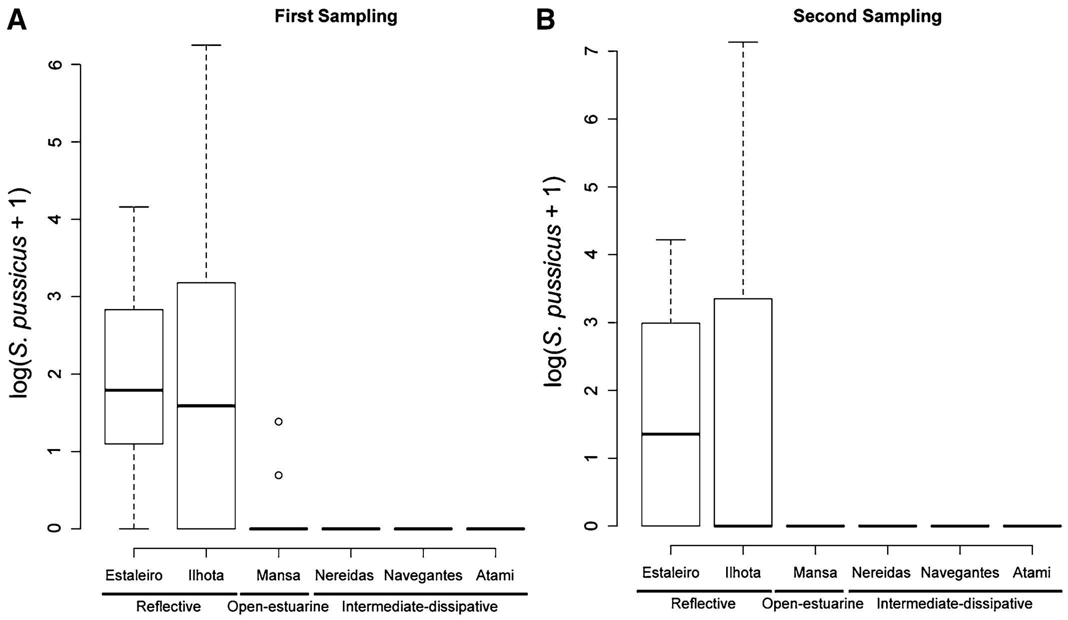

Fig. 4 Boxplot of *Saccocirrus pussicus* (log$X + 1$ transformed) in studied beaches for macroscale analyses during first sampling time (**A**) and second sampling time (**B**). Beaches were classified as reflective (Estaleiro and Ilhota), open-estuarine (Mansa), and intermediate-dissipative (Nereidas, Navegantes, and Atami). The line in the middle of the box represents the median, and the lower and upper ends of the box are the 25 and 75% quartiles, respectively. The lines indicate 1.5 times the size of the hinge, which is the 75% minus 25% quartiles (Note that the interval defined by these lines is not a confidence interval). Points beyond these lines are outliers

waves, AGS, SKW and percentage of carbonate of the beach.

Microscale: vertical distribution of *Saccocirrus pussicus* in centimetres

Saccocirrus pussicus was found between 0 and 40 cm depth, but average densities varied significantly among layers, with the highest abundances usually occurring in the top 20 cm of sediment (post hoc SNK, Table 3, Fig. 6).

The multiple regression applied for the microscale indicated that the model containing sediment $\mathring{T}$C, Chl-*a*, AGS, OM, and shelly gravel percentage best explained the data for vertical distribution of *S. pussicus*. Sediment $\mathring{T}$C and shelly gravel percentages were the significant predictors of the vertical distribution of *S. pussicus* (Table 4).

