TESTING THE HABITAT HARSHNESS HYPOTHESIS: REPRODUCTIVE BIOLOGY OF THE WEDGE CLAM *DONAX HANLEYANUS* (BIVALVIA: DONACIDAE) ON THREE ARGENTINEAN SANDY BEACHES WITH CONTRASTING MORPHODYNAMICS

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ABSTRACT

In order to test the habitat harshness hypothesis (HHH) the reproductive biology of *Donax hanleyanus* was studied histologically, comparing populations from three beaches with contrasting morphodynamics (dissipative, intermediate and reflective) over 25 months. The reproductive phase of *D. hanleyanus* was extended at the reflective beach compared to the other two. Males and females from the dissipative and intermediate beaches were significantly smaller and had lower biomass at maturity than those at the reflective beach. Recruits were significantly more abundant and the recruitment period was extended significantly at the dissipative beach. Spawning events took place twice each year at the dissipative (early spring and spring-summer) and the intermediate beach (winter and summer), whereas continuous gamete releases were noted at the reflective beach. Size and biomass at first maturity were lower at the dissipative beach, whereas monthly mean abundance of *D. hanleyanus* was higher at the reflective beach. The gametogenic cycle correlated significantly with sea-surface temperature, relative spermatozoon abundance, condition index, ash-free shell-free dry mass, and mean size and abundance of oocytes, for all three populations. At the population level, many of these reproductive responses to physical variables were opposite to those predicted by the HHH, including: greater abundance, extended reproductive cycle, extended period with spawning individuals, and larger size and higher biomass at first maturity at the reflective beach. This suggested that the hypothesis of habitat safety (HHS), originally proposed for supralittoral species, may be extended to intertidal species; a combination of narrow swashes and steep slopes makes reflective beaches a safer and more stable environment for intertidal species such as *D. hanleyanus*.

INTRODUCTION

Macrobenthic communities populating exposed sandy beaches demonstrate clear increases in ecological diversity, species richness, abundance and biomass from reflective to dissipative beach morphotypes (e.g. McLachlan, 1990; Ricciardi & Bourget, 1999; Defeo, Lercari & Gomez, 2003). In physically controlled environments such as sandy beaches, communities are structured by constituent species responding independently to the physical environment rather than by biological interactions, giving strong support to the 'autoecological hypothesis' (AH) (Noy-Meir, 1979). In agreement with this hypothesis, but restricted to the intertidal of sandy beaches, the 'swash exclusion hypothesis' (SEH) (McArdle & McLachlan, 1991, 1992) predicts a consistent increase in species richness, abundance and biomass from reflective to dissipative beaches. Furthermore, previous studies have shown that organisms on harsh reflective beaches need to invest more energy in maintenance processes than in growth and reproduction (Gómez & Defeo, 1999; Defeo, Gomez & Lercari, 2001). Defeo *et al.* (2001, 2003) combined the community level AH and SEH, to postulate the 'habitat harshness hypothesis' (HHH). The HHH predicts that (1) at the community level, reflective beaches will exhibit lower species richness, diversity and abundance, while (2) at the population level, they will be characterized by lower abundance, growth, fecundity, reproductive output and higher mortality rates. However, other recent investigations suggest that populations co-occurring on sandy beaches with a range of contrasting morphodynamics do not conform consistently to these predictions.

Veloso & Cardoso (2001) demonstrated no significant changes in abundance of macrobenthic communities between intermediate and reflective beaches. At the population level Defeo *et al.* (1997) recorded that the isopod *Excirolana braziliensis* exhibited higher abundance at a reflective beach than at a dissipative one, a finding that was confirmed by Defeo & Martínez (2003). In further contrast to the predictions of the HHH, the amphipod *Pseudorchestoidea brasiliensis* presented greater abundance, egg production potential and recruitment levels and lower natural mortality at a reflective beach (Gómez & Defeo, 1999). Following a 2-year study of seven Uruguayan sandy beaches with contrasting morphodynamics, the same authors recently demonstrated that the amphipod *Atlantorchestoidea brasiliensis* shows clear population responses to

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physical variables in direct opposition to those predicted by the HHH, including an increase in abundance and individual size from dissipative to reflective beaches (Defeo & Gómez, 2005). Furthermore, abundances of the decapod *Emerita brasiliensis* did not vary between dissipative and reflective beaches and at the latter beach type displayed higher male growth rates as well as lower natural mortality (Defeo *et al.*, 2001). In summary, these studies suggest that beach morphodynamics might not be the primary factor affecting abundance, population dynamics and life history traits of macrobenthic species. However, the HHH has not been tested comprehensively with respect to reproductive biology. The only investigation dealing with this subject to date was a 13-month study in which 150 wedge clams from two different beach morphotypes in Uruguay were examined. The results in that instance appeared to confirm the HHH (Delgado & Defeo, 2007).

The wedge clam *Donax hanleyanus* Philippi, 1847 is a numerically dominant intertidal warm-temperate species on South American sandy beaches and is distributed from tropical (17°S Caravelas, Brazil) to temperate regions (37°S Punta Mogotes in Mar del Plata, province of Buenos Aires) (de Castellanos & Fernandez, 1965; Penchaszadeh & Olivier, 1975; Narchi, 1978; Cardoso & Veloso, 2003). Wedge clams inhabit a range of Argentinean intertidal habitats (Marcomini *et al.*, 2002; Herrmann, 2009), providing an opportunity to assess responses to contrasting morphodynamic regimes. The present study tests the HHH at the population level, comparing the reproductive biology of *D. hanleyanus* from three Argentinean sandy beach habitats, one dissipative, one intermediate and one reflective. Following predictions of the HHH (Defeo *et al.*, 2001, 2003), we sought to determine whether *D. hanleyanus* at the dissipative beach does indeed exhibit greater abundance of recruits, larger size at first sexual maturity, larger maximum individual size and mass, and extended periods of reproduction, recruitment and spawning.

MATERIAL AND METHODS

Study area

The reproductive biology of *Donax hanleyanus* was studied in the Province of Buenos Aires at Santa Teresita (36°32′S, 56°41′W), Mar de las Pampas (37°19′S, 57°00′W) and Faro Querandí (37°29′S, 57°07′W); the last named locality is the southernmost extent of the species' distribution. These three open ocean sandy beaches show contrasting morphodynamics and flow continuously into one another with a north–south shoreline orientation, which is stable in the long term (Marcomini & López, 1993).

Abiotic factors

According to McLachlan's (1980) rating scale for exposure and Short & Wright's (1983) classifications of beach types, Santa Teresita is sheltered and dissipative, Mar de las Pampas exposed and intermediate, and Faro Querandí exposed and reflective (Table 1). The three sampling sites receive continuous wave action and are subject to semidiurnal tides, with a maximum tidal range of 1.6 m, a spring tide average of 1.7 m and a neap tide mean of 0.2 m. The sea-surface temperature (SST) (mean $\pm$ SE) varies between $11 \pm 0.14°C$ in winter and $23 \pm 0.21°C$ in summer. The study sites are composed of fine (Santa Teresita), medium (Mar de las Pampas) and coarse sands (Faro Querandí), with a mean particle diameter of 0.21, 0.37 and 0.48 mm, respectively (Table 1). All three beaches are affected by freshwater seepage, as confirmed by satellite images, and a southward current bringing water masses from the estuary of the Río de la Plata, 290 km long and up to 220 km wide. Mean salinity ranges between 31‰ and 34‰. All three beaches are well drained and oxygenated.

