Unravelling the role of local and large-scale factors in structuring sandy beach populations: the wedge clam *Donax hanleyanus*

Eleonora Celentano[1],#, Julio Gómez[2],#, Diego Lercari[1], Anita de Álava[1], Omar Defeo[1],*

[1]UNDECIMAR, Facultad de Ciencias, Universidad de la República, Montevideo 11400, Uruguay
[2]Centro Universitario Regional Este (CURE), Universidad de la República, Rocha 27000, Uruguay

ABSTRACT: Changes in the structure and dynamics of sandy beach macrofaunal populations result from the simultaneous action of local and regional factors acting synergistically. This is particularly noticeable in transitional interfaces between freshwater and marine ecosystems, where large-scale gradients affect local beach morphodynamics and resident fauna. The wedge clam *Donax hanleyanus* occurs on beaches with contrasting morphodynamics along the salinity gradient generated by the Rio de la Plata estuary. We conducted sampling surveys to determine a fine-grained comprehensive coverage of the species' distribution in Uruguay to assess the concurrent effects of large-scale variations in salinity and local beach morphodynamics on wedge clam populations along 400 km (16 sandy beaches) over 2 yr. The main factor controlling wedge clam occurrence was salinity, overriding the effects of local habitat features. On beaches where the species was present, total abundance was higher on oceanic dissipative shores, which also harbored a higher abundance and relative representation of recruits. Recruitment was almost lacking in reflective beaches. However, biomass of adults with larger body sizes prevailed on reflective beaches, suggesting a scaling of abundance to body size and potential density-dependent effects. In this metapopulation, estuarine beaches are sinks, whereas oceanic beaches act as source habitats. We concluded that large-scale gradients generated by salinity variations translated into local population patterns (distribution, abundance and population structure) and processes (recruitment), which were secondarily driven by local morphodynamics. The relative importance of pre- and post-settlement processes across the morphodynamic spectrum from reflective to dissipative beaches has yet to be elucidated.

KEY WORDS: Bivalve · Metapopulation · Morphodynamics · Recruitment · Body size · Uruguay

1. INTRODUCTION

Sandy beaches are one of the most extensive intertidal ecosystems worldwide (Luijendijk et al. 2018, Defeo et al. 2021). Their physical structure is determined by the interaction between sand, waves and tides, and the resident macrofauna is mainly controlled by these distinctive physical properties (McLachlan & Defeo 2018). Worldwide macrofaunal patterns highlight the role of local morphodynamic features as explanatory variables of species richness, abundance and biomass, which increase toward wide dissipative beaches with gentle slopes and fine-grain sands (Defeo & McLachlan 2013, Barboza & Defeo 2015). Oceanographic fronts, upwellings, primary production and estuarine discharges, operating

*Corresponding author: odefeo@dinara.gub.uy
#These authors contributed equally

at several temporal and spatial scales, also play pivotal roles as predictors of macrofaunal diversity and abundance on sandy shores (Gray 2016, Defeo et al. 2017, Risoli et al. 2022).

Estuaries, as transitional interfaces between freshwater environments and the sea (Elliott & Whitfield 2011), affect sandy beaches through drastic variations in environmental conditions resulting from mixing of marine waters with freshwater derived from continental runoff. The estuarine discharge acts as an aggregate variable that simultaneously affects beach morphodynamics and the resident fauna. Fluvial sediments are deposited in estuarine beaches, which are also affected by longshore currents, waves and tides that account for variations in physical beach characteristics (Jackson et al. 2002, Jackson & Short 2020). These beaches are generally low-energy; the highest swell waves occur in the outer estuarine sector, decreasing gradually toward the inner zone. As swell waves dissipate, wind waves increase in dominance until they finally exceed the attenuated swell waves (Jackson 1995, Jackson & Short 2020). Thus, freshwater flow and runoff-related variables can explain the longitudinal dissipation of wave energy and the decrease in wave height and period toward the inner estuary (Vila-Concejo et al. 2020). These hydrodynamic agents modify beach morphodynamics, and therefore distinct beach profiles are found in beaches along an estuarine gradient, including a reduction in swash and beach width toward the inner estuary (Jackson & Short 2020).

Salinity and related features associated with river runoff and regional circulation patterns also shape large-scale trends in species richness, abundance and biomass in sandy beach communities (Lercari & Defeo 2006, Barboza et al. 2012, Laurino & Turra 2021). Freshwater runoff increases the vertical stratification in the nearshore environment and causes substantial variations in salinity, leading to reduced diversity of macrobenthic communities (Lercari & Defeo 2015). Salinity-driven effects on beach populations have been detected at different spatial scales, including alongshore trends within a single beach (Defeo & de Álava 1995, Lercari & Defeo 1999, Schoeman & Richardson 2002) and large-scale variations generated by freshwater runoff from large rivers (Celentano et al. 2010, Gómez & Defeo 2012, Ortega-Cisneros et al. 2017).

In intertidal beach species, studies conducted at several spatial and temporal scales have lent support to the 'habitat harshness hypothesis' (HHH; Defeo & Martínez 2003, Defeo et al. 2003). The HHH states that the increasing stress imposed by reflective beaches (i.e. steep slope, coarse grain, harsh swash climate) causes a decline in fitness and life history traits of beach fauna compared to benign, dissipative shores. Under such harsh conditions, individuals may divert more energy to survival than growth and reproduction, thus resulting in decreased growth rates, individual sizes and reproductive outputs and increased mortality rates (McLachlan & Defeo 2018). These predictions have been successfully tested in intertidal beach-type generalist species (sensu McLachlan & Defeo 2018) that can colonize a wide spectrum of morphodynamic conditions (Celentano & Defeo 2006, Corte et al. 2014). However, in estuarine environments, local physical features and estuarine-related conditions affect sandy beach macrofauna in different ways that cannot be explained by only one factor (Rodil et al. 2014, Carcedo et al. 2015, Ortega-Cisneros et al. 2017, Risoli et al. 2022). Therefore, an overarching challenge in sandy beach ecology is to assess the effects of combined forces of local and regional factors on macrofauna structure, dynamics and function (Fanini et al. 2020).

Mollusks constitute the most important taxa on sandy beaches in terms of biomass (McLachlan et al. 1996). Among them, bivalves of the genus *Donax* (Bivalvia: Donacidae) are commonly found in the intertidal zone of tropical, subtropical and warm temperate beaches worldwide (Ansell 1983, McLachlan et al. 1996). These bivalves are well-suited to inhabit different beach morphodynamic types (McLachlan et al. 1995, 1996). On the Atlantic coast of South America, the wedge clam *D. hanleyanus* Philippi, 1945 inhabits sandy beaches spanning a broad range of morphodynamic types (Defeo & McLachlan 2011), from Caravelas, Brazil (17° S; Cardoso & Veloso 2003), through Uruguay (Delgado & Defeo 2007) to Mar del Plata, Argentina (38° S; Risoli et al. 2022). The Uruguayan coastline is characterized by microtidal sandy beaches with a wide variety of morphodynamic features, including transitional environments influenced by the Rio de la Plata (RdlP) estuary, which is the widest estuary in the world and strongly influences coastal marine waters (Piola et al. 2005, Lercari & Defeo 2006). In this context, the occurrence of *D. hanleyanus* in sandy beaches with contrasting morphodynamics along a coastline affected by a large-scale salinity gradient provides an opportunity to unravel the contribution of local and regional factors to population attributes. With this objective in mind, for 2 yr, we sampled 16 Uruguayan sandy beaches with contrasting physical characteristics along ~400 km covering the RdlP salinity gradient.

2. MATERIALS AND METHODS

2.1. Study sites

A total of 16 exposed microtidal (tidal range: 0.5 m) sandy beaches along ~400 km of Uruguayan coastline were sampled every 2 mo for 2 yr. The sampling design covered the salinity and morphodynamic gradients defined, respectively, by the RdlP and the continuum between reflective and dissipative states (Fig. 1). Contiguous pairs of beaches with different morphodynamic types and the same salinity range were considered (Lercari & Defeo 2006). Sampling sites were located from the westernmost Pascual beach in the inner estuarine zone (Beach 1: 34° 45′ S, 56° 27′ W) to the oceanic Barra del Chuy beach (Beach 16: 33° 40′ S, 53° 20′ W) (Fig. 1).

2.2. Sampling and laboratory analyses

At each site, beach width (m) was measured as the distance between the base of the dunes and the lower limit of the swash zone, where water moves over the beach face after a broken wave collapses on the sand. Swash width (m) was measured as the distance between upper and lower swash limits at sampling time. Water salinity and temperature were measured in the swash zone with an YSI 33 thermosalinometer. Breaker height (m) was determined visually, and the wave period (s) was estimated using a stopwatch as the time interval between breakers for 5 min.