Motility and feeding strategies

Under still-water conditions, and in a small amount of sediment, ca. 15 of the 20 observed specimens of *S. pussicus* displayed a sedentary behavior, whereby adhering to sand grains by the pygidial adhesive glands (Supplementary material 1). Muscular swimming behavior was observed in ca. five specimens placed in Petri dishes with a thin layer of sediment. Muscular swimming is produced by undulatory movements presumably depending on coordinated contractions of the trunk longitudinal musculature (Supplementary materials 2, 3). Under agitated-water conditions, all *S. pussicus* displayed a similar sedentary behavior whereby adhering to sand grains using the pygidial adhesive glands. After the water agitation was stopped, all saccocirrids remained adhered to the sand grains for more than 30 min. No gliding movements were observed.

Detritus and sand grains were observed in the gut of most individuals. Suspension feeding was observed on sedentary individuals that constantly waved their palps around their mouth to intercept food particles from the water column. Captured particles were carried to the mouth by helicoidal coiling of the entire palp. Active collection of particles (similar to suspension feeding strategy) is inferred both at the surface and subsurface of the sediment (see results of the vertical scale analysis). Direct ingestion of deposited

Table 1 Summary of the results from generalized linear mixed effect models used in analysis of data from Estaleiro and Ilhota

Models	No. par	LogLik	AIC	X^2	P
(A) Random effects structure					
R1: *S. pussicus* ~ (1|beach/transect)	5	−480.97	494		
(B) Fixed effects structure					
Model 1: *S. pussicus* ~ beach * zone * time|random = R1	12	−402.12	828		
Model 2: *S. pussicus* ~ (beach * zone * time)^2|random = R1	11	−402.13	**826**	0.026	0.8719
Model 3: *S. pussicus* ~ zone * beach|random = R1	8	−440.94	898	77.622	**<0.0001**
Model 4: *S. pussicus* ~ beach * time|random = R1	8	−479.94	976	78.008	**<0.0001**
Model 5: *S. pussicus* ~ zone * time|random = R1	8	−441.17	898	−77.548	**<0.0001**
Model 6: *S. pussicus* ~ beach|random = R1	6	−480.20	972	78.058	**<0.0001**
Model 7: *S. pussicus* ~ 1|random = R1	5	−480.97	972	1.534	0.2155

(C) Coefficients model 2	Estimate	SE	Z	P
Intercept	2.890	0.321	9.00	**<0.0001**
Time	−4.046	0.526	−7.69	**<0.0001**
Zone	−1.326	0.363	−3.65	**<0.001**
Beach	−3.694	0.572	−6.46	**<0.0001**
Zone × time	5.674	0.647	8.76	**<0.0001**
Beach × time	−2.498	0.502	−4.97	**<0.0001**
Beach × zone	5.994	0.608	9.85	**<0.0001**

(D) Random effects variances	Variance	SE
Beach	2.22×10^{-6}	4.71×10^{-2}
Transect (beach)	0.1329	0.3645

Bold values indicate $P < 0.05$ and lowest value of AIC

(A) Model of random effects structure that were used to described the data assessed using the AIC scores (lower scores equals better fit). (B) The significance of the fixed effects was then determined by comparing models of reduced complexity using the likelihood ratio test and AIC scores to assess the significance of each parameter. (C) Results of generalized linear mixed-effects models with negative binomial errors with zero inflation from fixed effects for the best model estimated (Model 2). (D) Estimated variance of random effects.

Zero inflation parameter: 0.000001 (SE = 0.0012436); negative binomial dispersion parameter: 11.177 (SE = 0.18)

particles by the mouth was also observed, indicating the possibility of deposit feeding. However, deposition of OM in the highly turbulent environment inhabited by *S. pussicus* is unlikely due to the high permeability of the sediments (see also Ramey & Bodnar, 2008). The sedentary behavior of adhering to sand grains by the pygidial adhesive glands and the active collecting of particles was favored regardless for the limited amount of sediment provided under the laboratory conditions.

