Testing macroecological hypotheses in sandy beach populations: the wedge clam *Donax hanleyanus* in South America

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ABSTRACT: Large-scale spatial and temporal variability in environmental conditions may result in differences in life-history traits, population demography, and abundance of sandy-beach species. We analyzed the effects of salinity, chlorophyll *a* (chl *a*), and sea surface temperature (SST) on population parameters of the wedge clam *Donax hanleyanus* from 75 South American sandy beaches covering a 15° latitudinal range. Generalized modeling results showed that between-beach differences in abundance, population structure, growth performance, productivity, mortality, and individual shell mass were mainly explained by salinity fluctuations, with chl *a* and SST as secondary contributors, overriding, in most cases, local habitat features (Dean's parameter, grain size, slope). Our results provide valuable insights into macroscale ecological processes, setting a basis to delineate conservation guidelines at large spatial scales that respond to the potential effects of climate variability and change on sandy beach populations.

KEY WORDS: Bivalve · Macroecology · Environmental correlates · Life-history traits

1. INTRODUCTION

Macrofaunal communities and populations from sandy beaches are mainly structured by physical and biological factors operating over many spatial and temporal scales (Defeo & McLachlan 2005, McLachlan & Dorvlo 2007, McLachlan & Defeo 2018). At the macroscale, community patterns consistently increase in species richness towards the tropics (McLachlan & Dorvlo 2005, Barboza & Defeo 2015, Defeo et al. 2017), following the latitudinal diversity gradient (Hillebrand 2004). Species richness also increases with sea surface temperature (SST), as pre-

dicted by the kinetic energy or temperature hypothesis (Clarke & Gaston 2006, Barboza & Defeo 2015), due to higher metabolic rates and lower thermal stress caused by warmer conditions. Salinity fluctuations govern community features in sandy beaches located along large-scale estuarine gradients, showing an exponential decrease in species richness towards beaches with high intra-annual salinity variations (Lercari & Defeo 2006, 2015). Surface chlorophyll *a* concentration (chl *a*; used here as a proxy of food supply) could also play an important role in structuring communities (Defeo et al. 2017), with more productive beaches promoting a greater

number of species according to the productivity-richness hypothesis or potential energy hypothesis (Evans et al. 2005). When operating at large spatial scales, these variables interact with local habitat characteristics such as waves, tides, and grain size, whose interaction defines a continuum of morphodynamic types ranging between microtidal reflective and macrotidal dissipative beaches (Short 1996, 1999, McLachlan et al. 2018). Species richness decreases from dissipative to reflective beaches, based on the species exclusion by a harsh swash climate associated with beach type (swash exclusion hypothesis; McLachlan et al. 1993).

Sandy-beach species with extensive distribution ranges also show latitudinal trends in their life-history traits that match many of the patterns found at the community level, as expected for a physically controlled environments (Defeo & McLachlan 2005). Abundance, individual growth, and mortality rates are higher in organisms inhabiting tropical beaches compared with temperate ones, whereas fecundity and longevity show the opposite trend (Defeo & Cardoso 2002, 2004, Cardoso & Defeo 2003, 2004). Latitudinal patterns in life-history traits have been observed in a broad range of intertidal organisms (Dugan et al. 1994, Defeo & McLachlan 2005, McLachlan & Defeo 2018), including bivalves that dominate sandy-beach biota (Cardoso & Veloso 2003, Fiori & Defeo 2006, Moss et al. 2016). These species also exhibit higher individual growth rates and lower longevity with increasing SSTs (Marquardt et al. 2022), and a reduced abundance, survival, growth, and fecundity in beaches affected by large-scale salinity gradients (Schoeman & Richardson 2002, Risoli et al. 2020, 2022, Celentano et al. 2022) or low food availability (Risoli et al. 2022). Concerning the role of local morphodynamics, a negative impact on life-history traits is expected in populations inhabiting reflective beaches compared to dissipative ones, according to the habitat harshness hypothesis (HHH). The HHH states that the increased stress imposed by reflective beaches (characterized by steep slopes, coarse grains, and a very harsh swash climate with short periods and short lengths) causes a reduction in fitness and life-history traits of beach macrofauna compared to benign, dissipative shores with gentle slopes, fine grains and a swash climate with long swashes and extended periods. Under the harsh conditions on reflective beaches, individuals may divert more energy to survival than growth and reproduction, thus resulting in decreased individual sizes and weights, growth and survival rates, and reproductive outputs (e.g. fecundity) (Defeo et al.

2001, 2003, Defeo & Martínez 2003). Several intertidal bivalve mollusks and crustaceans, which widely dominate sandy-beach biota, have conformed consistently to these predictions (McLachlan & Defeo 2018 and references therein).

The wedge clam *Donax hanleyanus* Philippi, 1845 (Bivalvia: Cardiida: Donacidae) is a conspicuous component of the sandy beach macrofauna that inhabits the intertidal zone of Atlantic beaches of South America (Penchaszadeh & Olivier 1975, Defeo & de Álava 1995), from Caravelas, Brazil, 17° S (Cardoso & Veloso 2003) to Mar del Plata, Argentina, 38° S (Risoli et al. 2021) (see Fig. 1a). This species plays a critical role in food webs, constituting the major link between primary production and higher trophic levels (Penchaszadeh & Olivier 1975, Cardoso & Veloso 2003). Along the >3000 km that encompass its distribution range, *D. hanleyanus* covers all morphodynamic types from reflective to dissipative beaches (Marcomini et al. 2002, Cardoso & Veloso 2003, Risoli et al. 2021), including those under the estuarine influence of the Río de la Plata (RdlP, near 35° S) and Lagoa dos Patos (LdP, near 32° S) (Risoli et al. 2022).