In order to estimate across-shore variations in physical variables, linear transects were performed at each beach from the base of the dunes to the lower swash limit, with sample units (SUs) located every 4 m. Beach slope was calculated for all SUs and beach face slope (BFS) from the elevation of low tide to the upper limit of swash action. Sediment samples were taken in each SU to determine grain size by sieving the sediment through a sieve column ranging from 2.0 to 0.063 mm mesh. The sediment retained in each sieve was weighed to estimate mean grain size using the GRADISTAT software (Blott & Pye 2001). A subsample was taken in each SU to estimate moisture (%) and organic matter (%) (by weight differences between wet, dry and burned samples).
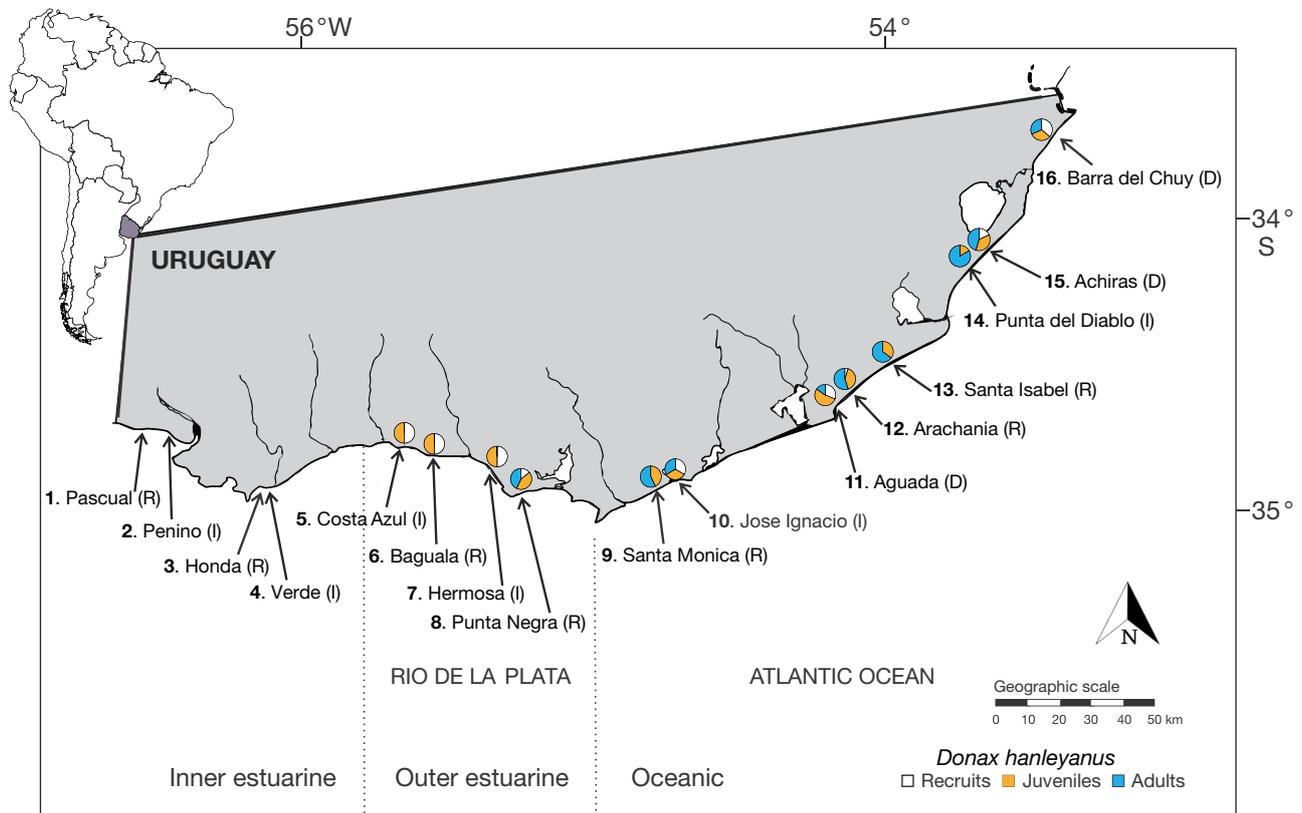
Fig. 1. Location of the 16 sandy beaches surveyed, named and numbered from west to east. Estuarine (inner and outer) and oceanic zones are also shown, along with the relative representation of population components of *Donax hanleyanus* at each beach. D: dissipative; I: intermediate; R: reflective

Biological sampling comprised 3 transects perpendicular to the shoreline, spaced 8 m apart, with SUs beginning at the base of the dunes and continuing at 4 m intervals in a seaward direction until at least 2 consecutive SUs yielded no more wedge clams. A sheet metal cylinder (27 cm in diameter) was used to remove the sediment of each SU to a depth of 40 cm, and the wedge clams retained were sieved through a 0.5 mm mesh, fixed and transported to the laboratory.

In the laboratory, wedge clams were measured to the nearest 0.1 mm and wet weighed (0.01 g precision), covering the full range of *Donax hanleyanus* sizes (1–34.4 mm). Wedge clams were classified into 3 population components following Defeo & de Álava (1995): recruits (≤5.0 mm), juveniles (5.1–15 mm) and adults (>15 mm). This operational definition of population components closely matches histological analysis, which showed that undifferentiated individuals (juveniles) ranged from 7 to 15 mm (Delgado & Defeo 2007). Abundance and biomass (total and by population component) were estimated by strip transect (IST, ind. m^{-1} and BST, g m^{-1}), where the mean density (in number of individuals or grams per square meter) of all samples taken in a transect was multiplied by the width (m) of the species distribution across the beach (McLachlan & Defeo 2018). Mean individual body size was calculated directly from the length frequency distributions (mm) and also estimated as the ratio between total biomass and total abundance (BST/IST, in grams).

2.3. Data analysis

Beaches were classified using Dean's parameter (Ω), defined as (Short 1996):

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

where *Hb* is breaker height (m), *Ws* is sand fall velocity (cm s^{-1}) and *T* is the wave period (s). $\Omega < 2$ characterizes reflective beaches, $\Omega > 5$ defines dissipative ones and $2 < \Omega < 5$ describes a wide range of intermediate beach states (Defeo & McLachlan 2005).

Length frequency distributions (LFDs) of *D. hanleyanus* were grouped into 1 mm size classes, and the index of recurrence of size classes (IRSC, Celentano et al. 2010) was estimated as follows:

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

where N_L defines the number of length (*L*) size classes in a given beach and *NT* is the total number

of size classes observed in all beaches sampled. IRSC ranges between 0 and 1 (all size classes present).

Generalized additive mixed models (GAMMs) were used to assess the relative effect of environmental variables (salinity, water temperature, beach and swash width, beach slope and BFS, grain size and Ω) on the occurrence, abundance and body size of the wedge clam. GAMMs were chosen as a modelling tool because of their flexibility to adjust for non-linear trends (Guisan et al. 2002). We performed a conditional 2-step procedure, avoiding the possible overdispersion caused by the presence of excessive zeroes in the database (Martin et al. 2005). First, we modelled species occurrence (i.e. presence/absence) and then abundance and body size. Binomial (occurrence) and Gaussian (abundance and body size) distributions and logit and identity link functions were respectively used for model fitting (Hastie & Tibshirani 1990).

The modelling process for biological variables started by setting a global model, which included all environmental variables (retained after testing for collinearity) as fixed effects. A categorical site variable and the date of each sampling event were included as random intercepts in all models to adjust the variability among sites and times, without consuming many degrees of freedom. The variables were included as smooth terms using penalized cubic regression splines. The maximum number of degrees of freedom of each smooth term was limited to 3 to avoid overfitting. Models were ranked according to the corrected Akaike's information criterion (AICc) for small sample size, selecting those with lower AICc. GAMMs were performed in R using the 'gamm4' package (Wood & Scheipl 2020) via the 'uGamm' function of the 'MuMIn' package (Bartoń 2020). The dredge function included in 'uGamm' assesses every possible model by generating all combinations of explanatory variables used as predictors.