In order to characterize the physical parameters of the *Donax* belt, particle size analyses from all studied sites were

Table 1. Characterization of physical and biological attributes of the three studied localities on north Argentinean Atlantic coast.

Beach features	Santa Teresita	Mar de las Pampas	Faro Querandí
Latitude	36°32′S	37°19′S	37°29′S
Longitude	56°41′W	57°00′W	57°07′W
Beach width (m)	<80	<70	<100
Intertidal zone width (m)	<70	<60	<60
Tidal range (m)	1.8	1.7	1.7
Mean grain size (phi/mm)*	2.26/0.21	1.43/0.37	1.05/0.48
Median grain size (phi)*	2.28	1.39	0.99
Sorting*,[†],[‡]	Good (0.36)	Moderate (0.68)	Moderate (0.51)
Skewness*,[†]	−0.11	+0.07	−0.11
Textural group[§]	Fine	Medium	Coarse
Mean slope of intertidal (%)	1/43	1/16	1/14
Exposure[¶]	Sheltered	Exposed	Exposed
Morphodyn. type[§]	Dissipative	Intermediate	Reflective
Dean parameter (Ω)[#],**	1.92–2.53	1.50–1.86	3.28–3.93
D. hanleyanus belt (m)	30	12	10
Macrofauna richness (species)	5	3	3

*After Flemming & Thum (1978) and after Flemming & Ziegler (1995).

[†]After Inman (1952).

[‡]After McLachlan and Brown (2006).

[§]After Short and Wright (1983).

[¶]After McLachlan (1980).

[#]After Dean (1973).

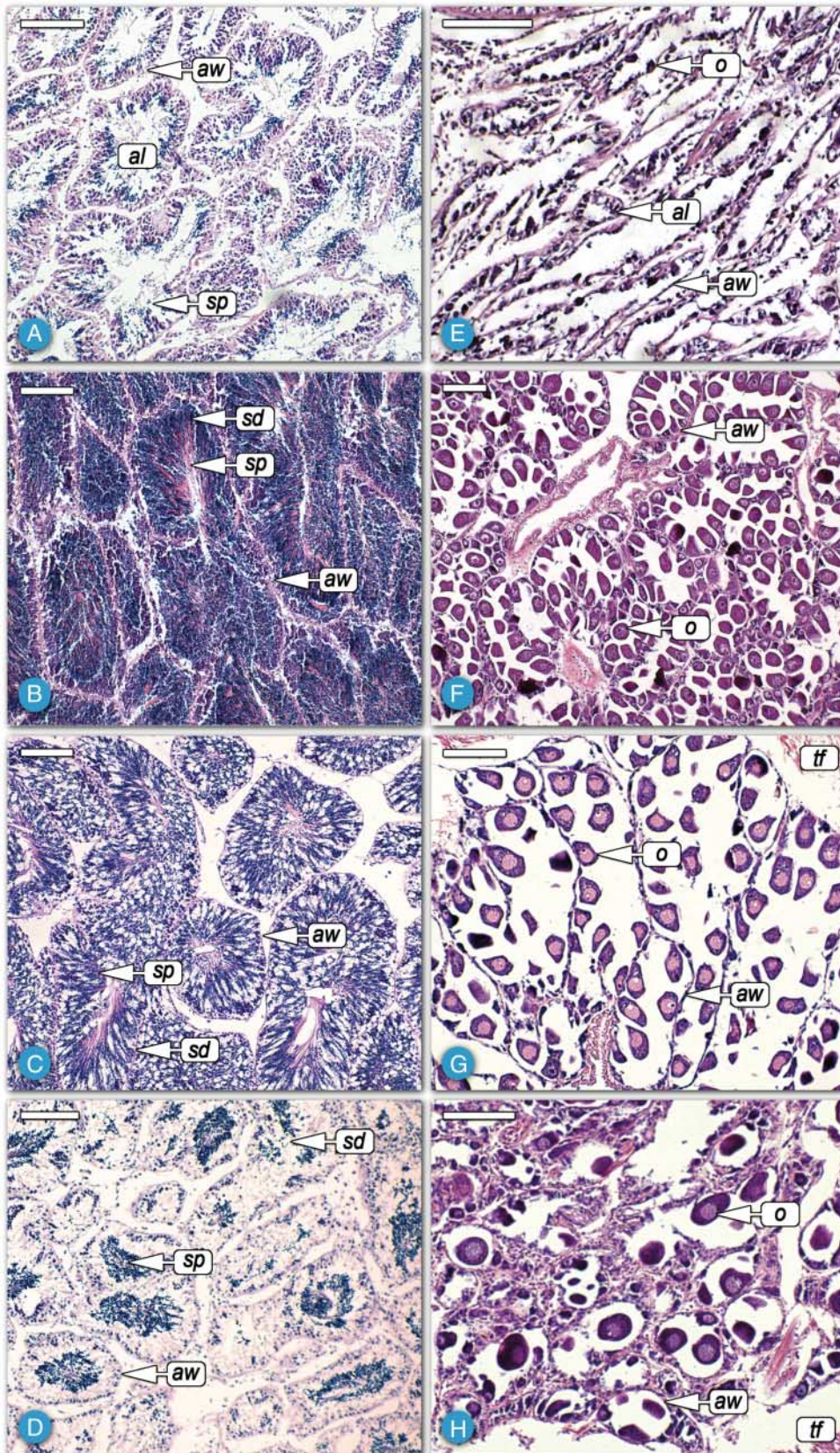**Calculated for specific seasonal SST from 9°C to 25°C.

Figure 1. Microphotography of male (**A–D**) and female (**E–H**) gonad stages of *Donax hanleyanus*: pre-active (**A, E**), active (**B, F**), spawning (**C, G**) and cytolysed (**D, H**). Abbreviations: aw, alveolar wall; al, alveolus; sp, spermatozoa; sd, spermatids; tf, transverse fibre. Scale bars = 100 μm.

carried out by sampling sediments to a depth of 10 cm with a plastic corer of 3.5 cm diameter. Sand samples were washed with freshwater overnight to remove salt and then dried at 70°C. Afterwards, any shell fragments were extracted and the remaining part of the samples was analysed using a MacroGranometer™ settling tube (e.g. Flemming & Thum, 1978; Flemming & Ziegler, 1995) and the SedVar™ V6.2p software package (Brezina, 1997), which is part of the system. The data processing software makes use of the more versatile equation of Brezina (1979) rather than that of Gibbs Matthews & Link (1971), which is applicable only to smooth glass spheres to calculate settling velocities. All textural parameters presented in this study were calculated using the percentile statistics of Inman (1952), while sediments were classified according to the Wentworth scale (1922).