Between 20 and 40° S, the western South Atlantic shelf is influenced by seasonally reversing winds, strong western boundary currents interacting with outer shelf waters, and a significant discharge of freshwater from the RdlP and, to a lesser extent, the LdP (see Palma et al. 2008, Matano et al. 2010). The seasonal amplitude of SST is highest (>7°C) in the outer RdlP (Rivas 2010), exceeds 6°C in the neighboring shelf, and decreases northward, reaching about 1.5°C near Cape Frío (23° S; Pacheco et al. 2022). In contrast, sea surface salinity and chl *a* present the highest seasonal amplitudes (exceeding 3 and 8 mg m^{-3}, respectively) over the southern Brazil continental shelf, south of Cape Santa Marta Grande (Piola et al. 2008, Pacheco et al. 2022). While salinity changes >10 may be observed along the coast in the outer RdlP estuary, particularly along the coast of Uruguay (Guerrero et al. 1997). Salinity and chl *a* variations are mediated by the seasonal reversal of alongshore winds, which drive northward penetration of low-salinity waters derived from the RdlP in austral fall–winter, and their southward retreat in spring–summer (Piola et al. 2000, Palma et al. 2008). Concerning latitudinal variations in beach morphodynamics, greater wave energy and a predominance of finer sands at higher latitudes result in the dominance of dissipative beaches, whereas reflective beaches tend to be more common in the tropics (McLachlan & Defeo 2018).
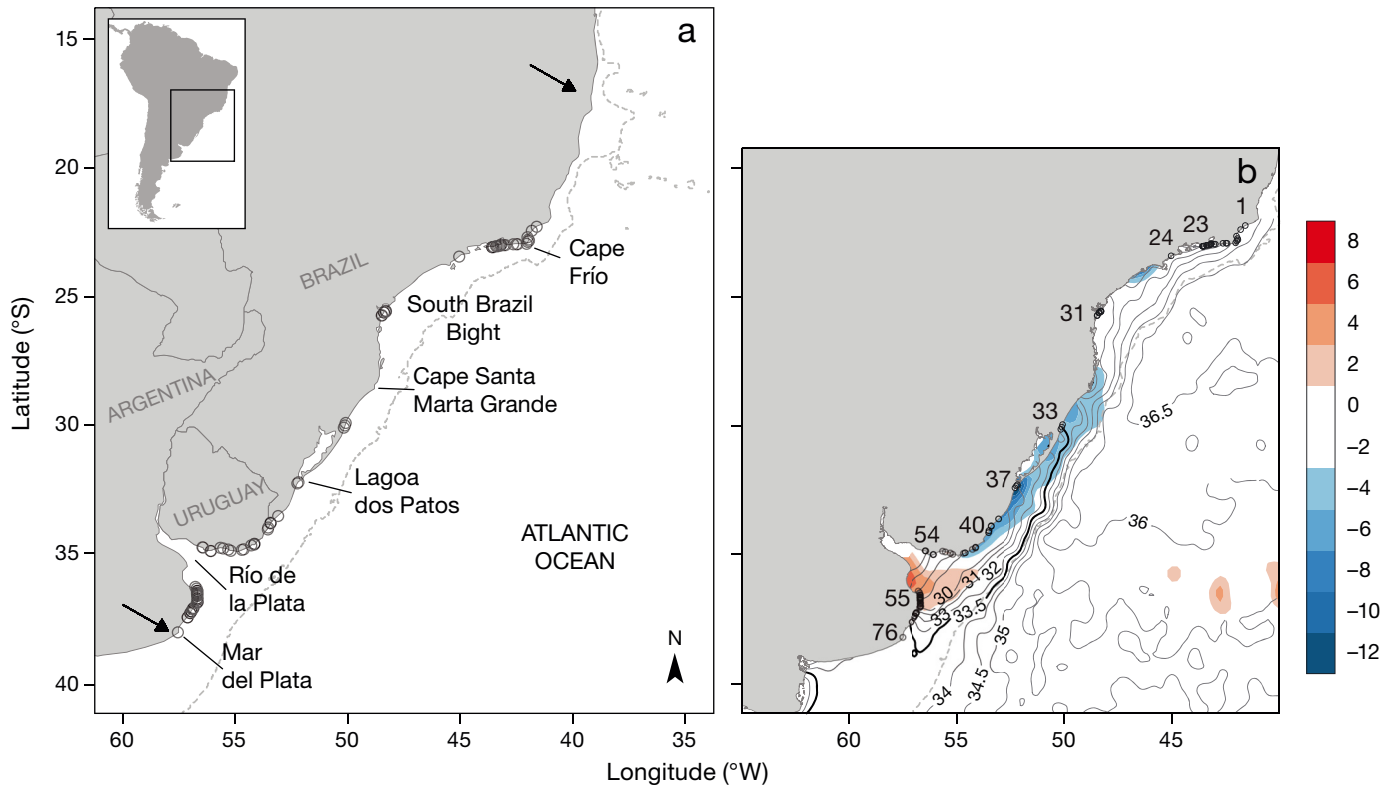
Fig. 1. (a) Geographic range of wedge clam *Donax hanleyanus* along eastern South American sandy beaches (indicated by arrows), including the location of the 75 beaches (black open circles) analyzed in this study. The grey dashed line indicates the 200 m isobath. (b) Annual mean salinity distribution (contours). The heavy contour indicates the annual mean location of the 33.5 isohaline, which marks the extent of the Río de la Plata plume waters. Color shading indicates the difference in winter salinity minus summer salinity (see color scale). Site locations are shown along the coast with selected sites numbered according to Table S1 in the Supplement. Bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO) are available at https://www.gebco.net/data_and_products

Ecological features of the wedge clam provide an outstanding opportunity to assess large-scale population responses to contrasting environments. In this paper, we analyzed macroscale patterns in life-history traits, productivity, population structure, and abundance of wedge clam *D. hanleyanus* populations on sandy beaches of South America. We then related these patterns to regional environmental variables (SST, salinity, chl *a*) and local beach morphodynamic characteristics. We expected that abundance, individual mass and size, survival, longevity, secondary production, total biomass, and production-to-biomass (*P*:*B*) ratio of *D. hanleyanus* would be lower in sandy beaches with low salinity and chl *a*, but greater (except for longevity) in beaches with high SST. We also predicted population structure to exhibit a lack of size classes under these conditions, overcoming the potential effects of local habitat characteristics. Following HHH pre-

dictions at the local scale, we expected an adverse effect of the harsh conditions in reflective beaches on the population features of *D. hanleyanus*.