3. RESULTS

3.1. The habitat

Salinity increased from estuarine to oceanic beaches, with the latter showing the lowest within-beach variation (evidenced by the SE values in Fig. 2a). Lowest salinity values were found in westernmost inner estuarine Beaches 1 (mean ± SE: 4.4 ± 1.7) and 2 (5.0 ± 1.8); the highest was in the easternmost oceanic Beach 16 (29.2 ± 1.0). A large-scale continuous salinity gradient was best explained ($R^2 = 0.98$, p < 0.001) by an asymptotic model of the form (Fig. 2a):
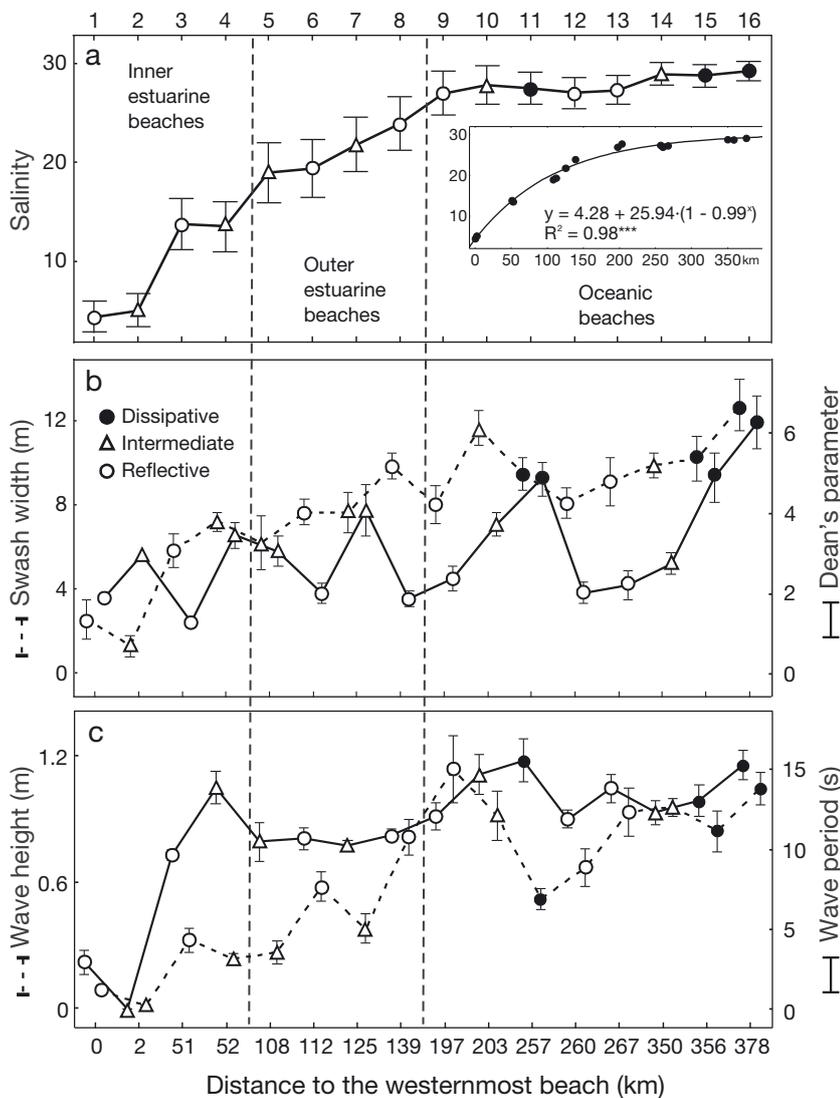
Fig. 2. Macroscale patterns of environmental variables (mean ± SE) in Uruguayan sandy beaches, ordered from the westernmost beach and numbered following Fig. 1. Inset in (a) shows the potential model relating salinity with distance from the westernmost site (km). *** p < 0.001

$$S = a + b \cdot (1 - c^D) \qquad (3)$$

where S is salinity, D is the distance from the westernmost site and a (4.28 ± 0.63), b (25.94 ± 0.78) and c (0.99 ± 0.001) are significant parameters (p < 0.001).

Swash width and Ω increased from estuarine to oceanic beaches, particularly dissipative ones (Fig. 2b). Breaker wave height and wave period significantly increased from inner estuarine beaches to oceanic beaches (Figs. 2c & S1 in the Supplement at www.int-res.com/articles/suppl/m696p029_supp.pdf). Beach slope, BFS (not shown), and grain size were highest in reflective beaches (Fig. S2a), whereas beach width increased toward dissipative beaches

(Fig. S2b). Neither of these variables followed an alongshore trend.

3.2. Occurrence, abundance and biomass

Donax hanleyanus was absent in the 4 westernmost beaches in the inner estuary (Figs. 1 & 3) and occurred in the 12 remaining beaches. Wedge clam abundance increased towards oceanic beaches, and this pattern was consistent for the whole population and each population component (Figs. 3 & 4). Total abundance was highest in the oceanic dissipative Beach 16, but total biomass was highest in oceanic reflective Beaches 12 and 13 (Fig. 3). In outer estuarine beaches (Beaches 5–7), only recruits and juveniles occurred throughout the study period (Fig. 4a–d). Recruits were most abundant and had the highest biomass in dissipative Beaches 11 and 16 (Figs. 4a,b & S3), whereas reflective Beaches 12 and 13 harbored the highest abundance and biomass of adults (Figs. 4e,f). It is worth noting that all these trends were consistent through time (Fig. S4).

3.3. Population structure and body size

D. hanleyanus showed a population structure skewed towards recruits and juveniles in estuarine beaches, with adults occurring only in Beach 8 at the outer estuary (Fig. 5). In contrast, oceanic dissipative beaches harbored LFDs represented by all size classes, mainly depicting a well-defined recruitment component (Fig. 5). Reflective beaches presented LFDs with a significant adult component and a virtual absence of recruit sizes (Fig. 5). Temporal variations in population structure for Beaches 8 (outer estuarine), 13 (oceanic reflective) and 16 (oceanic dissipative) that typified the salinity and morphodynamic gradients showed consistent patterns (Figs. 6, S4 & S5): (1) Beach 8 had irregular recruitment and a sporadic occurrence and low abundance of adults; (2) dissipative Beach 16 presented well-defined recruitments in
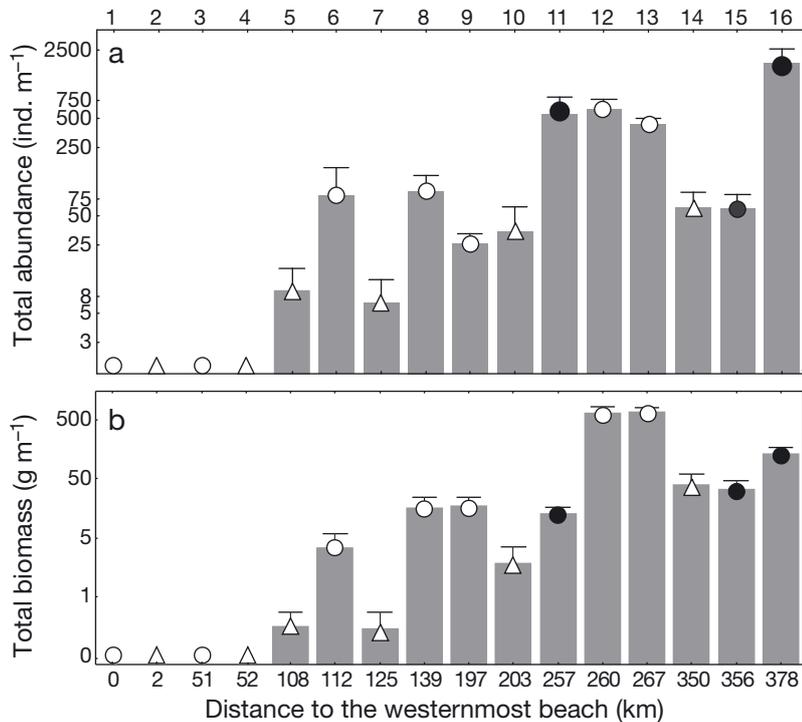
Fig. 3. Total *Donax hanleyanus* (a) abundance and (b) biomass (mean + SE) in Uruguayan beaches, ordered and numbered following Fig. 1. ●: Dissipative; △: intermediate; ○: reflective. Note the different *y*-axis (logarithmic) scales

7 of the 11 sampling events; and (3) reflective Beach 13 did not show recruits throughout the study period and registered a sporadic presence of juveniles and a regular and persistent dominance of adults at all sampled months (Fig. 6). In line with these results, the IRSC was positively correlated with salinity, indicating a better representation of size classes in oceanic beaches (Fig. 7a). A linear model also explained spatial variations in maximum individual size, with the largest organisms occurring in oceanic reflective Beaches 12 and 13 (Fig. 7b).