Wave height was approximated by measuring the height of breaking waves $(n = 10)$ with graduated poles against the horizon, and adding the result to the height difference between the location of the observer and the lowest point at which the backwash met the next incoming swash bore. The wave period was measured as the time interval between breakers $(\mathcal{N} = 50)$. The morphodynamic state of each site studied was described by the Dean parameter (Ω) (Dean, 1973):

$$\Omega = H_b \frac{100}{WT}, \qquad \text{(Eq. 1)}$$

which is based on mean wave height H_b (m) divided by wave period T (s) and sand fall velocity W (m/s). The slope of the beach face was measured by the height difference (Emery, 1961) between the drift and the water line. The swash period was estimated according to McArdle & McLachlan (1991). Salinity (Optech portable refractometer, model RSM) as well as the SST (hand-held digital thermometer) were measured monthly *in situ* at the three sample locations. For additional detailed information the SST was measured daily at Santa Teresita between October 2005 and December 2006 (Herrmann *et al.*, 2008a) and was supplemented with data of the Argentinean Marine Institute (CEADO: Centro Argentino de Datos Oceanográficos, Servicio de Hidrografía Naval, Buenos Aires, Argentina), which operates a permanent weather station at this beach.

Sampling and histological examination

Following the systematic approach described by Herrmann (2009), a total of 22,519 *D. hanleyanus* were collected from the three study beaches between December 2004 and December 2006. Quantitative sampling of clams was carried out at monthly intervals (Santa Teresita and Mar de las Pampas: December 2004 to December 2006; Faro Querandí: March 2005 to December 2006) at a series of survey stations set at 4 m intervals along three transects. The transects ran perpendicular to the shoreline between the spring tide high water mark and the spring tide low water mark and were separated by 20 m intervals. At each station, three replicate sand samples (40 × 40 cm) were excavated to 35 cm depth using a 0.16 m² steel corer, and sieved individually on a 1-mm mesh. Specimens of *D. hanleyanus* were measured to the nearest 0.1 mm with a digital vernier calliper and returned alive to their habitat. For biomass determinations, as well as for calculations of the condition index (CI), 2,205 specimens were preserved in 70% ethanol and subsequently analysed in the laboratory. For histological examinations a total of 35 clams, covering the full range of antero-posterior shell lengths (apSL) (Santa Teresita: 5–28 mm, Mar de las Pampas: 9–38 mm and Faro Querandí: 9–39 mm), was collected monthly from the three beaches $(\mathcal{N}_{\text{total}} = 2,275$ specimens).

Table 2. Qualitative descriptions of histological preparations of *Donax hanleyanus* gonad used to assess gametogenic stages.

Stage	Definition	Brief description of gonad	Figure 1
0	Sexual rest	Follicles few and small, sex indistinguishable, protogonia and gonia in mitosis	–
I	Pre-active	Reproductive material is scant and intersected by transverse muscular fascicle cells, alveoli appear loosely arranged, phagocytes are common	A, E
II	Active	Germ cells are in various stages of development and fill the alveoli, alveoli are large with complete and closed walls	B, F
III	Spawning	Clear loss of gametes, reproductive material varies in quantity but it is fairly abundant, alveolar pattern is disturbed, walls are broken and alveoli appear flattened	C, G
IV	Cytolysed	Reproductive material is completely degenerated; alveoli are very small and wide apart, massive numbers of phagocytic cells	D, H

Individual stages of male and female gonads are shown in Figure 1.

Clams with severed adductor muscles were fixed in Bouin's solution for 2 h, then transferred to 70% ethanol and later processed in the laboratory using standard histological methods, i.e. embedding in paraffin, sectioning at 5 μm and staining with haematoxylin–eosin (following Howard *et al.*, 2004). Gonads were examined with a light microscope and assigned to one of five developmental stages [rest, pre-active (Fig. 1A, E), active (Fig. 1B, F), spawning (Fig. 1C, G) and cytolysed (Fig. 1D, H); Table 2]. Images of each sample were captured using a Sound Vision digital camera and processed using the imaging software AxioVision version 4.4 (2008). For all developmental stages except sexual rest, the mean oocyte diameter was determined by measuring 30 oocytes per specimen $(\mathcal{N}_{\text{total}} = 17,286$ oocytes measured). In addition, the abundance of oocytes in each sectioned female gonad was examined by counting oocytes from 1 mm² surface area $(\mathcal{N}_{\text{total}} = 15,450$ oocytes counted). SST was measured daily (at 13.00) at Santa Teresita using a digital thermometer with a precision of 0.1°C. Since monthly SSTs taken at Mar de las Pampas and Faro Querandí did not vary from those of Santa Teresita (one-way ANOVA, $F_{2,69} = 0.089$, $P > 0.05$), daily SSTs from the latter were used for all three beaches.

Data analysis

Estimation of relative spermatozoon abundance: Relative spermatozoon abundance (RSA) is a measure of male gonad activity. RSA values were used to simplify the classification of male gonadal tissue and to analyse seasonal variations in the gametogenic cycle. RSA was calculated as:

$$\text{RSA} = \frac{1}{\text{grey value} \times 10^9}, \qquad \text{(Eq. 2)}$$

where the grey value per mm² was measured from greyscale digital images of histological sections using the digital imaging software package Adobe Photoshop version CS3 Extended (2008). The grey value is equal to the brightness of pixels in a

digital image, commonly expressed in integers ranging from 0 (black) to 255 (white) on an 8-bit digital signal.

Condition index, biomass and recruitment: CI was calculated to detect seasonal variations in the mass of the visceral mass of *D. hanleyanus*. The total shell-free, wet mass (SFWM) of each ethanol-preserved clam was recorded to the nearest 0.1 mg immediately after dabbing on blotting paper. Mantle, siphons, retractor and adductor muscles were then removed, and the SFWM of the resulting unit comprising the visceral mass and foot was recorded. Following the equation of de Villiers (1975), CI was calculated as:

$$\text{CI} = \frac{100 M_\text{v}}{(M_\text{t} - M_\text{v})}, \tag{Eq. 3}$$

where M_v is the wet ethanol-preserved visceral mass (including the foot) and M_t is the total ethanol-preserved SFWM. Additionally the ash-free, shell-free dry mass (AFDM) was estimated as an indicator of clam condition, using the conversion factor 0.186 provided by Brey, Rumohr & Ankar (1988).

Clams were measured monthly at each beach (data from Herrmann, 2009) and a pooled 2-year length–frequency distribution was plotted for each of the three populations ('population' in this paper refers to all specimens of *D. hanleyanus* inhabiting the geographic location without any genetic implication). On the basis of the histological results, these length–frequency distributions represented three discrete ontogenetic stages: (1) recruits (<11 mm), (2) juveniles (11–22 mm, the size class where sex can be differentiated for the first time) and

(3) adults (>22 mm, size where individuals were 100% mature).

Size and biomass at sexual maturity: The size at which 100% of the population is mature was estimated from the proportion of mature females and males, respectively, in different size classes, using the logistic equation of McGullagh & Nelder (1997):

$$B_\text{apSL} = \frac{a}{1 + e^{\left[\frac{-(x-x_0)}{b}\right]}}, \tag{Eq. 4}$$

where B_apSL is the proportion of females and males, respectively, with mature gonads in each size class (apSL), and a, b and x_0 are parameters. The biomass at which 50% of the population is mature was estimated using to the same formula, whereby B_SFWM is the proportion of females and males, respectively, with mature gonads in each biomass class (SFWM).