Live animals when stressed or disturbed, under agitated-water conditions, produced a strong metallic smell similar to that described in *Protodrilus hypoleucus* Armenante, 1903 (see Jouin, 1970) or *Saccocirrus goodrichi* (Jouin & Gambi, 2007). Usually in winter, storms or swells events (pers. obs.), this smell is stronger and can even be felt in the swash and breaking wave zones of the studied beaches.

Discussion

Saccocirrus pussicus was restricted to reflective beaches, and never found in dissipative beaches with fine sand. This is congruent with previous studies, which reported high abundances of *Saccocirrus* only in the turbulent hydrodynamic zones (du Bois-Reymond Marcus, 1948; Di Domenico et al., 2009). At a regional and local scale, the steeper slope, H_b, percentage of carbonate, AGS and SKW mainly determined their maximum abundance. Over time, geological history and wave regimes have strongly

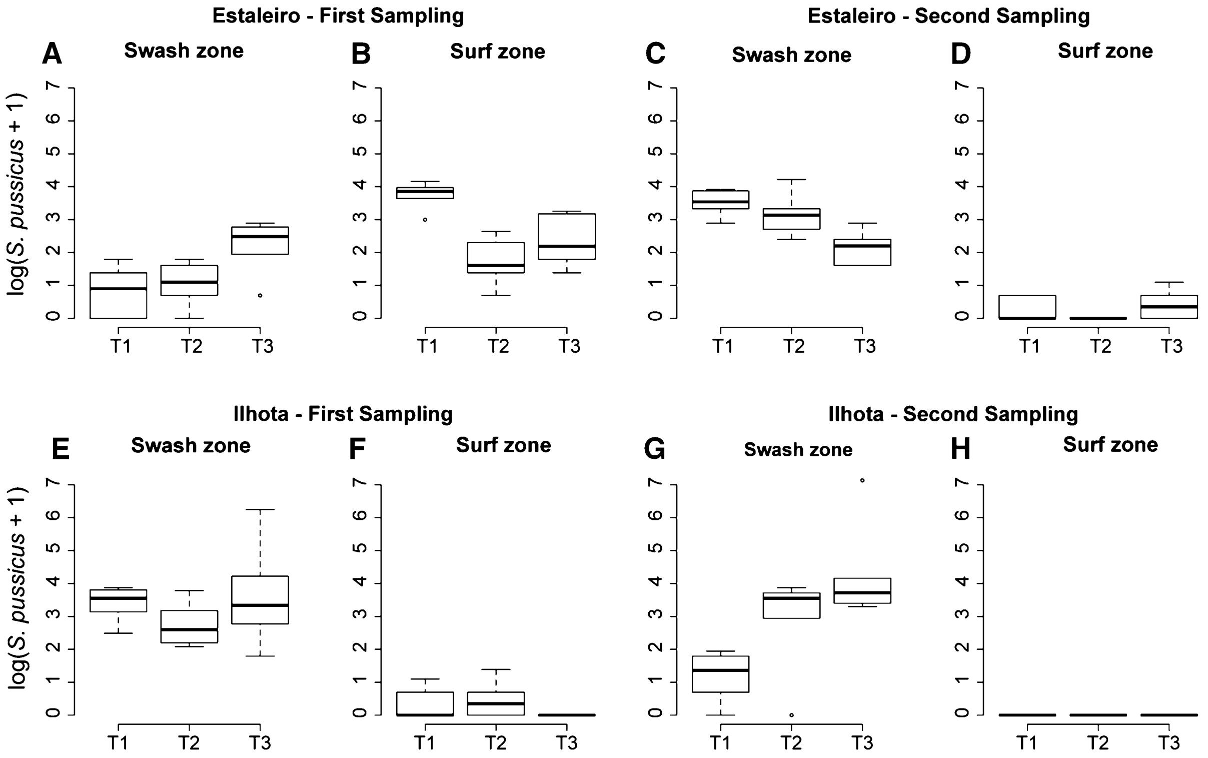

Fig. 5 Boxplot of *Saccocirrus pussicus* ($\log X + 1$ transformed) in the swash and surf zones (breaking wave zone of reflective beaches) along each transect (T1, T2, and T3) of the Estaleiro (**A**–**D**) and Ilhota (**E**–**H**) beaches during first sampling time and second sampling time. Beaches with high percentage (>50%) of zero counted of *Saccocirrus pussicus* were omitted, i.e., Atami, Mansa, Nereidas, and Navegantes (see Fig. 4). The line in the middle of the box represents the median, and the lower and upper ends of the box are the 25 and 75% quartiles, respectively. The lines indicate 1.5 times the size of the hinge, which is the 75% minus 25% quartiles (Note that the interval defined by these lines is not a confidence interval). Points beyond these lines are outliers

Table 2 Results of multiple regression analyses for the best model choice by AICc for regional- and local-scale distribution of *Saccocirrus pussicus* density ($\log_{10}X + 1$ transformed) within environmental variables

Variable	Estimate	SE	t value	Pr(>|t|)
Intercept	0.436588	0.237195	1.841	0.070
H_b	**0.002934**	**0.001148**	**2.556**	**0.013***
Slp	**4.613966**	**1.413634**	**3.264**	**0.002****
AGS	−0.164225	0.091944	−1.786	0.079
SKW	0.821776	0.458634	1.792	0.078