3.4. The species and its relationship with the environment

The conditional procedure using a 2-step GAMM showed different effects of salinity and beach morphodynamics on the occurrence and abun-
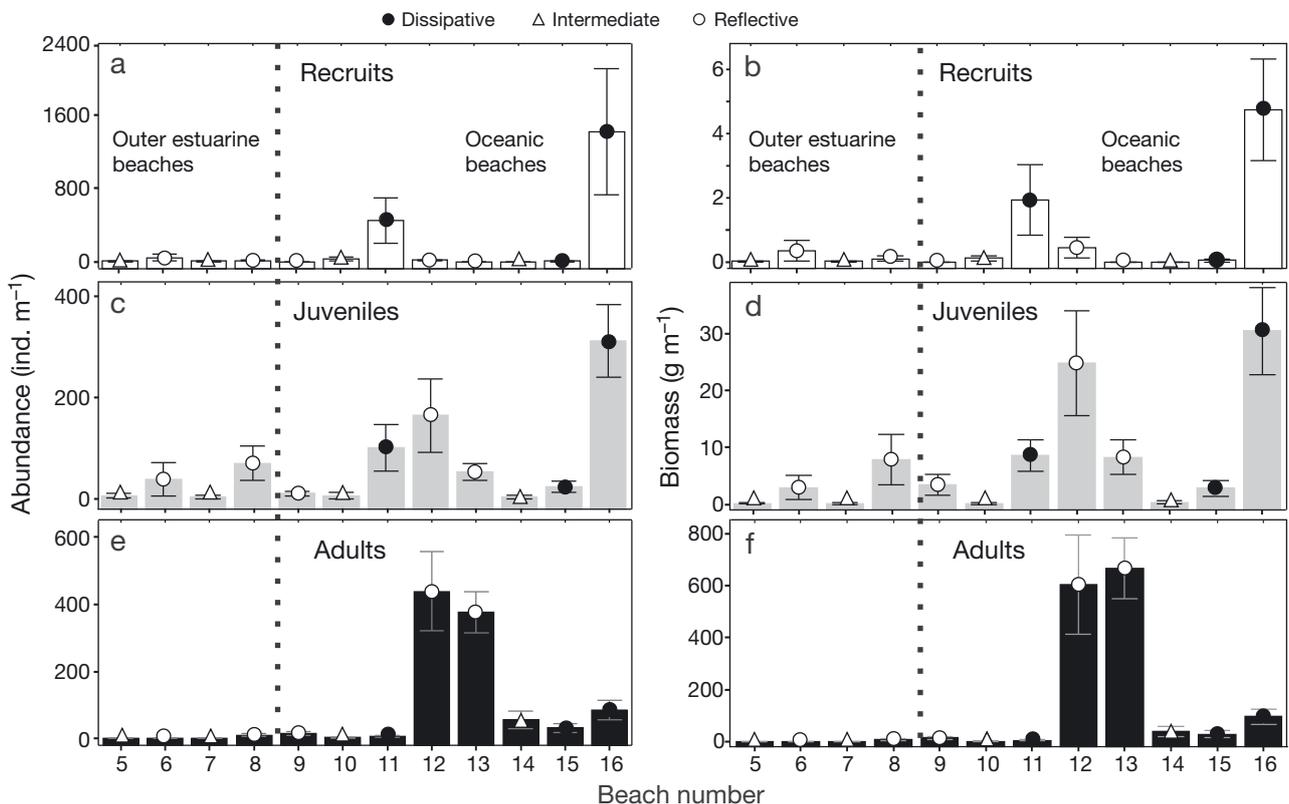
Fig. 4. *Donax hanleyanus* (a,c,e) abundance and (b,d,f) biomass (mean ± SE) by population component in Uruguayan beaches ordered and numbered following Fig. 1. No wedge clams were collected in estuarine Beaches 1–4. Note the different *y*-axis scales
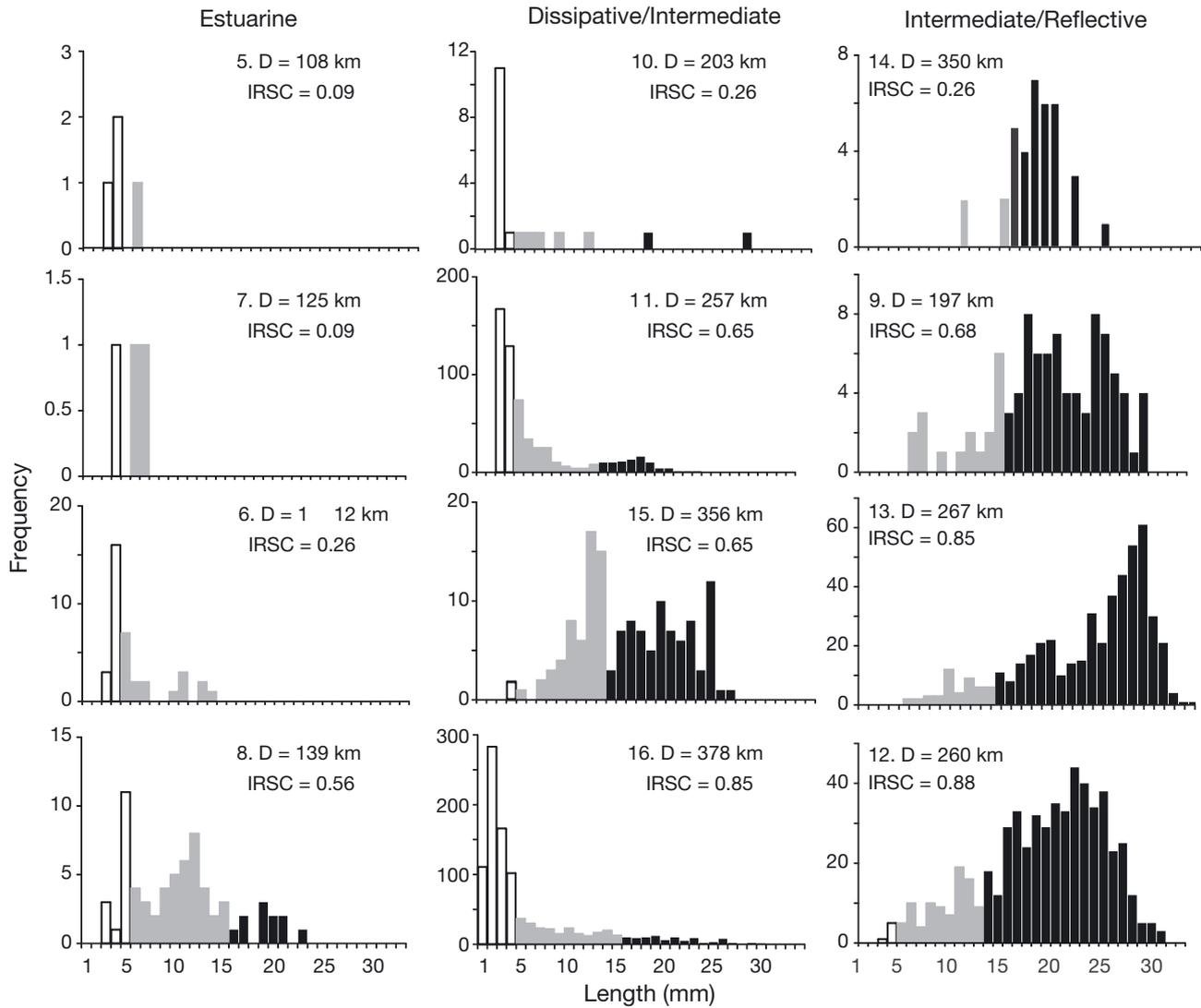
Fig. 5. *Donax hanleyanus* length frequency distributions (combined for the whole study), discriminated by beach and population component: recruits (white), juveniles (gray) and adults (black). Beach number, distance from the westernmost beach (D: km), and the estimated index of recurrence of size classes (IRSC) are shown. Beaches are ordered by their (1) estuarine/oceanic condition, (2) morphodynamic state, and (3) increasing IRSC value. Note the different *y*-axis scales

dance of the wedge clam. Occurrence (1st step GAMM) significantly increased with salinity, i.e. towards oceanic beaches (Table 1, Fig. 8a). Abundance (2nd step GAMM) for the total population was significantly predicted by beach width and Ω, denoting an increase towards dissipative conditions and a predominance of local physical factors over the regional estuarine gradient (Table 1, Fig. 8b,c). Abundance of recruits was significantly explained by beach width and water temperature as the leading environmental predictors of temporal and large-scale trends (Table 1, Fig. 8d,e), denoting increasing recruitment towards dissipative beaches during the warmest months.

Wedge clam body size increased with beach slope and grain size, meaning larger individuals were found at reflective beaches (Table 1). Body size followed the opposite trend of abundance and was best explained by local morphodynamic variables (Table 1), increasing with beach slope (all population components combined; Fig. 8f) and toward coarser grains in recruits and juveniles (Fig. 8g).