Mature clams were allocated to the developmental stages 'active' and 'spawning', while immature individuals were deemed to be in the sexual rest stage. Equation (3) was fitted by non-linear least squares, using the quasi-Newton algorithm of the software package SigmaPlot version 11 (2008) to estimate the standard error of parameters. Size at 50% population maturity ($\text{apSL}_{50\%}$) was estimated as:

$$\text{apSL}_{50\%} = -b^* \ln\left[\frac{a}{50} - 1\right] + x_0 \tag{Eq. 5}$$

Table 3. Results of statistical analysis of the gametogenic cycle of *Donax hanleyanus* in relation to abiotic and biotic factors at the three beaches.

	Parameter	Statistical results at the beaches		
		Santa Teresita (dissipative)	Mar de las Pampas (intermediate)	Faro Querandí (reflective)
a	Sex ratio (females:males)*	For values see text	$\chi^2 = 0.718$, df = 1, **P > 0.397**	$\chi^2 = 1.029$, df = 1, **P = 0.310**
b	Gametogenic cycle *vs* time course[†]	$F_{11,9} = 5.644$, **P = 0.007**	$F_{11,10} = 15.595$, **P = 0.000**	$F_{11,10} = 8.861$, **P = 0.001**
c	Gametogenic cycle *vs* SST[‡]	$r_\text{s} = 0.726$, **P = 0.000**, n = 21	$r_\text{s} = 0.787$, **P = 0.000**, n = 22	$r_\text{s} = 0.799$, **P = 0.000**, n = 22
d	Gametogenic cycle *vs* CI[‡]	$r_\text{s} = -0.556$, **P = 0.025**, n = 16	$r_\text{s} = 0.480$, **P = 0.024**, n = 22	$r_\text{s} = 0.575$, **P = 0.005**, n = 22
e	Gametogenic cycle *vs* AFDM[‡]	$r_\text{s} = 0.557$, **P = 0.016**, n = 18	$r_\text{s} = 0.669$, **P = 0.001**, n = 22	$r_\text{s} = 0.445$, **P = 0.043**, n = 21
f	Gametogenic cycle *vs* mean size of oocytes[‡]	$r_\text{s} = 0.721$, **P = 0.004**, n = 14	$r_\text{s} = 0.501$, **P = 0.021**, n = 21	$r_\text{s} = 0.443$, **P = 0.039**, n = 22
g	Gametogenic cycle *vs* abundance of oocytes[‡]	$r_\text{s} = 0.708$, **P = 0.000**, n = 21	$r_\text{s} = 0.779$, **P = 0.000**, n = 22	$r_\text{s} = 0.639$, **P = 0.001**, n = 22
h	CI *vs* SST[‡]	$r_\text{s} = 0.507$, **P = 0.032**, n = 18	$r_\text{s} = 0.337$, P = 0.125, n = 22	$r_\text{s} = 0.673$, **P = 0.001**, n = 22
i	AFDM *vs* SST[‡]	$r_\text{s} = 0.574$, **P = 0.016**, n = 17	$r_\text{s} = 0.600$, **P = 0.003**, n = 22	$r_\text{s} = 0.581$, **P = 0.005**, n = 22
j	Oocyte mean size *vs* SST[‡]	$r_\text{s} = 0.741$, **P = 0.002**, n = 14	$r_\text{s} = 0.334$, P = 0.139, n = 21	$r_\text{s} = 0.448$, **P = 0.037**, n = 22
k	Abundance of oocytes *vs* SST[‡]	$r_\text{s} = 0.504$, **P = 0.020**, n = 21	$r_\text{s} = 0.743$, **P = 0.000**, n = 22	$r_\text{s} = 0.701$, **P = 0.000**, n = 22
l	Oocyte modal size *vs* seasons (spawning)[†]	$F_{1,12} = 10.154$, **P = 0.008**	$F_{1,19} = 4.777$, **P = 0.042**	$F_{1,12} = 5.680$, **P = 0.027**
m	Oocyte abundance increases *vs* seasons[†]	$F_{1,19} = 10.864$, **P = 0.004**	$F_{1,20} = 6.214$, **P = 0.022**	$F_{1,20} = 5.609$, **P = 0.028**
n	Oocyte abundance decreases *vs* seasons[†]	$F_{1,19} = 10.142$, **P = 0.005**	$F_{1,20} = 9.346$, **P = 0.006**	$F_{1,20} = 14.107$, **P = 0.001**
o	Settling period of recruits *vs* SST[†]	$r_\text{s} = -0.327$, P = 0.119, n = 24	$r_\text{s} = -0.123$, P = 0.584, n = 22	$r_\text{s} = -0.356$, P = 0.104, n = 22
p	Appearances of recruits	$F_{1,22} = 224.266$, **P = 0.000**	$F_{1,20} = 16.064$, **P = 0.001**	$F_{1,20} = 25.997$, **P = 0.000**
q	Gametogenic cycle *vs* RSA[‡]	$r_\text{s} = 0.804$, **P = 0.000**, n = 21	$r_\text{s} = 0.856$, **P = 0.000**, n = 22	$r_\text{s} = 0.822$, **P = 0.000**, n = 22
r	RSA increases *vs* seasons[†]	$F_{1,19} = 6.889$, **P = 0.017**	$F_{1,20} = 11.661$, **P = 0.003**	$F_{1,20} = 35.507$, **P = 0.000**
s	RSA decreases *vs* seasons[†]	$F_{1,19} = 15.366$, **P = 0.001**	$F_{1,20} = 30.139$, **P = 0.000**	$F_{1,20} = 55.621$, **P = 0.000**
t	Gonad in active and spawning stage[†]	$F_{1,40} = 33.454$, **P = 0.000**	$F_{1,42} = 8.032$, **P = 0.007**	$F_{1,42} = 17.539$, **P = 0.000**
u	Gonad in cytolysed stage[†]	$F_{1,19} = 17.898$, **P = 0.000**	$F_{1,20} = 4.542$, **P = 0.046**	$F_{1,20} = 9.767$, **P = 0.005**
v	Gonad in sexual rest stage[†]	$F_{1,19} = 46.143$, **P = 0.000**	$F_{1,20} = 5.301$, **P = 0.032**	$F_{1,20} = 4.484$, **P = 0.047**

Bold indicates significant correlation ($P < 5\%$).

