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

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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
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 distribution 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 Donax 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 Donax 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 RdP 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).
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):

\[ \Omega = \frac{Hb}{Ws \cdot T} \]  

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:

\[ \text{IRSC} = \frac{N_L}{NT} \]  

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

Swash width and $\Omega$ 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/supp/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
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-
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 $\Omega$, 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...
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 $\Omega$ 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. 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.
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 RdIP 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 RdIP (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 Argentinian 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 RdIP. The comparable results obtained at meso- and macroscales highlight the crit-

![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](image)

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![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](image)
The ecological 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).

**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.
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 RdIP, 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).

*Donax 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.

Acknowledgements. We thank the UNDECIMAR Benthic Ecology Group for field and laboratory assistance. Financial support from CONICYT (Project N° 4034) and CSIC (Grupo 32) is acknowledged. Dr. R. Lipcius and 2 anonymous reviewers provided suggestions that greatly improved the manuscript.

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