4. DISCUSSION

Donax hanleyanus showed marked large-scale variability along 400 km of sandy coastline, driven
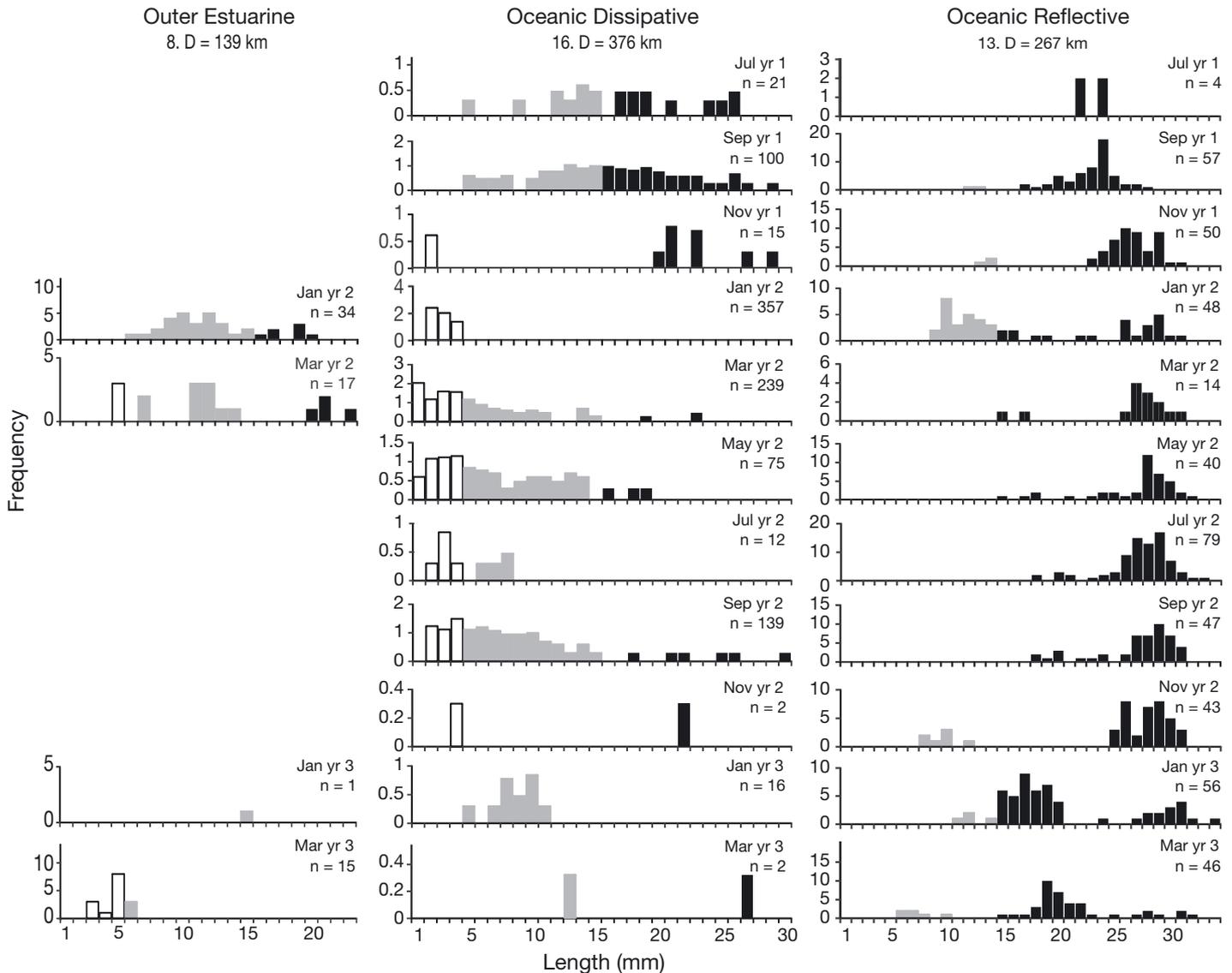
Fig. 6. *Donax hanleyanus* size frequency distributions by sampling event in 3 beaches typifying salinity and morphodynamic gradients. Beach number and distance from the westernmost beach (D: km) are shown. Population components: recruits (white), juveniles (gray) and adults (black). Note the different *y*-axis scales. Data were converted to log (*x*+1) in Beach 16 for better visualization

by spatial variations in salinity and beach morphodynamics. This fine-grained comprehensive coverage, not seen in previous analyses for a sandy beach bivalve population, showed that local habitat characteristics (e.g. beach width, slope), acting together with salinity as an estuarine-related stressor at larger spatial scales, affected the wedge clam in several ways. The main factor controlling wedge clam occurrence was salinity, overriding the effects of local habitat features. On beaches where the species occurred, total abundance was higher on oceanic dissipative shores, with beach width and Ω being significant predictors. Recruits

were also more abundant on dissipative beaches and represented a vast proportion of the population, whereas adult abundance and biomass were higher in reflective environments. Local morphodynamic factors can benefit the wedge clam under dissipative conditions (i.e. higher abundance, well-represented population structure, higher recruitment), thus supporting the HHH. These findings suggest that large-scale gradients in environmental suitability generated by salinity variations can translate into local population patterns and processes, which are secondarily driven by local morphodynamics in oceanic beaches.
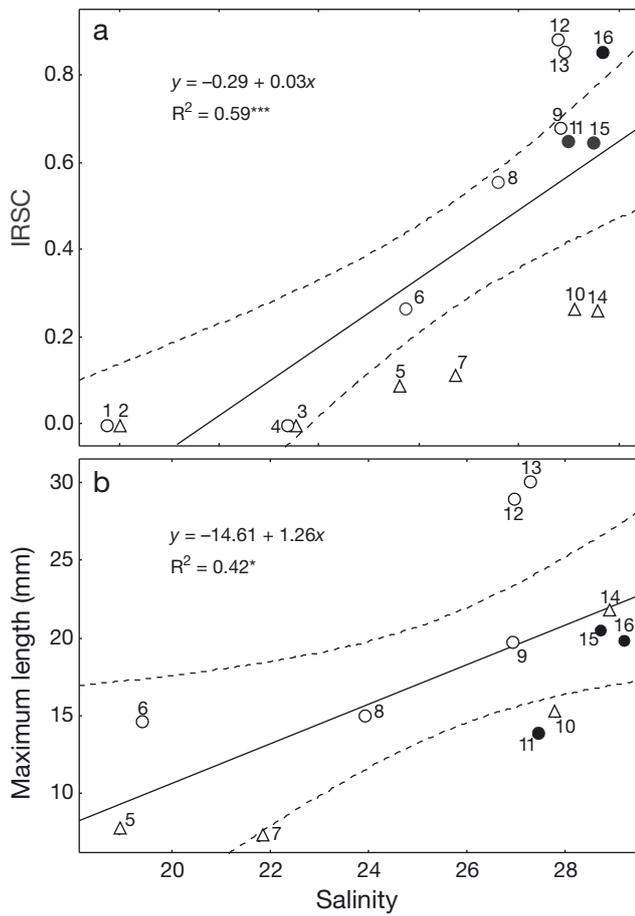
Fig. 7. *Donax hanleyanus*. Best bivariate models between water salinity and (a) index of recurrence of size classes (IRSC) and (b) maximum length (mm). Only beaches with species occurrence are shown. Dotted lines: 95% CIs. Beaches are numbered following Fig. 1. ●: Dissipative; △: intermediate; ○: reflective. * p < 0.05, *** p < 0.001

Salinity was the best predictor of wedge clam occurrence, modulating the species' presence at a large spatial scale. The wedge clam was not recorded in the inner RdlP estuary throughout the 2 yr period, and only recruits and juveniles were found in outer estuarine Beaches 5, 6 and 7. Similarly, in Argentina, *D. hanleyanus* does not occur on beaches under a significant freshwater influence of the RdlP (Marcomini et al. 2002). An experimental study of the congeneric *D. trunculus* found that juveniles resisted lower salinities and presented higher survival than adults (Reyes-Martínez et al. 2020). In addition, osmotic constraints inflicted by salinity variations and high metabolic demand during gonad development diminish their efficiency of absorbing nutrients and generating reserves, increasing mortality rates. Thus, environmental unsuitability can affect fitness through organisms' survival, resulting in populations that lack an adult component on most estuarine beaches (Figs. 4, 6 & 7).