*Chi-square test.
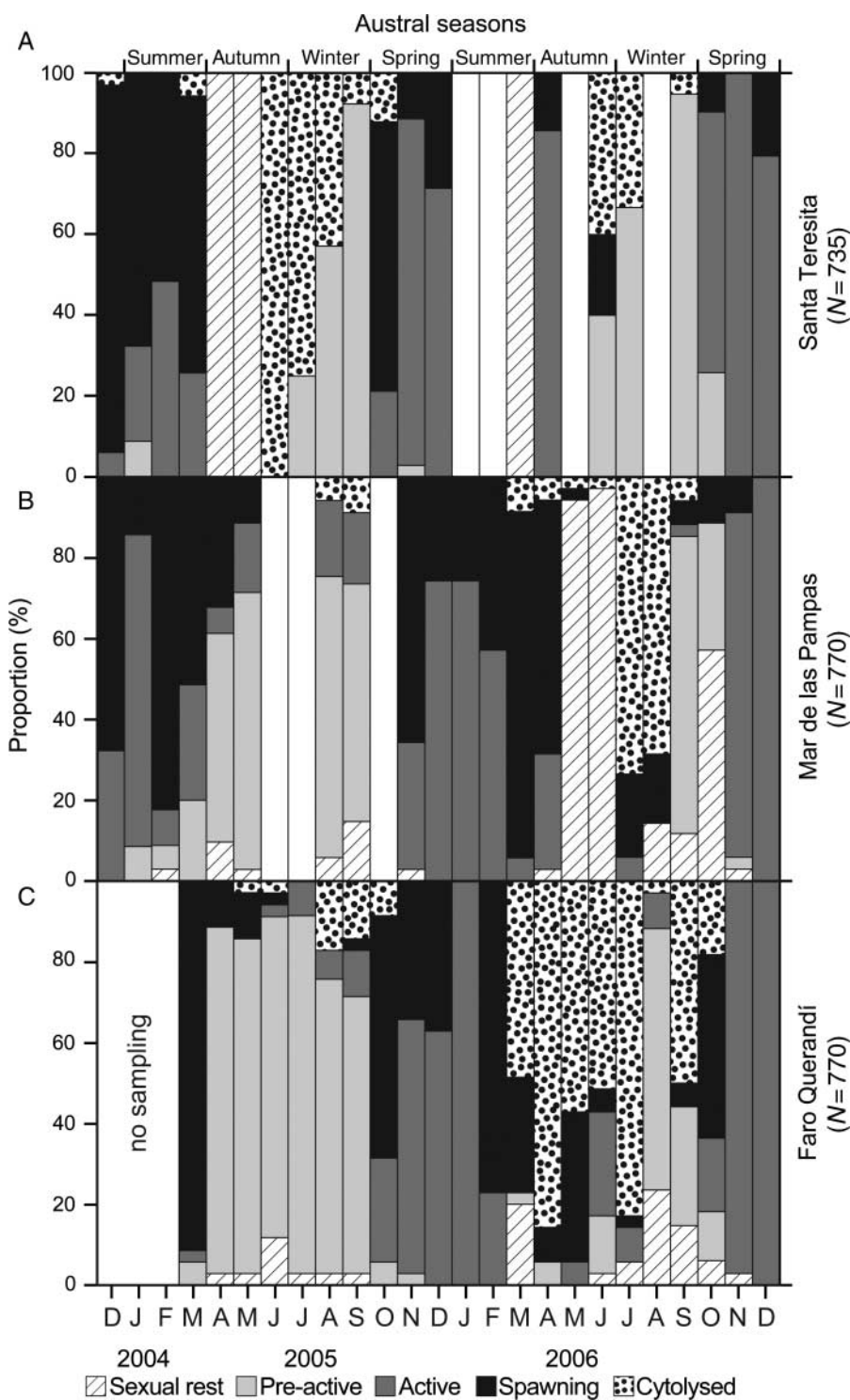
[†]One-way ANOVA.

[‡]Spearman's rank order correlation.

Figure 2. Gametogenic cycle of *Donax hanleyanus* indicating proportions of distinct gonad stages of individuals sampled at the dissipative (**A**), intermediate (**B**) and reflective (**C**) beaches. White bars: no individuals found. *N*, numbers of analysed clams per beach.

and the biomass at which 100% of the population is mature (SFWM$_{50\%}$) was estimated accordingly.

Statistical analysis: Sex ratios (male:female) of *D. hanleyanus* were calculated according to the presence of oocytes and spermatozoa using chi-square analysis. The influence of SST on the gametogenic cycle, as well as its relationship with RSA, CI, AFDM, abundance and size of oocytes within the population inhabiting each of the sampled beaches were statistically analysed by Spearman's rank order correlation. Spatial and temporal differences in the gametogenic cycle and oocyte abundance as well as mean and modal sizes of oocytes were tested by one-way analysis of variance (ANOVA). For all beaches the three ontogenetic groups were tested for differences by two-way ANOVA using the factors 'beach' and 'ontogenetic group'. Based on the Durbin–Watson coefficient, residuals of
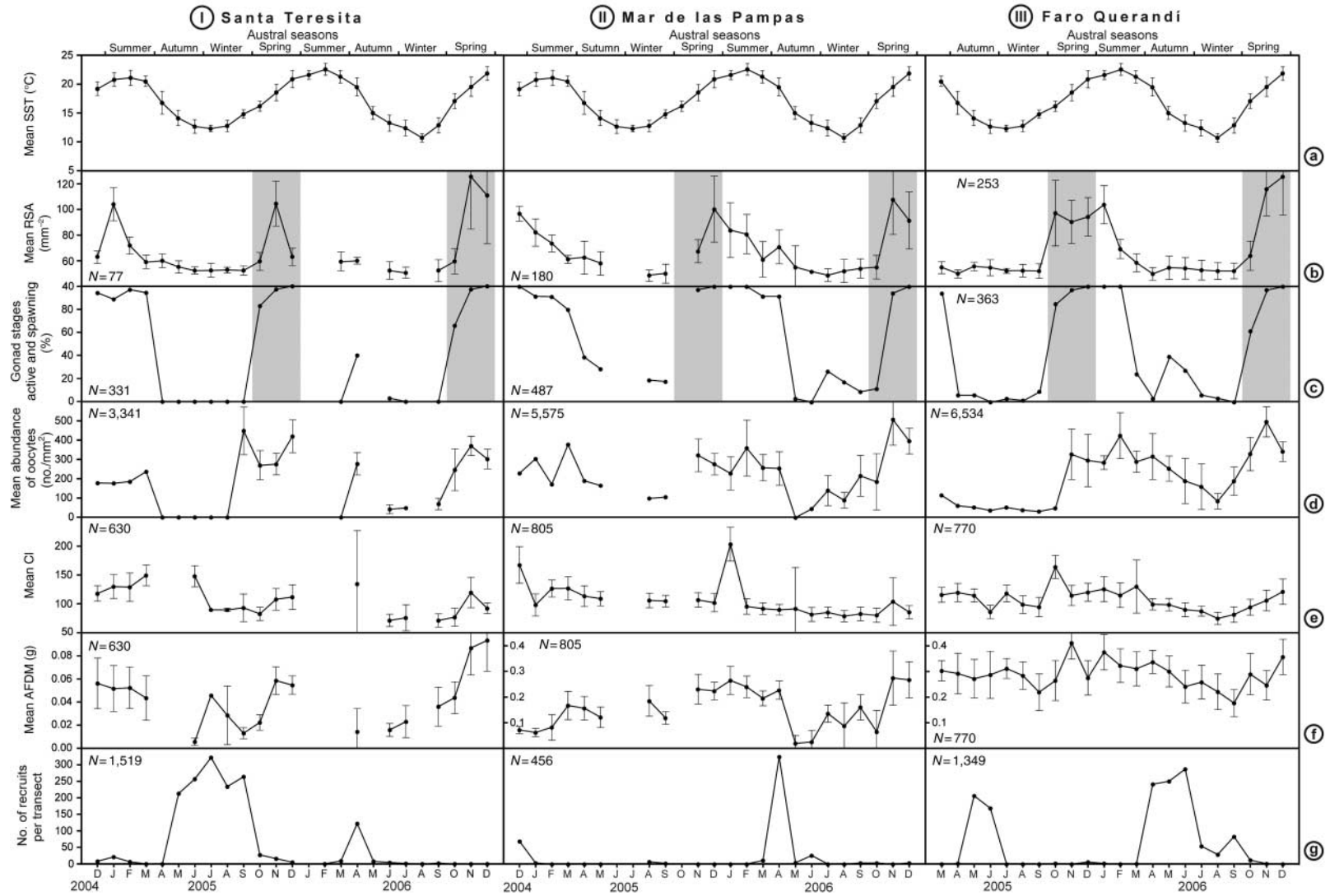
Figure 3. Gametogenic cycle of *Donax hanleyanus* in relation to abiotic and biotic factors at the dissipative (**I**), intermediate (**II**) and reflective (**III**) beaches; (**a**) mean SST (°C), (**b**) mean RSA (mm^{-2}), (**c**) percentage of gonad stages 'ripe' and 'spawning', (**d**) mean abundance of oocytes (numbers/mm^2), (**e**) mean CI, (**f**) mean AFDM (g) and (**g**) numbers of recruits (<11 mm) per transect. Grey bars indicate seasons where Carreto *et al.* (1995) observed chlorophyll *a* maxima in the Buenos Aires shelf region. Error bars are standard deviation (SD). Note different scale on *Y* axes in graphs **IIf** and **IIIf**.