2. MATERIALS AND METHODS

2.1. Environmental data

This study incorporated 75 Atlantic mesotidal/microtidal sandy beaches of South America, between Carapebus, Brazil (22° 15′ S) and Mar del Plata, Argentina (38° 04′ S) (Fig. 1a; details in Table S1 in the Supplement at www.int-res.com/articles/suppl/m707 p043_supp.pdf), covering most of the distribution range of the wedge clam *Donax hanleyanus*. The spatial scale was prioritized over the temporal one, based on the idea that large-scale datasets help determine macroscale patterns in these populations and/or com-

munities. SST, salinity, and chl *a* concentration for each beach were gathered from online database sources. Daily 1/4° resolution satellite and *in situ* derived SST data were obtained from NOAA's Optimum Interpolation Sea Surface Temperature version 2.1 (Reynolds et al. 2007, Huang et al. 2020). This SST product used advanced very high-resolution radiometer data based on the Pathfinder processing product from January 1985 to December 2005 and operational data since 2006. To compensate for sensor and platform differences, all satellite data were biased-adjusted based on *in situ* observations. The SST data used are from September 1981 to April 2020. Since *in situ* chl *a* observations near the coast are scarce, we used 8 d averaged, 4 km resolution sea surface chl *a* concentration data from MODIS Aqua obtained from NASA's Giovanni (https://giovanni.gsfc.nasa.gov/giovanni/) and gridded over 1/4°Cells. Spatial averaging reduces the pixel-noise level associated with signal digitization noise and atmospheric correction band errors (Hu et al. 2001). The optical complexity of coastal waters frequently leads to overestimates of satellite-derived chl *a* concentration. To attenuate this impact, we used monthly mean values, which tend to sharply reduce the amplitude of spuriously high chl *a* values. The chl *a* data used are from July 2002 to June 2021. Surface salinity data were used because the wedge clam inhabits beaches affected by continental freshwater discharge (Celentano et al. 2022, Risoli et al. 2022). Salinity data were obtained from the World Ocean Database (Boyer et al. 2018; https://www.ncei.noaa.gov/products/world-ocean-database), and from the 'Base Regional de Datos Oceanográficos (BaRDO) - INIDEP' oceanographic database (https://www.argentina.gob.ar/inidep). The data for each site were gridded on 1/4° cells. These data were averaged over 1/4° cells for consistency with the satellite-based SST and chl *a* data. The adopted 1/4° resolution in the environmental variables is expected to capture the details of regional patterns (Fig. 1b).

Additional physical characteristics of each beach were gathered from the reviewed articles used to build the dataset. The main physical variables included in the analyses were grain size and beach slope, which constitute meaningful descriptors of macroecological trends in sandy beaches (Defeo & McLachlan 2013, Barboza & Defeo 2015). In cases where physical information was unavailable, we reviewed the primary literature, using search strings that combined the beach name with one of the following terms: Dean's parameter, wave height, wave period, beach slope, grain size, and sediment. When

information on wave height and period was available, beach morphodynamics was assessed using Dean's parameter (Ω) (Short 1996):

$$\Omega = \frac{Hb \times 100}{Ws \times T} \qquad (1)$$

where Hb is wave height (m), Ws is sand fall velocity at 20°C (cm s^{-1}), and T is wave period (s). Settling velocities based on particle size were calculated using tables from Gibbs et al. (1971). Reflective beaches are characterized by $\Omega < 2$, dissipative ones are defined by $\Omega > 5$, and $2 < \Omega < 5$ describes intermediate beach states. In narrow and steep reflective beaches, all sediment is stored in the intertidal zone and backshore, there is no surf zone, and swashes have short periods and lengths. By contrast, in dissipative beaches the wave energy is dissipated in a well-developed surf zone, and the benign swash climate is characterized by long periods and lengths (McLachlan et al. 2018).

2.2. Population parameters

The database used for analyses was built using information on population parameters of the wedge clam *D. hanleyanus* collected from the available literature. Search strings used in Google Scholar, Scopus, and JSTOR databases combined the species name and one of the following terms: phi prime, age, growth, longevity, lifespan, abundance, density, production, *P*:*B* ratio, biomass, or mortality. Only surveys that sampled the entire species distribution across the beach were considered to provide unbiased abundance estimates (Defeo & Rueda 2002, Schoeman et al. 2003). Observations reported in monthly or seasonal surveys were pooled to provide one representative estimate of the long-term mean conditions for each beach. Information coming from 11 sandy beaches of Argentina and Uruguay (M. C. Risoli et al. unpubl. data) was also included in the analysis (see Table S1).

Variations in abundance of *D. hanleyanus* were analyzed in terms of individuals per linear meter of beach or strip transect (IST; ind. m^{-1}; Defeo & Rueda 2002), matching the most commonly used unit in the literature. This measure was employed instead of density (ind. m^{-2}) to avoid biased results due to changing beach profile during rough and calm conditions. When abundance was available as density (ind. m^{-2}), data were converted to IST values by multiplying the density by the corresponding width of the species distribution across each beach. Population structure

in each beach was analyzed according to the frequency distribution of 1 mm size classes (LFDs). Then, an index of recurrence of size classes (IRSC; Celentano et al. 2010) was calculated as follows:

$$IRSC = \frac{N_L}{N_T} \qquad (2)$$

where N_L defines the number of length (L) size classes on a beach, and N_T is the total number of size classes observed in all beaches surveyed. The IRSC ranges from 0 to 1 (all size classes present) (Caddy & Defeo 2003). Data on individual growth and longevity were gathered from literature, and when von Bertalanffy growth function parameters (asymptotic shell length SL_∞ and growth constant K) were available, the phi prime (φ') growth index (Pauly & Munro 1984) was used to assess growth performance: $\varphi' = 2 \log_{10} (SL_\infty) + \log_{10} (K)$. Secondary production and mean total biomass data (dry) were analyzed per mass per linear meter (g m^{-1}). Data on annual *P:B* ratio and the total mortality coefficient (Z, yr^{-1}), as well as individual body size (SL, height, and width) and mass (total and shell mass), were gathered from all the reviewed articles used to build the dataset. When available, ash-free dry mass was calculated using conversion factors provided by Ricciardi & Bourget (1998).