Population structure and body size of *D. hanleyanus* varied markedly between beaches along the salinity gradient. Oceanic beaches harbored a population structure fully represented by all size classes and higher body size than estuarine beaches. Similar macroscale patterns were detected for this species on the Argentinean coast (Risoli et al. 2022) and for other macrofaunal species on Uruguayan beaches (Celentano et al. 2010, Lozoya et al. 2010, Gómez & Defeo 2012). Freshwater runoff also affected *D. serra* abundance and population structure on a South African beach (Schoeman & Richardson 2002). Freshwater discharged by an artificial canal on a sandy beach in Uruguay also accounted for a decline in abundance, biomass, body size and reproductive output in the suspension-feeding guild comprising the clams *D. hanleyanus* and *Mesodesma mactroides* and the mole crab *Emerita brasiliensis* (McLachlan & Defeo 2018). These mesoscale (i.e. one beach) trends clearly match macroscale variations in wedge clam population features along the full salinity gradient generated by the RdlP. The comparable results obtained at meso- and macroscales highlight the crit-

Table 1. *Donax hanleyanus*. Significant generalized additive mixed model results for species occurrence, abundance and body size (in g and mm; see Section 2.2 for details). Approximate significance of smooth terms for each environmental variable is shown

Response	Predictor	df	χ^2	F	p	Adjusted R^2
Occurrence	Salinity	1.00	10.59		0.001	0.24
Total population abundance (ind. m^{-1})	Beach width (m)	2.95		43.14	<0.001	0.70
	Dean's parameter	2.76		5.19	0.019	
Recruit abundance (ind. m^{-1})	Beach width (m)	2.76		15.85	<0.001	0.94
	Water temperature (°C)	2.88		26.55	<0.001	
Body size (g) (total population)	Beach slope (cm m^{-1})	1.00		5.69	0.020	0.18
Body size (mm) (recruits and juveniles)	Grain size (mm)	1.00		6.64	<0.005	0.21
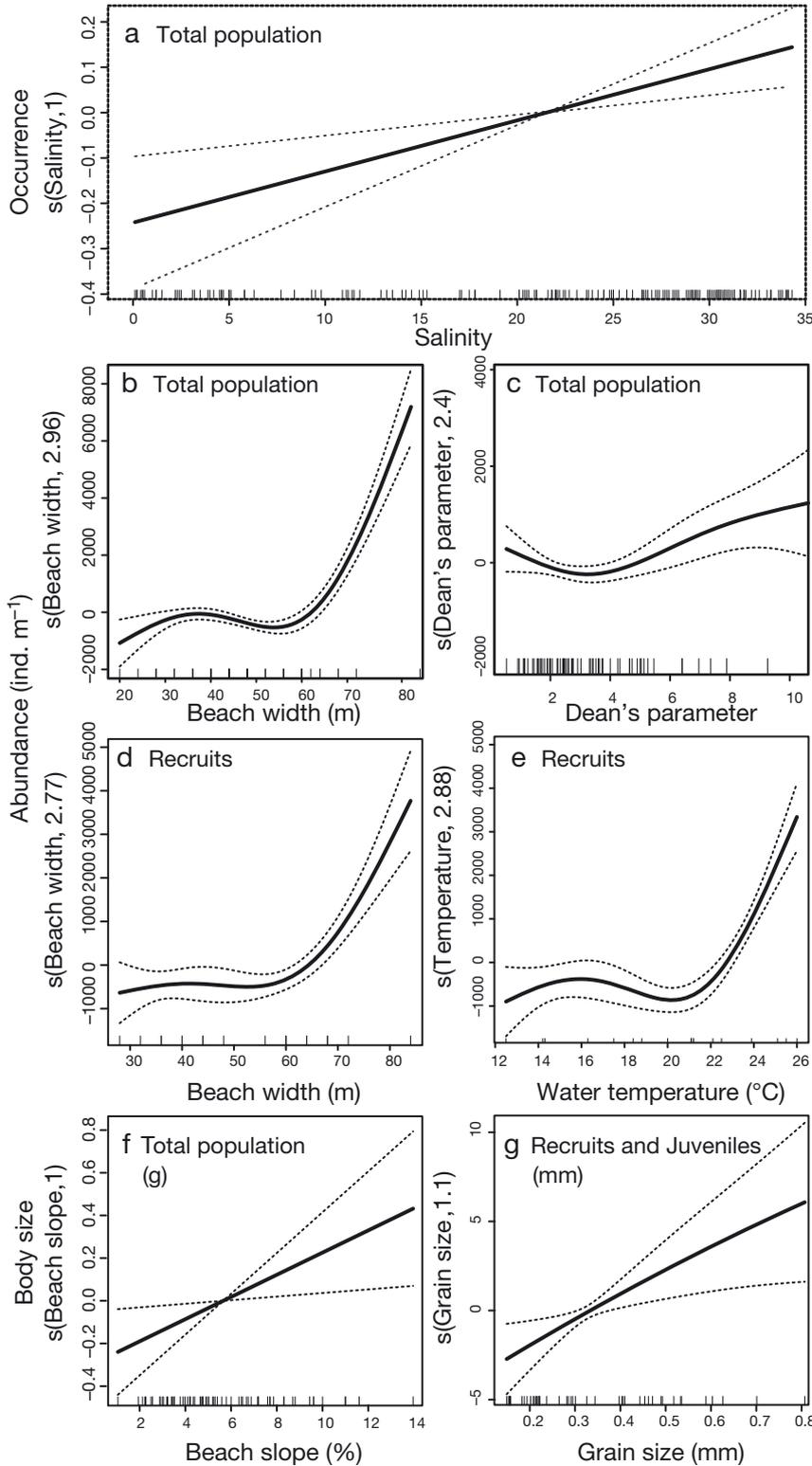
Fig. 8. *Donax hanleyanus.* Best generalized additive mixed models showing the relationship (solid line) between (a) species occurrence, (b–e) abundance and (f,g) body size and environmental predictors. Dotted lines: ±2 SE above and below the estimate of the smooth curve. Numbers on the *y*-axis labels indicate the estimated degrees of freedom of the smoothed curve. Marks on the *x*-axis indicate the measured values of each variable. Note the different *y*-axis scales

ical role of environmental variability in controlling the distribution and abundance of beach populations at multiple spatial scales.

The foregoing results have important implications in a metapopulation context. Estuarine beaches act as absolute sinks that depend exclusively on imported larvae, whereas oceanic beaches harboring a wide range of sizes act as source habitats. In the former, juveniles and adults perish annually before reproduction, suggesting an ecological trap (Robertson & Hutto 2006, Lipcius & Ralph 2011). Probable mechanisms underlying these trends involve advective transport from the oceanic beaches back to their natal populations and subsidies to estuarine beaches. These patterns reinforce the role of oceanic beaches as essential source habitats, according to the metapopulation theory developed for sandy beaches (Defeo & McLachlan 2005). This source–sink hypothesis was also verified for intertidal mole crabs of the genus *Emerita* on Pacific and Atlantic beaches in South America (Celentano et al. 2010, Veas et al. 2013).

D. hanleyanus is an intertidal beach-type generalist capable of inhabiting beaches under a broad range of morphodynamic states. Beach width and Ω were the most important GAMM predictors of abundance, which increased toward wider dissipative beaches. Beach width, together with tide range, defines the dimensions of the intertidal habitat and the number of species/niches that can be accommodated (Checon et al. 2018, McLachlan & Defeo 2018). Wider dissipative beaches could (1) support larger populations, thus reducing the probability of local extirpations, and (2) favor across-shore segregation between recruits, juveniles and adults (reviewed in McLachlan & Jaramillo 1995). Beach

width was also a critical correlate of wedge clam abundance on Argentinean beaches (Thompson & Sánchez de Bock 2009). In Uruguay, the marked decrease in swash width (and thus clam habitat availability) toward narrower estuarine beaches (Fig. 2b) could be explained by the longitudinal dissipation of wave energy by the RdlP, which significantly reduced breaker wave height and period (Fig. 2c). These concatenated effects generate low-energy environments with drastic salinity variations and reductions in food and habitat quality for the wedge clam.

Greater wedge clam total biomass and larger body sizes prevailed on oceanic reflective beaches. This capacity of an intertidal species to prosper in harsh environments with coarse sediments, a turbulent swash climate and low food availability is favored by morphological, behavioral and trophic adaptations (Nel et al. 2001), which in the case of the wedge clam are given by the following: (1) changing the trophic niche according to local conditions (Bergamino et al. 2016); (2) an efficient and fast burrowing capacity to cope with short swash periods (McLachlan et al. 1995); and (3) a more streamlined shape (wedge-shaped) with higher density, which is a function of shell thickness (McLachlan et al. 1995).