the logistic functions of size and biomass at sexual maturity were tested for autocorrelation. The closer the coefficient to value '2' (within the range 0–4), the less significant the autocorrelation (SigmaStat, 2004). To compare results of size and biomass at 50% population maturity, as estimated for both sexes and for each of the three beaches, analyses of the residual sum squares (ARSS) were performed (Chen, Jackson & Harvey, 1992). All statistical analyses were carried out using the statistical package SPSS version 16.0.1 (2007). Differences were considered significant at the level of $\alpha = 5\%$ (Zar, 1999).

RESULTS

Abiotic factors

Results of grain size and sand fall velocity analyses, as well as associated parameters are summarized in Table 1.

Gametogenic cycle

Histological examinations of gonadal tissue from a 25-month sampling series demonstrated that sex ratios did not significantly deviate from 1:1 at the intermediate and reflective beaches (Table 3a), but that there was a greater proportion of females at the dissipative beach in December 2004 ($\chi^2 = 8.758$, df = 1, $P < 0.05$), January 2005 ($\chi^2 = 11.765$, df = 1, $P < 0.05$) and April 2006 ($\chi^2 = 4.571$, df = 1, $P < 0.05$). No case of hermaphroditism was found. Histological analysis revealed that the reproductive cycle of both male and female *Donax hanleyanus* undergoes a distinct seasonality at all three beaches (Fig. 1; Table 3b). Sexual activity was detectable mainly during spring and summer (Fig. 2; Table 3t) at all three beaches. At the dissipative beach, the spawning period of wedge clams was restricted mainly to spring and summer, while gamete release continued all year round at the intermediate (except in July, August 2005 and July, December 2006) and reflective beach (except July, August 2005 and August, November, December 2006) populations, respectively (Fig. 2). In both years of the study, cytolysed specimens dominated the population in autumn and winter at all three beaches (Fig. 2; Table 3u). Wedge clams of indistinguishable sex were found at the reflective and intermediate beaches during all months except during summer, while a high proportion of individuals in the sexual rest stage appeared at the dissipative site in early autumn 2005 and in late summer 2006 (Fig. 2; Table 3v).

The gametogenic cycle (active and spawning) of *D. hanleyanus* was correlated significantly with SST (Fig. 3A, C; Table 3c). In both years, the size of oocytes (Tables 3f, 4) and their abundance (Fig. 3D; Table 3g) was correlated significantly with the gametogenic cycle (Fig. 3C) at all three beaches. Furthermore, both parameters correlated significantly with SST at the dissipative and reflective beaches (Table 3j, k). At all three beaches, oocytes showed increased abundance in spring (Fig. 3D; Table 3 m), and decreased abundance in autumn–winter (Fig. 3D; Table 3n), when most specimens were in the cytolysed stage (Fig. 1D, H).

Analyses of monthly oocyte size classes showed a unimodal distribution, with size ranges from 2 to 70 µm (Fig. 4), a situation which did not vary significantly between beaches (ANOVA, $F_{2,54} = 0.194$, $P > 0.05$). At the dissipative beach the modal oocyte size decreased twice each year, in early spring (September) and in spring–summer (December). A twice-annual decrease was also recorded at the intermediate beach each year, in winter (August) and in summer (twice in

Table 4. *Donax hanleyanus*: monthly SST (°C), mean oocyte size (µm) ($x \pm$ SD in µm), number of females per month (n_f) and number of measured oocytes (n_o) from individuals inhabiting one of the three sampling localities Santa Teresita, Mar de las Pampas and Faro Querandí.

Year	Month	SST (°C)	Santa Teresita (dissipative)			Mar de las Pampas (intermediate)			Faro Querandí (reflective)		
			$\bar{x} \pm$ SD (µm)	n_o	n_f	$\bar{x} \pm$ SD (µm)	n_o	n_f	$\bar{x} \pm$ SD (µm)	n_o	n_f
2004	Dec	18.42	35.52 (9.53)	177	25	39.10 (11.23)	141	17	No sampling		
2005	Jan	20.79	37.52 (8.45)	176	27	40.14 (10.67)	187	19			
	Feb	21.08	41.79 (10.15)	185	16	35.53 (10.09)	106	13			
	Mar	20.49	39.78 (9.45)	237	21	40.96 (10.07)	233	12	38.09 (10.05)	116	14
	Apr	16.75	–	–	–	36.97 (10.58)	117	13	30.49 (11.19)	61	16
	May	14.14	–	–	–	39.41 (9.40)	102	15	32.55 (10.43)	53	21
	Jun	12.67	–	–	–	–	–	–	39.34 (12.69)	38	19
	Jul	12.31	–	–	–	–	–	–	37.51 (12.13)	53	16
	Aug	12.74	–	–	–	35.65 (11.89)	122	35	33.97 (11.12)	71	41
	Sep	14.84	7.62 (2.41)	73	8	29.36 (11.08)	65	12	23.01 (11.42)	49	14
	Oct	16.18	28.14 (9.85)	454	16	–	–	–	29.52 (9.89)	591	20
	Nov	18.53	38.24 (4.64)	570	20	36.22 (5.83)	510	17	40.14 (5.60)	514	18
	Dec	20.87	35.32 (5.66)	540	18	36.88 (5.99)	612	20	40.09 (4.46)	660	22
2006	Jan	21.59	–	–	–	38.10 (5.04)	540	18	36.34 (4.59)	390	13
	Feb	22.55	–	–	–	34.84 (7.14)	360	12	37.61 (5.33)	330	11
	Mar	21.29	–	–	–	30.78 (8.19)	540	18	26.54 (8.21)	359	12
	Apr	19.51	34.89 (5.74)	90	3	29.70 (12.07)	390	13	32.78 (9.89)	390	13
	May	14.99	–	–	–	–	–	–	30.91 (10.87)	457	17
	Jun	13.24	–	–	–	32.56 (9.62)	30	1	29.98 (11.53)	556	20
	Jul	12.40	28.49 (12.61)	66	1	31.03 (11.89)	554	19	21.16 (12.40)	460	14
	Aug	10.69	–	–	–	18.91 (12.44)	480	16	14.79 (8.29)	237	9
	Sep	12.86	9.29 (4.22)	208	12	12.90 (7.65)	347	13	12.90 (7.80)	460	17
	Oct	17.07	21.56 (9.28)	410	15	15.52 (5.62)	162	9	20.73 (9.27)	180	6
	Nov	19.54	38.64 (5.06)	420	14	34.11 (8.36)	480	16	37.45 (4.27)	540	18
	Dec	21.84	36.28 (4.14)	17		35.26 (8.10)	570	19	39.66 (7.68)	450	16