Carbonate	−0.064728	0.034996	−1.85	0.069

Bold values indicate $P < 0.05$

Residual standard error: 0.4379 on 66 degrees of freedom; multiple R^2: 0.4426, adjusted R^2: 0.4003; F-statistic: 10.48 on 5 and 66 DF, P value <0.001

H_b significantive wave height, *Slp* slope, *ASG* average grain size, *SKW* skewness, *carbonate* percentage of carbonate

* $P < 0.05$, ** $P < 0.01$

influenced beach morphology and evolution (Short, 1999; Jackson et al., 2005). Geological history in itself establishes a theoretical framework model for the genesis and morphological evolution of the shape and volume of a given beach (see Pettermann et al., 2006), and predicts the nature and source of sediments (Jackson et al., 2005). The reflective beach conditions with coarse sediments found in Estaleiro, Ilhota, and also Estaleirinho (sampled only at microscale) seemingly offered an optimal environment for the establishment of *S. pussicus*.

At a local scale, the highest abundances of *S. pussicus* shifted from the swash zone to the surf zone, revealing temporary changes in the distribution and abundance of the species among different beach hydrodynamic zones. Interestingly, these movements may be correlated with changes in the wave circulations throughout the two sampling periods, reflected by the

Table 3 Summary of mixed ANOVA analyzing *Saccocirrus pussicus* mean densities and post hoc SNK

	gf	*S. pussicus*		
		MS	*F*	*P*
Beach = Be	1	0.00001	0.00001	0.995
Layer = Ly	**3**	**1.297**	**4.041**	**0.034**
Ly × Be	3	0.029	0.091	0.963
Plot (Be)	4	0.146	0.624	0.646
Ly × Pl(Be)	12	0.321	1.373	0.192
Residual	96	0.233		
SNK		Ly: **0–10** = **10–20** > 20–30 = 30–40		

Bold values indicate $P < 0.05$

Table 4 Results of multiple regression analyses for the best model choice by AICc for vertical distribution of *Saccocirrus pussicus* density ($\log_{10}X + 1$ transformed) within environmental variables

Variable	Estimate	SE	*t* value	Pr(>|*t*|)
Intercept	**4.7149108**	**1.5028705**	**−3.137**	**0.0057****
T°C sed	**0.1909202**	**0.0648246**	**2.945**	**0.00866****
Chl-*a*	0.0013122	0.0008297	1.582	0.13116
AGS	0.3236413	0.165024	1.961	0.06552
OM	1.6017396	0.8728271	1.835	0.08307
Grv	**0.1253332**	**0.0491573**	**2.55**	**0.02012***