D. hanleyanus populations inhabiting oceanic dissipative beaches were composed mainly of recruits, which were almost lacking in reflective beaches. Previous studies also found greater *D. hanleyanus* recruitment and a more extended recruitment period in dissipative beaches (Delgado & Defeo 2007, Herrmann et al. 2010). The wide surf zones of dissipative beaches could harbor orders-of-magnitude higher concentrations of surf zone diatoms (i.e. primary nutrition source for the wedge clam; Bergamino et al. 2016) and dense larval settlement in the intertidal because of the presence of rip currents, which tend to be absent in the narrow surf zones of reflective beaches (Shanks et al. 2010, Morgan et al. 2018, Salant & Shanks 2018). The much higher recruitment of intertidal species in dissipative beaches has been widely ascribed to the nearshore hydrodynamics of their extended surf zones, which retain a high abundance of larvae and phytoplankton, forming semi-closed ecosystems (reviewed in McLachlan & Defeo 2018). In contrast, the low retention rates of floating material in the surf zones of reflective beaches (Shanks et al. 2017) could explain the poor recruitment observed throughout the 2 yr sampled. This pattern has also been documented in intertidal species inhabiting exposed rocky shores and beach rocks (Shanks et al. 2017), suggesting that variations in nearshore

hydrodynamics could play a critical role in recruitment dynamics across ecosystem types.

The comparatively lower abundance of wedge clam adults on dissipative beaches with high recruitment suggests that post-settlement density-dependent processes could be important regulating forces (Lima et al. 2000, McLachlan & Defeo 2018, Ferguson et al. 2021). In contrast, lower post-settlement mortality could explain the increase in the relative representation of adults with larger individual size and biomass on reflective beaches. These findings, taken together, suggest a scaling of abundance to body size, reinforcing the role that density-dependent processes play in sandy beach macrofauna, where abundance increases from reflective to dissipative beaches as mirrored by a decrease in body size (Defeo & McLachlan 2011, 2013). Thus, both beach types acting as metapopulation sources seem to be driven by different demographic processes. Low recruitment rates (and probably larval supply) on reflective beaches are decoupled from adult abundance, possibly driven by low larval retention rates in the surf zone and the effects of the harsh habitat quality at settlement. Adult abundance is also decoupled from recruitment: dissipative beaches had higher recruitment abundance but lower adult abundance than reflective beaches, implying higher density-dependent mortality rates from recruitment to adult stages (Defeo 1996, Lipcius et al. 1997).

Secondary settlement, in which newly settled bivalves undergo a second dispersal stage, has been documented in other *Donax* species (Ansell 1983, McLachlan et al. 1996) and could explain the patterns reported for reflective beaches. At settlement, beach clams attach to sand grains with a byssus but can detach and undergo a pelagic phase by using the byssus as a float, allowing resuspension and transport (Ansell 1983). Redistribution of recruits <6 mm of *D. gouldi* attached to pelagic algae stages has been documented in surf zones with strong currents (Ansell 1983). In contrast, large-scale movements of adults are unfeasible, as demonstrated by tagging studies in *D. serra* (Dugan & McLachlan 1999) and other intertidal species (Harris et al. 2017). Additionally, the beaches studied here are separated mainly by rocky heads, precluding alongshore movements from one beach to another.

In summary, the large-scale estuarine gradient, acting jointly with local habitat features, shapes the population characteristics of *D. hanleyanus*. The main factor controlling wedge clam occurrence was salinity, overriding the effects of local habitat features. Sporadic occurrence, low abundance and a

lack of adults were registered on outer estuarine beaches, which act as sinks in this metapopulation. Wedge clam abundance was higher on wide and dissipative oceanic beaches, whereas reflective beaches were skewed toward adults with larger body size and biomass, suggesting a scaling of abundance to body size and potential density-dependent effects shaping population patterns. Assessing metapopulation connectivity with high-resolution hydrodynamic models will provide insights into the role of subsidies across beach types (Harris et al. 2014, Nel et al. 2014, Meerhoff et al. 2020) and will be helpful to define suitable beaches and critical minimum larval supply for metapopulation growth and persistence (Lipcius et al. 2015, 2021). A physical–biological coupling at different scales generates significant variation in pre- and post-settlement processes; the relative importance of these processes across the morphodynamic spectrum has yet to be elucidated.

LITERATURE CITED

Ansell AD (1983) The biology of the genus *Donax*. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. W Junk, The Hague, p 607–635

Barboza FR, Defeo O (2015) Global diversity patterns in sandy beach macrofauna: a biogeographic analysis. Sci Rep 5:14515

Barboza FR, Gómez J, Lercari D, Defeo O (2012) Disentangling diversity patterns in sandy beaches along environmental gradients. PLOS ONE 7:e40468

Bartoń K (2020) MuMIn: multi-model inference. R package version 1.43.17, https://cran.r-project.org/web/packages/MuMIn/index.html

Bergamino L, Martínez A, Han E, Lercari D, Defeo O (2016) Trophic niche shifts driven by phytoplankton in sandy beach ecosystems. Estuar Coast Shelf Sci 180:33–40

Blott SJ, Pye K (2001) GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf Process Landf 26:1237–1248

Carcedo MC, Fiori SM, Piccolo MC, Abbate MCL, Bremec CS (2015) Variations in macrobenthic community structure in relation to changing environmental conditions in sandy beaches of Argentina. Estuar Coast Shelf Sci 166:56–64

Cardoso R, Veloso VG (2003) Population dynamics and secondary production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) on a high-energy, subtropical beach of Brazil. Mar Biol 142:153–162

Celentano E, Defeo O (2006) Habitat harshness and morphodynamics: life history traits of the mole crab *Emerita brasiliensis* in Uruguayan sandy beaches. Mar Biol 149: 1453–1461

Celentano E, Gutiérrez NL, Defeo O (2010) Effects of morphodynamic and estuarine gradients on the demography and distribution of a sandy beach mole crab: implications for source–sink habitat dynamics. Mar Ecol Prog Ser 398: 193–205

Checon HH, Corte GN, Shah Esmaeili YM, Amaral ACZ (2018) Nestedness patterns and the role of morphodynamics and spatial distance on sandy beach fauna: ecological hypotheses and conservation strategies. Sci Rep 8:3759

Corte GN, Yokoyama LQ, Amaral ACZ (2014) An attempt to extend the habitat harshness hypothesis to tidal flats: a case study of *Anomalocardia brasiliana* (Bivalvia: Veneridae) reproductive biology. Estuar Coast Shelf Sci 150: 136–141

Defeo O (1996) Recruitment variability in sandy beach macroinfauna: much to learn yet. Rev Chil Hist Nat 69: 615–630

Defeo O, de Álava A (1995) Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. Mar Ecol Prog Ser 123:73–82

Defeo O, Martínez G (2003) The habitat harshness hypothesis revisited: life history of the isopod *Excirolana braziliensis* in sandy beaches with contrasting morphodynamics. J Mar Biol Assoc UK 83:331–340

Defeo O, McLachlan A (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multiscale analysis. Mar Ecol Prog Ser 295:1–20

Defeo O, McLachlan A (2011) Coupling between macrofauna community structure and beach type: a deconstructive meta-analysis. Mar Ecol Prog Ser 433:29–41

Defeo O, McLachlan A (2013) Global patterns in sandy beach macrofauna: species richness, abundance, biomass and body size. Geomorphology 199:106–114

Defeo O, Lercari D, Gómez J (2003) The role of morphodynamics in structuring sandy beach populations and communities: What should be expected? J Coast Res Spec Issue 35:352–362

Defeo O, Barboza CAM, Barboza FR, Aeberhard WH and others (2017) Aggregate patterns of macrofaunal diversity: an interocean comparison. Glob Ecol Biogeogr 26: 823–834

Defeo O, McLachlan A, Armitage D, Elliott M, Pittman J (2021) Sandy beach social–ecological systems at risk: regime shifts, collapses and governance challenges. Front Ecol Environ 19:564–573

Delgado E, Defeo O (2007) Tisular and population level responses to habitat harshness in sandy beaches: the reproductive strategy of *Donax hanleyanus*. Mar Biol 152:919–927

Dugan JE, McLachlan A (1999) An assessment of longshore movement in *Donax serra* Röding (Bivalvia: Donacidae) on an exposed sandy beach. J Exp Mar Biol Ecol 234: 111–124

Elliott M, Whitfield AK (2011) Challenging paradigms in estuarine ecology and management. Estuar Coast Shelf Sci 94:306–314

Fanini L, Defeo O, Elliott M (2020) Advances in sandy beach research—local and global perspectives. Estuar Coast Shelf Sci 234:106646

Ferguson GJ, Hooper G, Mayfield S (2021) Temporal and spatial variability in the life-history of the surf clam *Donax deltoides*: influences of density dependent processes. Estuar Coast Shelf Sci 249:107104

Gómez J, Defeo O (2012) Predictive distribution modeling of the sandy-beach supralittoral amphipod *Atlantorchestoidea brasiliensis* along a macroscale estuarine gradient. Estuar Coast Shelf Sci 98:84−93