February, once in December 2006), while at the reflective site decreases were observed during all seasons (autumn: April 2005 and March 2006; winter: June and July 2006; spring: September 2005; and summer: January 2006) (Table 3l), suggesting two spawning events at the dissipative and intermediate beaches and more continuous gamete releases at the reflective beach (Fig. 4).

Relative spermatozoon abundance

RSA correlated significantly with the gametogenic cycle (active and spawning gonad stages) of *D. hanleyanus* at all three beaches (Fig. 3B; Table 3q), whereby RSA showed significant increases at the dissipative and intermediate beaches in spring and at the reflective beach in spring–summer (Fig. 3B;
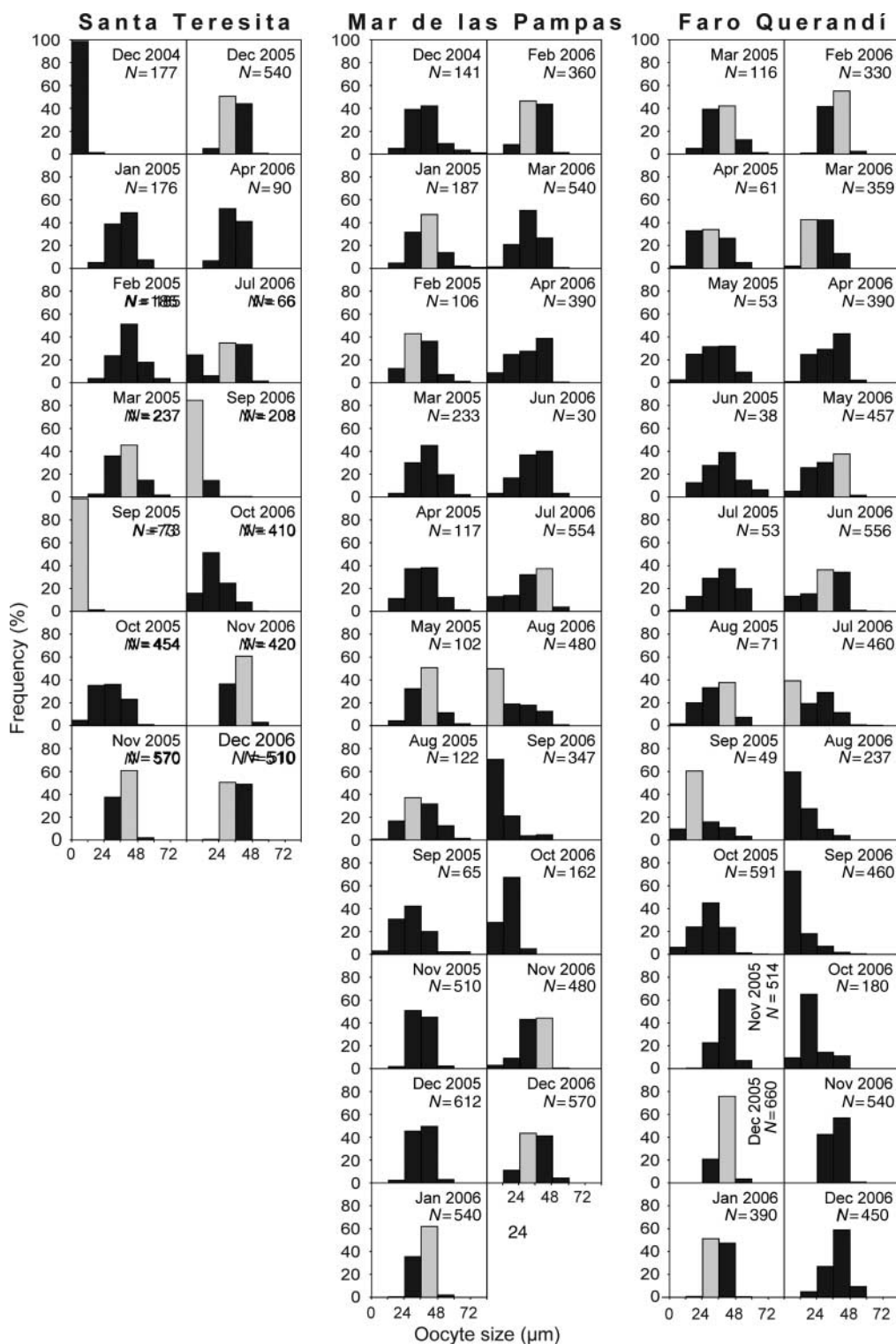
Figure 4. Monthly oocyte size–frequency distribution of *Donax hanleyanus*. Grey bars show modal values indicating the record prior to and after a sudden reduction of oocyte sizes. N, numbers of measured oocytes per month.
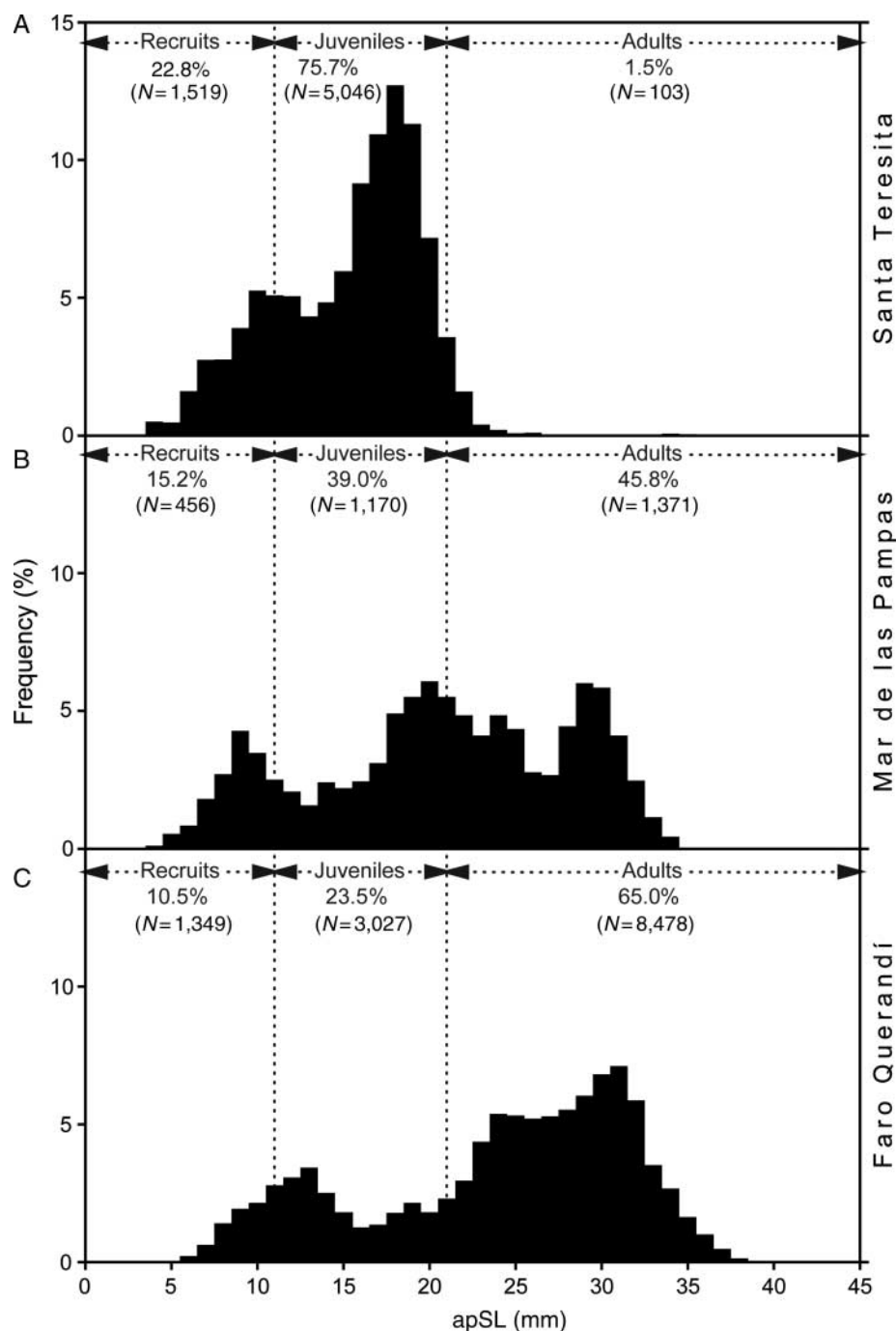
Figure 5. Length–frequency distribution (pooled from 25 monthly samples) of *Donax hanleyanus* at the dissipative (**A**), intermediate (**B**) and reflective (**C**) beaches, classified into three ontogenetic groups: recruits (<11 mm), juveniles (11–22 mm) and adults (>22 mm). Note the different scale on the *Y* axes.