2.3. Statistical analyses

Individual relationships between population parameters and environmental variables were first evaluated by univariate linear and nonlinear models. Generalized linear mixed models (GLMM; Zuur et al. 2009) were used to assess the relative effect of environmental variables on abundance, IRSC, φ', longevity, secondary production, total biomass, *P:B* ratio, mortality, and individual shell mass. Using GLMMs was preferred whenever possible because the random effect 'Beach' may include site- or region-specific attributes outside of the environmental variables analyzed in this study, which could account for differences in population parameters (Barboza & Defeo 2015). In addition, not all datasets contained the same number of observations for each biological variable. Generalized linear models (GLM; Zuur et al. 2009) were used in cases where GLMMs were not applicable due to the data characteristics (e.g. where singularity occurs). Response variables were log-transformed when necessary to improve model validations. Additionally, climatological chl *a* data were log-transformed and then antilog transformations

were computed, because the natural distribution of chl *a* concentrations is lognormal (Campbell 1995). At each site, SST, salinity, and chl *a* were spatially averaged over the same domains. Environmental variables (Dean's parameter, grain size, beach slope, SST, chl *a*, salinity) were included as fixed factors in each model and analyzed in terms of mean values for each beach. Minimum and maximum values were also included for SST, chl *a*, and salinity, as well as salinity range, which has been shown to be a reliable predictor of macrofaunal species richness and abundance in sandy beaches across estuarine gradients (Attrill 2002, Lercari & Defeo 2006). The best combination of fixed predictors (mean, minimum, maximum, or range values) for each initial model was selected *a priori* based on the relationships observed in the univariate models, and the model R^2 was selected as an indicator of goodness of fit. A significant effort was made in this selection *a priori* because models cannot withstand too many correlated variables (such as the minimum, mean, maximum, and range of the same variable) that could lead to overfitting. Therefore, an *a priori* selection of independent variables was considered the best option for reducing the number of explanatory variables included in the models. The variance inflation factor (VIF) was used to check collinearity, with a VIF > 10 considered as evidence of high collinearity and 10 > VIF > 5 as weak collinearity (Menard 2001, Vittinghoff et al. 2012). Models were evaluated with information-theoretical procedures (Burnham & Anderson 2002), using additive combinations of the fixed variables to run all possible candidate models. For each model, the Akaike's information criterion corrected for small sample size (AICc), and AICc weights (AICcw) were estimated and then used for model inference (Burnham & Anderson 2002). Model weights were used to calculate the relative likelihood that a certain model is the best of all candidate models. Models were ranked by AICc values, excluding from the analyses those with a difference between AICc values (ΔAICc) > 4, and using the remaining models to obtain model-averaged parameter estimates and their standard errors. Support for predictor variables was assessed by calculating the sum of the AICcw across all models containing the parameter of interest (parameter likelihood; Burnham & Anderson 2002), i.e. variables with an importance < 0.3 considered to have very low influence on predicted values (Burnham & Anderson 2002). RStudio software, version 2022.02.2 (RStudio Team 2022) was used to carry out statistical analyses, and the DHARMa package (Hartig 2020) was used to perform model validation. The Performance package
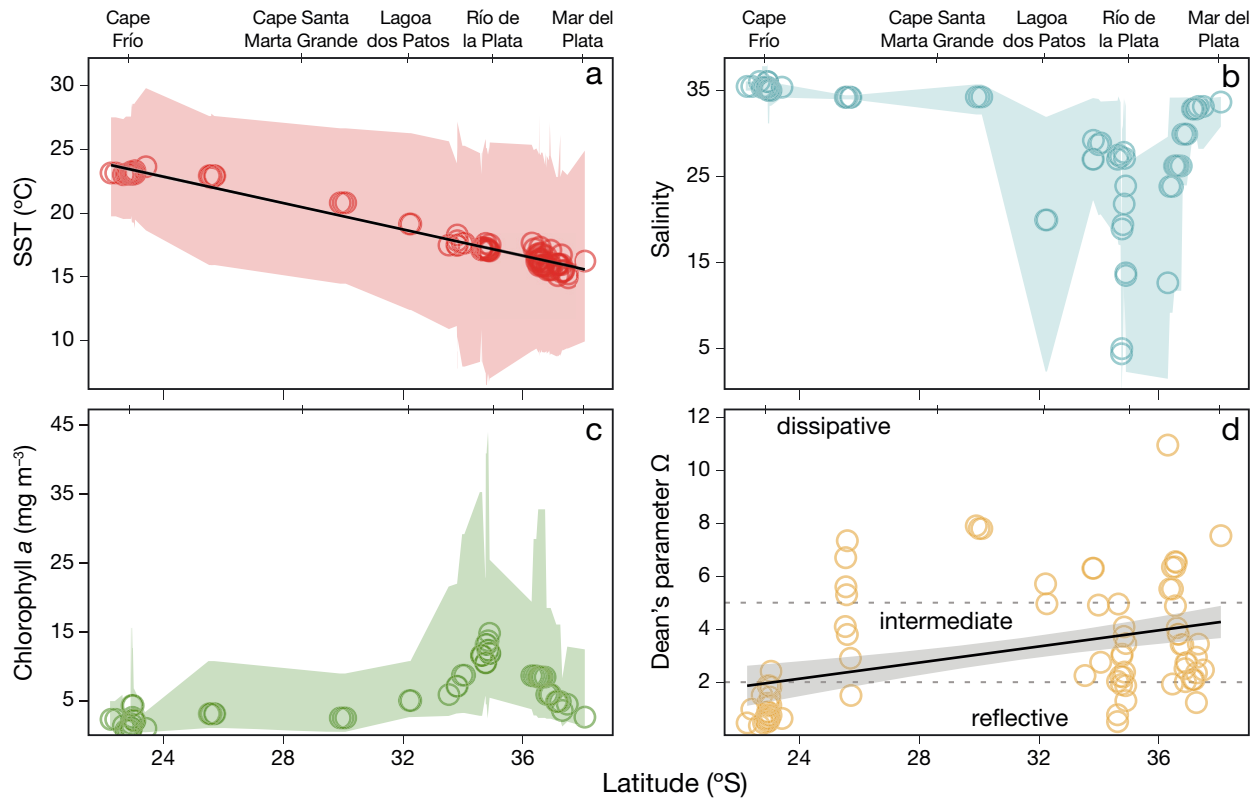
Fig. 2. Latitudinal patterns in selected environmental variables in South American sandy beaches (mean ± minimum and maximum values, shaded), denoted by (a) sea surface temperature (SST; n = 97), (b) salinity (n = 75), (c) chlorophyll *a* (chl *a*; n = 75), and (d) Dean's parameter Ω (n = 86); dashed lines indicate the limits between reflective, intermediate, and dissipative beaches. Main geographical locations are given along the upper *x*-axis. Regression lines (and 95 % CI) are shown for SST and Ω