Bold values indicate $P < 0.05$

Residual standard error: 0.1118 on 18 degrees of freedom; multiple R^2: 0.4334, adjusted R^2: 0.276; *F*-statistic: 2.754 on 5 and 18 DF, *P* value <0.05

T°C sed sediment temperature, *Chl-a* chlorophyll *a*, *ASG* average grain size, *OM* organic matter, *Grv* percentage of shelly gravels

* $P < 0.05$, ** $P < 0.01$

H_b and ε. During the first sampling period, the reflective beaches were affected by larger plunging waves which shifted to short surging waves during the second sampling period. The higher energy of these waves simultaneously increases the amount of sediment being transported from the swash zone to the breaking wave zone (Horn & Manson, 1994; Masselink & Puleo, 2006; Hoefel & Elgar, 2003). This is further indicated by correlation of *S. pussicus* with sediment variables as AGS, SKW, and percentage of carbonate. The changes in the sediment SKW from positive in the surf zone during the first sampling period (which indicates sediment transportation) to negative in the swash zone (indicating deposition) may indicate two different hydrodynamic moments in Estaleiro and Ilhota. This bedload sediment transport suspends and transports sand between the hydrodynamic zones of both habitats (Horn & Manson, 1994; Masselink & Puleo, 2006), and may explain the changes in abundance of *S. pussicus*.

The *S. pussicus* preference for hydrodynamic zones and known sediment transportation patterns may provide clues for surfing in this species. The surfing behavior hypothesis is congruent with the results from the microscale analysis of vertical distribution patterns. The highest abundance of *S. pussicus* was always recorded at the uppermost layers of sediment (0–20 cm), which are more prone to sediment transportation (Masselink & Puleo, 2006). Conversely, most meiofaunal animals respond to sediment disturbance by migrating downward or by simply living in the deeper layers (Meineke & Westheide, 1979; Foy & Thistle, 1991). Consistently lower abundances of *S. pussicus* in the deeper sediment layers contradict the idea that all interstitial species undergo vertical migrations or occupy the deeper layers as a strategy to avoid the mechanical stress of heightened wave energy. Only the gastrotrich *Turbanella hyalina* (Boaden, 1968), and now *S. pussicus* are known to potentially get displaced from the substrate by wave action. *Saccocirrus pussicus* attaches to grains with their pygidial adhesive glands while actively collecting particles with their palps (as a suspension feeding strategy), and may swim by undulatory muscular movements of the trunk. These behaviors may be essential adaptations for surviving in the surface layers of reflective beaches exposed to swells. This is an advantageous strategy, since food is mostly available in the upper sediment layers or in the water column of the breaking-swash zones of reflective beaches (Jesus et al., 2006; Ramey & Bodnar, 2008). The role of palps in feeding by gathering suspended particles seems crucial in high flow environments (Boaden, 1962; Miller et al., 1992; Martínez et al., 2013a, b). The high turbulent swash and surf zones of reflective beaches, together with the coarse and highly permeable sediments where *S. pussicus* is found, prevents the deposition of OM. Though palps lack motile ciliary bands in Saccocirridae (Westheide, 2008), as in other interstitial annelids (Gelder & Uglow, 1973; Worsaae et al., 2009; Di Domenico et al., 2014a), our observations have shown that *S. pussicus* can effectively intercept food particles even among these highly