Gray CA (2016) Tide, time and space: scales of variation and influences on structuring and sampling beach clams. J Exp Mar Biol Ecol 474:1−10

Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Modell 157:89−100

Harris L, Campbell EE, Nel R, Schoeman D (2014) Rich diversity, strong endemism, but poor protection: addressing the neglect of sandy beach ecosystems in coastal conservation planning. Divers Distrib 20:1120−1135

Harris LR, Abrahams K, Bezuidenhout K, Nel R (2017) The relative role of intrinsic and extrinsic factors driving alongshore swash-riding smooth plough shells, *Bullia rhodostoma*. J Exp Mar Biol Ecol 486:77−86

Hastie T, Tibshirani R (1990) Exploring the nature of covariate effects in the proportional hazards model. Biometrics 46:1005−1016

Herrmann M, de Almeida Rocha Barreira C, Arntz WE, Laudien J, Penchaszadeh PE (2010) Testing the habitat harshness hypothesis: reproductive biology of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) on three Argentinean sandy beaches with contrasting morphodynamics. J Molluscan Stud 76:33−47

Jackson DWT, Short AD (eds) (2020) Sandy beach morphodynamics. Elsevier, Amsterdam

Jackson NL (1995) Wind and waves: influence of local and non-local waves on mesoscale beach behavior in estuarine environments. Ann Assoc Am Geogr 85:21−37

Jackson NL, Nordstrom KF, Eliot I, Masselink G (2002) 'Low energy' sandy beaches in marine and estuarine environments: a review. Geomorphology 48:147−162

Laurino IR, Turra A (2021) The threat of freshwater input on sandy beaches: a small-scale approach to assess macrofaunal changes related to salinity reduction. Mar Environ Res 171:105459

Lercari D, Defeo O (1999) Effects of freshwater discharge in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. Estuar Coast Shelf Sci 49:457−468

Lercari D, Defeo O (2006) Large-scale diversity and abundance trends in sandy beach macrofauna along full gradients of salinity and morphodynamics. Estuar Coast Shelf Sci 68:27−35

Lercari D, Defeo O (2015) Large-scale dynamics of sandy beach ecosystems in transitional waters of the southwestern Atlantic Ocean: species turnover, stability and spatial synchrony. Estuar Coast Shelf Sci 154:184−193

Lima M, Brazeiro A, Defeo O (2000) Population dynamics of the yellow clam *Mesodesma mactroides*: recruitment variability, density-dependence and stochastic processes. Mar Ecol Prog Ser 207:97−108

Lipcius RN, Ralph GM (2011) Evidence of source−sink dynamics in marine and estuarine species. In: Liu J, Hull V, Morzillo AT, Wiens JA (eds) Sources, sinks, and sustainability. Cambridge University Press, Cambridge, p 361−381

Lipcius RN, Stockhausen WT, Eggleston DB, Marshall LS Jr, Hickey B (1997) Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: Source−sink dynamics? Mar Freshw Res 48:807−816

Lipcius RN, Burke RP, McCulloch DN, Schreiber SJ, Schulte DM, Seitz RD, Shen J (2015) Overcoming restoration paradigms: value of the historical record and metapopulation dynamics in native oyster restoration. Front Mar Sci 2:65

Lipcius RN, Zhang Y, Zhou J, Shaw LB, Shi J (2021) Modeling oyster reef restoration: larval supply and reef geometry jointly determine population resilience and performance. Front Mar Sci 8:677640

Lozoya JP, Gómez J, Defeo O (2010) Modelling large-scale effects of estuarine and morphodynamic gradients on distribution and abundance of the sandy beach isopod *Excirolana armata.* Estuar Coast Shelf Sci 87:472−478

Luijendijk A, Hagenaars G, Ranasinghe R, Baart F, Donchyts G, Aarninkhof S (2018) The state of the world's beaches. Sci Rep 8:6641

Marcomini SC, Penchaszadeh P, López RA, Luzzatto D (2002) Beach morphodynamics and clam (*Donax hanleyanus*) densities in Buenos Aires, Argentina. J Coast Res 18:601−611

Martin TG, Wintle BA, Rhodes JR, Kuhnert PM and others (2005) Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecol Lett 8:1235−1246

McLachlan A, Defeo O (2018) The ecology of sandy shores, 3rd edn. Elsevier, London

McLachlan A, Jaramillo E (1995) Zonation on sandy beaches. Oceanogr Mar Biol Annu Rev 33:305−335

McLachlan A, Jaramillo E, Defeo O, Dugan J, de Ruyck A, Coetzee P (1995) Adaptations of bivalves to different beach types. J Exp Mar Biol Ecol 187:147−160

McLachlan A, Dugan JE, Defeo O, Ansell AD, Hubbard DM, Jaramillo E, Penchaszadeh P (1996) Beach clam fisheries. Oceanogr Mar Biol Annu Rev 34:163−232

Meerhoff E, Defeo O, Combes V, Franco B and others (2020) Assessment of larval connectivity in a sandy beach mole crab through a coupled bio-oceanographic model. Estuar Coast Shelf Sci 246:107035

Morgan SG, Shanks AL, MacMahan JH, Reniers AJ, Feddersen F (2018) Planktonic subsidies to surf-zone and intertidal communities. Annu Rev Mar Sci 10:345−369

Nel R, McLachlan A, Winter DP (2001) The effect of grain size on the burrowing of two *Donax* species. J Exp Mar Biol Ecol 265:219−238

Nel R, Campbell EE, Harris L, Hauser L and others (2014) The status of sandy beach science: past trends, progress, and possible futures. Estuar Coast Shelf Sci 150:1−10

Ortega-Cisneros K, de Lecea AM, Smit AJ, Schoeman DS (2017) Resource utilization and trophic niche width in sandy beach macrobenthos from an oligotrophic coast. Estuar Coast Shelf Sci 184:115−125

Piola AR, Matano RP, Palma ED, Möller OO, Campos EJD (2005) The influence of the Plata River discharge on the western South Atlantic shelf. Geophys Res Lett 32:1−4

Reyes-Martínez MJ, Martínez-Pita I, Soler-Navarro D, García-García FJ (2020) The impact of salinity changes associated with size on the wedge clam *Donax trunculus* Linnaeus, 1758 (Mollusca: Bivalvia): a laboratory assay. Estuar Coast Shelf Sci 241:106838

Risoli MC, Defeo O, Yusseppone MS, Piola AR, Luz Clara M, Lomovasky BJ (2022) Disentangling patterns in population parameters of the wedge clam *Donax hanleyanus* from sandy beaches of Argentina: the role of environmental variability. Mar Environ Res 174:105564

Robertson BA, Hutto RL (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085

Rodil IF, Compton TJ, Lastra M (2014) Geographic variation in sandy beach macrofauna community and functional traits. Estuar Coast Shelf Sci 150:102–110

Salant CD, Shanks AL (2018) Surf-zone hydrodynamics alter phytoplankton subsidies affecting reproductive output and growth of tidal filter feeders. Ecology 99:1878–1889

Schoeman DS, Richardson AJ (2002) Investigating biotic and abiotic factors affecting the recruitment of an intertidal clam on an exposed sandy beach using a generalized additive model. J Exp Mar Biol Ecol 276:67–81

Shanks AL, Morgan SG, MacMahan J, Reniers AJ (2010) Surf zone physical and morphological regime as determinants of temporal and spatial variation in larval recruitment. J Exp Mar Biol Ecol 392:140–150

Shanks AL, Morgan SG, MacMahan J, Reniers AJ (2017) Alongshore variation in barnacle populations is determined by surf zone hydrodynamics. Ecol Monogr 87:508–532

Short AD (1996) The role of wave height, period, slope, tide range and embaymentization in beach classifications: a review. Rev Chil Hist Nat 69:589–604

Thompson GA, Sánchez de Bock MA (2009) Influence of beach morphodynamics on the bivalve *Donax hanleyanus* and *Mesodesma mactroides* populations in Argentina. Mar Ecol 30:198–211

Veas R, Hernández-Miranda E, Quiñones RA, Díaz-Cabrera E, Rojas JM, Fariña JM (2013) The influence of environmental factors on the abundance and recruitment of the sand crab *Emerita analoga* (Stimpson 1857): Source–sink dynamics? Mar Environ Res 89:9–20

Vila-Concejo A, Gallop SL, Largier JL (2020) Sandy beaches in estuaries and bays. In: Jackson DWT, Short AD (eds) Sandy beach morphodynamics. Elsevier, Amsterdam, p 343–362

Wood S, Scheipl F (2020) gamm4: generalized additive mixed models using 'mgcv' and 'lme4'. R package version 0.2-6. https://cran.R-project.org/web/packages/gamm4/index.html