(Lüdecke et al. 2021) was used to obtain the marginal and conditional R^2 of the models. Differences were considered significant at p < 0.05.

3. RESULTS

SST increased towards the tropics (Fig. 2a), whereas salinity and chl *a* did not show well-defined patterns (Fig. 2b,c). However, both variables exhibited large variability near RdlP (~36° S) and LdP (~32° S) estuaries (see Figs. 1b & S1). Salinity showed an abrupt decline between 33 and 37° S (Fig. 2b), while chl *a* peaked near 35° S (Fig. 2c). Dean's parameter decreased at higher latitudes, suggesting an increase of reflective beaches toward the tropics (Fig. 2d).

Abundance increased with Dean's parameter and mean salinity (Tables 1 & S2; Fig. 3a,e, all variables are statistically significant hereafter). Population structure given by the IRSC significantly decreased with salinity range and increased with maximum chl *a* (Tables 1 & S3; Fig. 3b,f). Growth performance

φ′ decreased with salinity range, and increased with mean chl *a* (Tables 1 & S4; Fig. 3c,g), whereas longevity decreased with mean SST and increased with grain size (Tables 1 & S5; Fig. 3d,h).

Secondary production increased with maximum salinity and decreased with maximum SST (Tables 1 & S6; Fig. 4a,e). Total biomass decreased with salinity range and increased with mean chl *a* (Tables 1 & S7; Fig. 4b,f). The *P:B* ratio significantly increased with maximum chl *a* (Tables 1 & S8; Fig. 4c), and the total mortality coefficient *Z* decreased with maximum salinity (Tables 1 & S9; Fig. 4g). Individual shell mass increased with mean salinity and beach slope (Tables 1 & S10; Fig. 4d,h). Results obtained from the models are summarized in Table 2.

4. DISCUSSION

The present study analyzed the concurrent role of a range of environmental variables in explaining large-scale trends in population parameters of the wedge clam *Donax hanleyanus* in South Atlantic

Table 1. Models relating *Donax hanleyanus* population parameters with key environmental variables for South American sandy beaches. GLMM: generalized linear mixed model; GLM: generalized linear model. R^2_m: marginal R^2 value associated with fixed effects; R^2_c: conditional R^2 value associated with fixed and random effects

	Estimate	SE	p	R^2_m	R^2_c
Abundance ~ Mean salinity + Dean's parameter				0.60	0.69
Model: GLMM, Poisson error distribution, log link function					
Intercept	−0.028	1.02	0.98		
Dean's parameter	0.178	0.07	**<0.05**		
Mean salinity	0.180	0.03	**<0.05**		
IRSC ~ Salinity range + Maximum chl *a*				0.52	
Model: GLM, Gaussian error distribution, identity link function					
Intercept	0.664	0.12	**<0.05**		
Salinity range	−0.046	0.01	**<0.05**		
Maximum chl *a*	0.022	0.01	**<0.05**		
Growth performance φ′ ~ Mean chl *a* + Salinity range				0.38	0.38
Model: GLMM, Gaussian error distribution, identity link function					
Intercept	2.832	0.04	**<0.05**		
Mean chl *a*	0.043	0.01	**<0.05**		
Salinity range	−0.011	0.00	**<0.05**		
Longevity ~ Mean SST + Grain size				0.97	
Model: GLM, Gaussian error distribution, identity link function					
Intercept	9.386	0.87	**<0.05**		
Mean SST	−0.386	0.04	**<0.05**		
Grain size	2.620	0.95	**<0.05**		
log Secondary production ~ Maximum salinity + Maximum SST				0.36	0.93
Model: GLMM, Gaussian error distribution, identity link function					
Intercept	−94.460	24.17	**<0.05**		
Maximum salinity	3.028	0.75	**<0.05**		
Maximum SST	−0.426	0.13	**<0.05**		
Log Total biomass ~ Mean chl *a* + Salinity range				0.41	0.66
Model: GLMM, Gaussian error distribution, identity link function					
Intercept	−2.231	0.64	**<0.05**		
Mean chl *a*	0.701	0.15	**<0.05**		
Salinity range	−0.271	0.06	**<0.05**		
P:B* ~ Maximum chl *a				0.28	
Model: GLM, Gaussian error distribution, identity link function					
Intercept	1.019	0.43	**<0.05**		
Maximum chl *a*	0.055	0.02	**<0.05**		
Mortality ~ Maximum salinity				0.31	
Model: GLM, inverse Gaussian error distribution, $1/\mu^2$ link function					
Intercept	−6.255	1.93	**<0.05**		
Maximum salinity	0.186	0.06	**<0.05**		
log Individual shell mass ~ Mean salinity + Beach slope				0.38	
Model: GLM, Gaussian error distribution, identity link function					
Intercept	−3.430	0.79	**<0.05**		
Mean salinity	0.092	0.03	**<0.05**		
Beach slope	0.089	0.03	**<0.05**		

sandy beach systems. Salinity, followed by chl *a* and SST, were the most relevant factors that may trigger large-scale differences in wedge clam population attributes, whereas local habitat features (Dean's parameter, grain size, beach slope) played a secondary role. Our observations reinforce regional-scale findings that highlighted salinity as the main factor controlling wedge clam populations in sandy beaches (Celentano et al. 2022, Risoli et al. 2022).