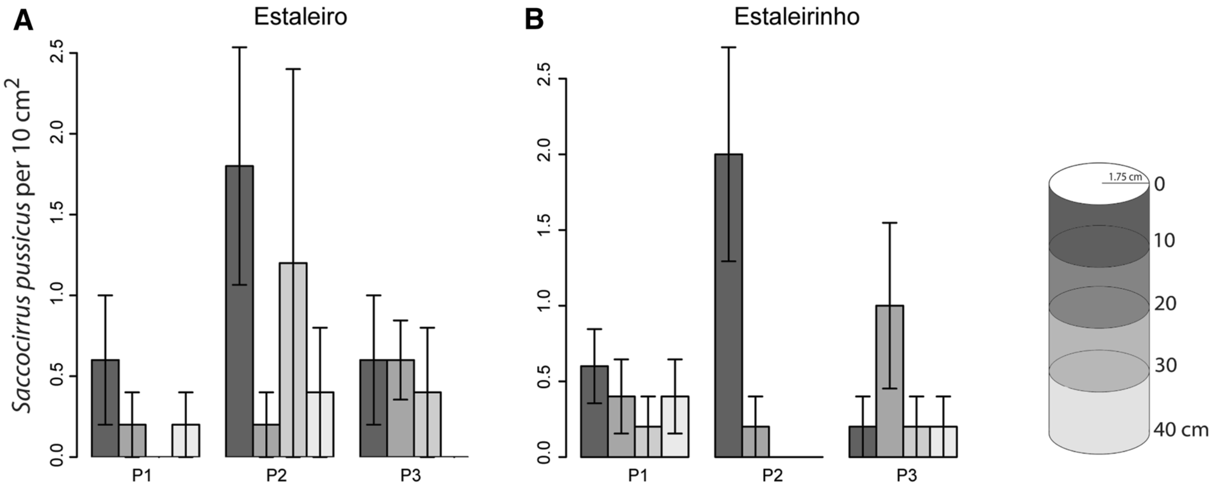

Fig. 6 Mean density (±SE) of *Saccocirrus pussicus* in different sediment layers (0–10, 10–20, 20–30, 30–40) of the plots (P1, P2, and P3) examined at Estaleiro (**A**) and Estaleirinho (**B**) beaches

permeable sediments. Previously, palps in *Saccocirrus* were considered as mainly sensory (Purschke, 1993).

The macroscale and vertical distribution analyses, coupled with the behavioral studies and morphological traits of *S. pussicus* (Di Domenico et al., 2014a, b), may provide consistent evidence for a well-adapted species to morphodynamic processes at reflective beaches. *Saccocirrus pussicus* individuals adhered to sand grains may be driven offshore during heightened wave conditions, and during offshore sediment transport, as suggested by the variation of subareal volume at Estaleiro and Ilhota beaches. Though this complex transportation mechanism needs to be better understood, it is rather difficult to envisage other vectors in which saccocirrids are transported among the hydrodynamic zones. The swash and surf zone mechanism of transport in reflective beaches are well studied, and the bedload transport is found to dominate the backwash (Horn & Manson, 1994; Masselink & Puleo, 2006). *Saccocirrus pussicus* individuals adhered to sand grains may be driven offshore during heightened wave conditions, and during offshore sediment transport. Their ecological tolerance to such destructive habitat changes may be in part due to modifications of their foraging behavior (see examples as; Taghon et al., 1980; Dauer et al., 1981; Taghon & Greene, 1992; Pardo & Amaral, 2004).

Saccocirrus pussicus is a common species in the Southwestern Atlantic, inhabiting reflective beaches from Rio de Janeiro, in Brazil (Di Domenico et al., 2014a) to Uruguay (Rodriguez et al., 2013). The temporal changes in its abundance patterns among the swash and surf zones is documented in this study. This is a prime example of coupling morphodynamics and biological processes in a sandy beach system. Other saccocirrids such as *Saccocirrus papillocercus* Bobretzky, 1872, *Saccocirrus major* Pierantoni, 1907, and *Saccocirrus minor* Aiyar & Alikunhi, 1944, all of which are morphologically similar to *S. pussicus*, are also found in similar environments and may depict the same coupling (Brown, 1981; Jouin & Gambi, 2007; Di Domenico et al., 2014b). The coupling between the ecology of this widely distributed group with beach morphodynamics throughout the world can be explained by shared morphological and behavioral adaptations to harsh sandy environments, may lead to an exceptional and successful surfing life strategy.

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