Donax hanleyanus abundance significantly decreased in response to a lower mean salinity and, as expected by the HHH, towards reflective beaches. This result is also supported by the habitat availability hypothesis (Defeo & McLachlan 2005, 2013), which predicts that beaches with larger areas (wider dissipative beaches) could harbor larger populations due to an increase in habitat heterogeneity and availability. Although the annual mean distribution of low salinity waters (salinity < 33.5; see heavy con-
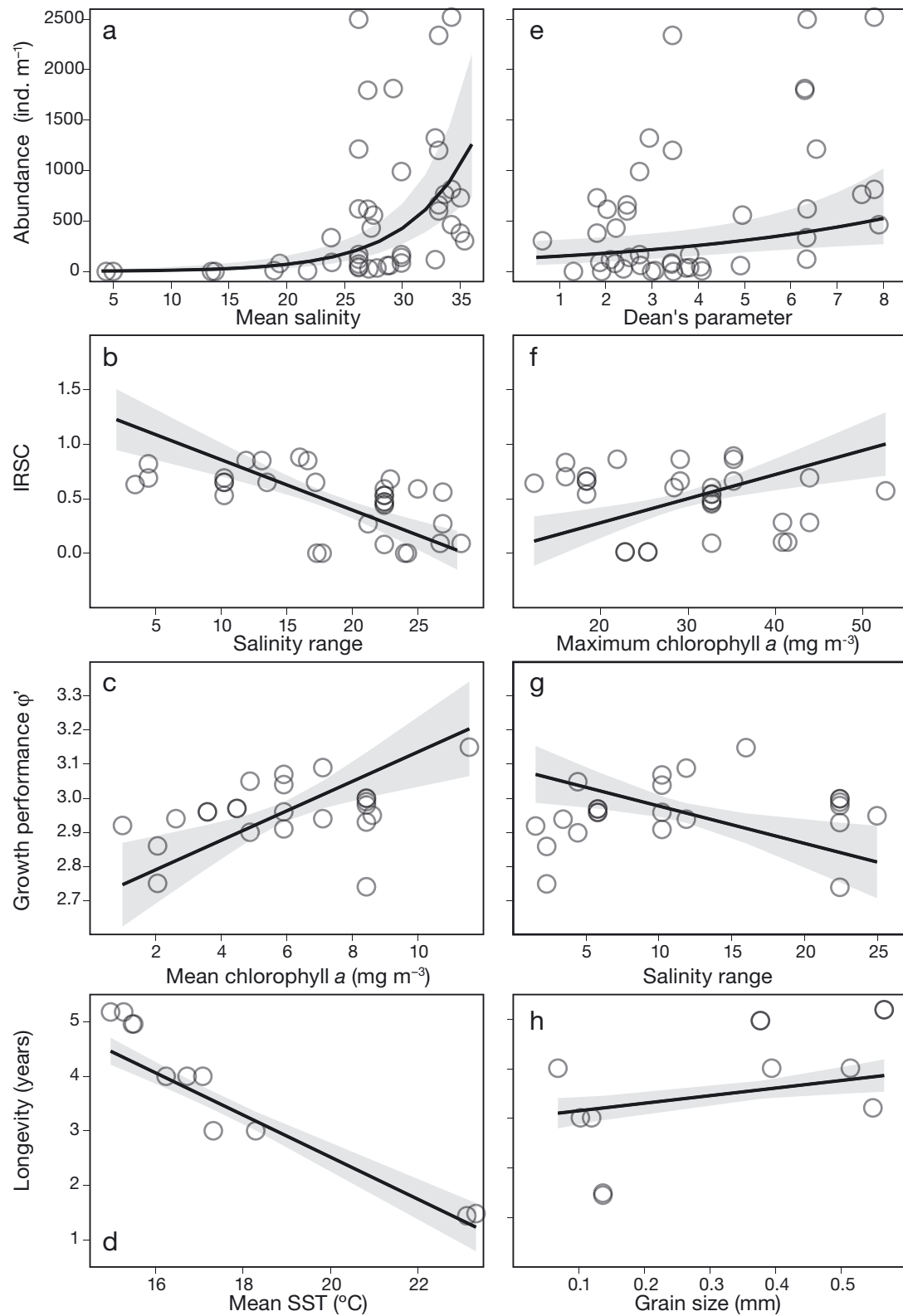
Fig. 3. Models relating wedge clam *Donax hanleyanus* (a,e) abundance, (b,f) population structure denoted by IRSC (index of recurrence of size classes), (c,g) growth performance, and (d,h) longevity with environmental variables in South American sandy beaches; mean partial effects of environmental variables are shown in order of importance, as solid lines with a shaded envelope representing the 95% CI; raw data used for the models are shown as open circles. See Table 1 for model details
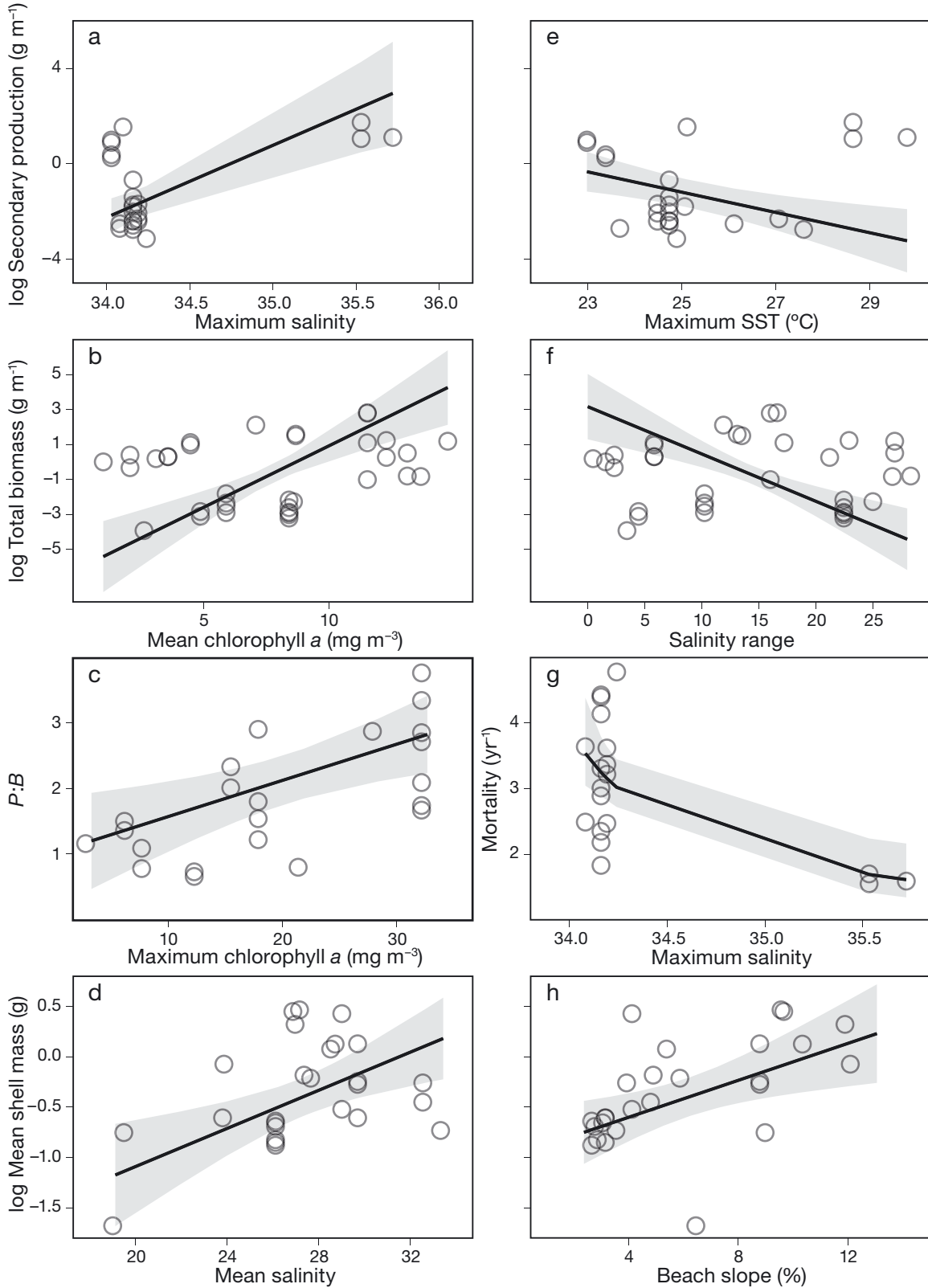
Fig. 4. Models relating wedge clam *Donax hanleyanus* (a,e) secondary production, (b,f) total biomass, (c) production:biomass (*P*:*B*) ratio, (d,h) individual shell mass, and (g) mortality with environmental variables in South American sandy beaches; mean partial effects of environmental variables are shown in order of importance, as solid lines with a shaded envelope representing the 95% CI; raw data used for the models are shown as open circles. See Table 1 for model details. SST: sea surface temperature

Table 2. Summary of the relationships found between population parameters and environmental variables in *Donax hanleyanus* from South American sandy beaches. IRSC: index of recurrence of size classes; *P:B*: production:biomass ratio; +: positive relationship; –: negative relationship; empty cells: no relationship

	Salinity	Chl *a*	SST	Dean's parameter	Grain size	Beach slope
Abundance	+ (mean)			+		
IRSC	– (range)	+ (maximum)				
Growth performance φ′	– (range)	+ (mean)				
Longevity			– (mean)		+	
Secondary production	+ (maximum)		– (maximum)			
Total biomass	– (range)	+ (mean)				
P:B		+ (maximum)				
Mortality *Z*	– (maximum)					
Mean shell mass	+ (mean)					+

tour in Fig. 1b) extends along the coast from approximately 37° 35′ S to 30° 04′ S, the RdlP plume undergoes large seasonal variations, extending farther north in austral fall and winter, and farther south in spring and summer (Piola et al. 2000, Möller et al. 2008). Along the coast, these seasonal variations are relatively large (~2–4) on the western side of the outer estuary. As the RdlP plume shifts northward during winter, the region south of the river mouth presents substantially lower salinities in austral summer than winter (light red shading in Fig. 1b). Similarly, large seasonal salinity differences span over a much longer coastal strip north of the estuary, extending northward beyond Cape Santa Marta Grande (blue shading in Fig. 1b). Sites within this region experience anomalously low surface salinities in austral fall and winter. The largest seasonal salinity fluctuations are observed in the northern shore of the outer estuary and along the coast between the mouth of LdP and 34° 46′ S. Salinity may have a strong influence on the spatio-temporal distribution of sandy beach macrofauna, impacting several physiological processes that translate into population traits. In turn, salinity may affect abundance, growth, survival, and recruitment success (McLachlan & Defeo 2018). Low abundances of this species were documented in beaches under the influence of the RdlP in both Argentina and Uruguay (Celentano et al. 2022, Risoli et al. 2022), as well as in other *Donax* populations around the world (Ansell 1983, Schoeman & Richardson 2002).

Population structure (depicted here by the IRSC) showed a lack of size classes and a reduced growth performance φ′ under estuarine conditions with high salinity ranges. When exposed to fluctuating salinity regimes, bivalves close their valves and reduce their feeding rates, which could be reflected in decreasing growth rates (Navarro 1988, Marsden 2004). In the context of the source–sink hypothesis for intertidal sandy beach populations (Defeo & McLachlan 2005), our results suggest that estuarine beaches could act as sink habitats, where wedge clam recruitment is insufficient to balance mortality rates (Celentano et al. 2010, Risoli et al. 2022). Additionally, IRSC and φ′ were positively correlated with mean and maximum chl *a* values, which are proxies of food supply in filter-feeding organisms such as *D. hanleyanus* (Penchaszadeh & Olivier 1975). Chl *a* was highest at 34–35° S (see Fig. 2c), where high wave energy creates hundreds of km of dissipative beaches (gentle slopes and fine grain sizes) characterized by high biomass accumulations of phytoplankton in their surf zones. These accumulations provide vast amounts of food for macrofaunal suspension feeders (McLachlan et al. 1996, McLachlan & Defeo 2018). Seasonal variations in chl *a* followed an inverse pattern to those observed for salinity, likely due to the fact that high chl *a* is associated with low salinity waters (Piola et al. 2008). Therefore, sites located between the RdlP estuary and Cape Santa Marta Grande exhibited high chl *a* values in austral fall and winter, with the largest variations observed along the southeast coast of Uruguay (Fig. S1). High food availability maximizes growth (in size and mass) and promotes healthy population structures by minimizing energy expenditure for basal maintenance (e.g. feeding) (Pörtner et al. 2005). Primary productivity (also approximated by chl *a* concentration) was also identified as a key explanatory variable in structuring biogeographical patterns in sandy beach ecosystems (Defeo et al. 2017). Our results are supported by field observations in sandy beach bivalves (McLachlan et al. 1996, McLachlan & Defeo 2018). Macroscale studies in both northern (Lastra et al. 2006, Rodil et al. 2014) and southern hemispheres (Defeo et al. 2017) showed that food availability impacts directly on

biotic features of filter-feeders (Ansell 1983, McLachlan & Defeo 2018). High food supply supported high abundance in other *Donax* species such as *D. denticulatus* Linnaeus, 1758 (Sastre 1984), *D. serra* Röding, 1798 (Donn 1987), and *D. trunculus* Linnaeus, 1758 (McLachlan et al. 1996).

Longevity clearly decreased towards the tropics, probably triggered by increasing metabolic rates caused by warmer conditions (Clarke & Gaston 2006, Tittensor et al. 2010, Barboza & Defeo 2015). This trend was noticed in other intertidal and marine bivalves (Cardoso & Veloso 2003, Lomovasky et al. 2008, Moss et al. 2016); however, long-lived animals were observed on reflective beaches, unlike the HHH predictions. Although sandy beaches are physically driven, biological factors (e.g. interspecific competition, top-down and/or bottom-up processes, or density-dependence at population level) could play a role (McLachlan & Defeo 2018). In agreement with our findings, Celentano et al. (2022) found a higher abundance of wedge clams in dissipative beaches (see Fig. 3e) and an increased relative representation of older adults with higher body size on reflective beaches (see Fig. 4h). This suggests a scaling of abundance to body size and reinforces the role of density-dependent processes in sandy beach macrofauna. Moreover, predation pressure may be less intense on reflective beaches with harsh swash conditions (McLachlan et al. 1995), favoring prolonged longevity. These results also reinforce the idea that, even though sandy beaches are thought to be mainly physically controlled, the relative influence of biotic interactions (e.g. competition, predation) increases toward dissipative beaches, which could be biologically controlled at high abundances (McLachlan & Defeo 2018). The total mortality coefficient Z also increased in lower salinity areas, reinforcing salinity as a critical driver of wedge clam population attributes. Salinity fluctuations also outlined between-beach differences in secondary production and biomass of *D. hanleyanus*, which increased under fully marine conditions. Secondary production and longevity decreased at lower latitudes with higher SSTs, probably triggered by temperature-induced higher metabolic rates (Pörtner et al. 2005). Biomass and $P{:}B$ increased with higher chl *a* values, showing that more productive beaches were mirrored by more productive populations (Evans et al. 2005). Individual shell mass decreased at low salinities and increased with higher beach slopes, which characterize reflective beaches. Low salinity reduces the shell deposition rate (Malone & Dodd 1967) and leads to more fragile valves, as ob-

served in the sympatric yellow clam *Mesodesma mactroides* (Risoli et al. 2020). Thicker valves found on reflective beaches may constitute an adaptation to the harsh swash climate, and considering that coarse sediments affect the burrowing capacity of *D. hanleyanus* (Marcomini et al. 2002), thickness could reduce the risk of damage during burial (see also McLachlan et al. 1995).

In summary, our study, based on a comprehensive dataset spanning thousands of kilometers, provides a new level of understanding of large-scale patterns in sandy beach populations, with broad macroecological implications for sandy shore macrofauna. We deciphered the relative contribution of environmental variables, revealing a key role of salinity as a driver of between-beach differences in almost all the traits analyzed, with chl *a* and SST as secondary contributors that override local morphodynamic features of the habitat (Dean's parameter, grain size, and beach slope). Consistent with previous findings at the community level (Defeo et al. 2017), chl *a* played a more important role than SST. Our findings provide insight into the ecological processes underlying macroscale patterns, which could help elucidate changes in sandy beach macrofaunal populations resulting from environmental variations. In the past decades, the eastern coast of South America from Cape Frío to 40° S has experienced warming, which is most intense in the RdlP and the South Brazil Bight (Franco et al. 2020). Warming has caused widespread clam mortalities, slow recovery, and habitat narrowing of a clam population (Gianelli et al. 2021). The expected continued warming as a response to climate change (Franco et al. 2020), paired with future changes in the salinity distribution due to changes in continental discharge (Pasquini & Depetris 2007) and wind patterns, may have further negative impacts on the regional *D. hanleyanus* populations. However, given its tropical/subtropical origin, the species could also extend its distribution range to higher latitudes. Considering the threats posed to sandy beach ecosystems by climate change, and the sensitivity of their biota to changes in the physical environment (Fanini et al. 2020, Defeo et al. 2021), clarification of macroecological patterns as those provided in this paper could set the basis for establishing conservation guidelines at large spatial scales. This strategy is also of utmost importance under a projected escalation in extreme climatic events in this region, which will continue to increase the exposure and vulnerability of sandy beaches and their resident fauna.

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