Table 3r). At all three beaches RSA decreased significantly in autumn–winter (Fig. 3B; Table 3s).

Condition index, biomass and recruitment

At all three study beaches, the annual reproductive cycle of *D. hanleyanus* correlated significantly with CI (Table 3d). CI was correlated significantly with SST at both the dissipative and the reflective beach (Table 3 h). Seasonal variations in clam biomass (AFDM) within the respective beach populations correlated significantly with SST (Table 3i) and with mature

gonad stages (ripe and spawning) at all three beaches (Table 3e), but did not vary between beaches (ANOVA, $F_{2,59} = 0.425$, $P > 0.05$). Recruits of *D. hanleyanus* were found in all seasons at all three beaches during both sampling years (except at the dissipative beach in January 2006 and at the intermediate beach in June, July and October 2005). However, the peak of settlement was recorded at the intermediate beach in summer 2005 and in summer–autumn 2006 [Fig. 3 (IIg); Table 3p], at the reflective beach in autumn 2005 and autumn–winter 2006 [Fig. 3 (IIIg); Table 3p], and at the dissipative beach for extended periods during autumn–winter 2005

and summer-autumn 2006 [Fig. 3 (Ig); Table 3p]. Despite this apparent seasonality, the settlement period of recruits was not significantly correlated with SST (Table 3o). The length–frequency distributions covering 2 years revealed that the intermediate and reflective beaches were populated by considerably larger clams than the dissipative site ($F_{2,21836} = 63.618$, $P < 0.05$). The mean apSL of juveniles found at the dissipative beach was significantly higher than that of both other populations, but adult apSL was considerably smaller ($F_{2,21836} = 11,302.263$, $P < 0.05$). The analysis of the population structure indicated that at the dissipative beach, recruits represented 22.8% of the population and adults accounted for only 1.5%, whereas the reflective beach population comprised a mere 10.5% recruits and 65% adult wedge clams (Figs 4, 5).

Size and biomass at sexual maturity

Single individuals of *D. hanleyanus* matured when smaller (apSL) and lighter (SFWM) at the dissipative beach (males: 8.61 mm, 0.02 g; females: 9.35 mm, 0.04 g) than at the intermediate (males: 12.72 mm, 0.10 g; females: 13.21 mm, 0.12 g) or reflective (males: 22.92 mm, 0.55 g; females 22.44 mm, 0.39 g) beaches. At all three study locations, the relationship between size and biomass at 50% population maturity was explained convincingly ($P < 0.05$) by the non-linear regression given as Eq. 5, for both males and females (Fig. 6; Table 5). At the dissipative beach, clams were 100% mature on reaching an apSL of *c.* 23 mm (both sexes) and an SFWM of 0.4 g. Females at the intermediate beach reached up to 20 mm apSL and 0.9 g SFWM before attaining 100% maturity, while for males apSL

and SFWM at 100% maturity were even higher, 27 mm and 0.5 g, respectively. In contrast, at the reflective beach clams were largest and heaviest (*c.* 30 mm apSL and 1.8 g SFWM, both sexes) when reaching 100% maturity (Fig. 6; Table 5). The logistic function of male wedge clam apSL was significantly steeper at the dissipative (ARSS $F_{2,21} = 324.631$, $P < 0.05$) and intermediate beaches (ARSS $F_{2,23} = 418.321$, $P < 0.05$), indicating that 50% population maturity was reached at a significantly larger size (apSL$_{50\%}$) at the reflective beach (Fig. 6A; Table 5). A similar pattern was found in female specimens, where the slope of the logistic function was also significantly steeper at the dissipative (ARSS $F_{2,20} = 658.950$, $P < 0.05$) and intermediate beach (ARSS $F_{2,23} = 973.554$, $P < 0.05$), resulting in significantly larger female clams in a 50% mature population (apSL$_{50\%}$) at the reflective beach (Fig. 6B; Table 5). Size and biomass (both sexes) at 50% population maturity (SFWM$_{50\%}$) were significantly higher at the reflective beach (Fig. 6C, D), leading to significantly steeper logistic SFWM function at the dissipative (ARSS: males $F_{2,50} = 253.423$, $P < 0.05$, females $F_{2,53} = 579.924$, $P < 0.05$) and intermediate beaches (ARSS: males $F_{2,152} = 481.643$, $P < 0.05$, females $F_{2,125} = 761.464$, $P < 0.05$) (Table 5).

DISCUSSION

Comparison of reproductive biology on morphodynamically distinct beach types

Histological analyses from the 25-month sampling series revealed differences in the reproductive biology of *Donax*
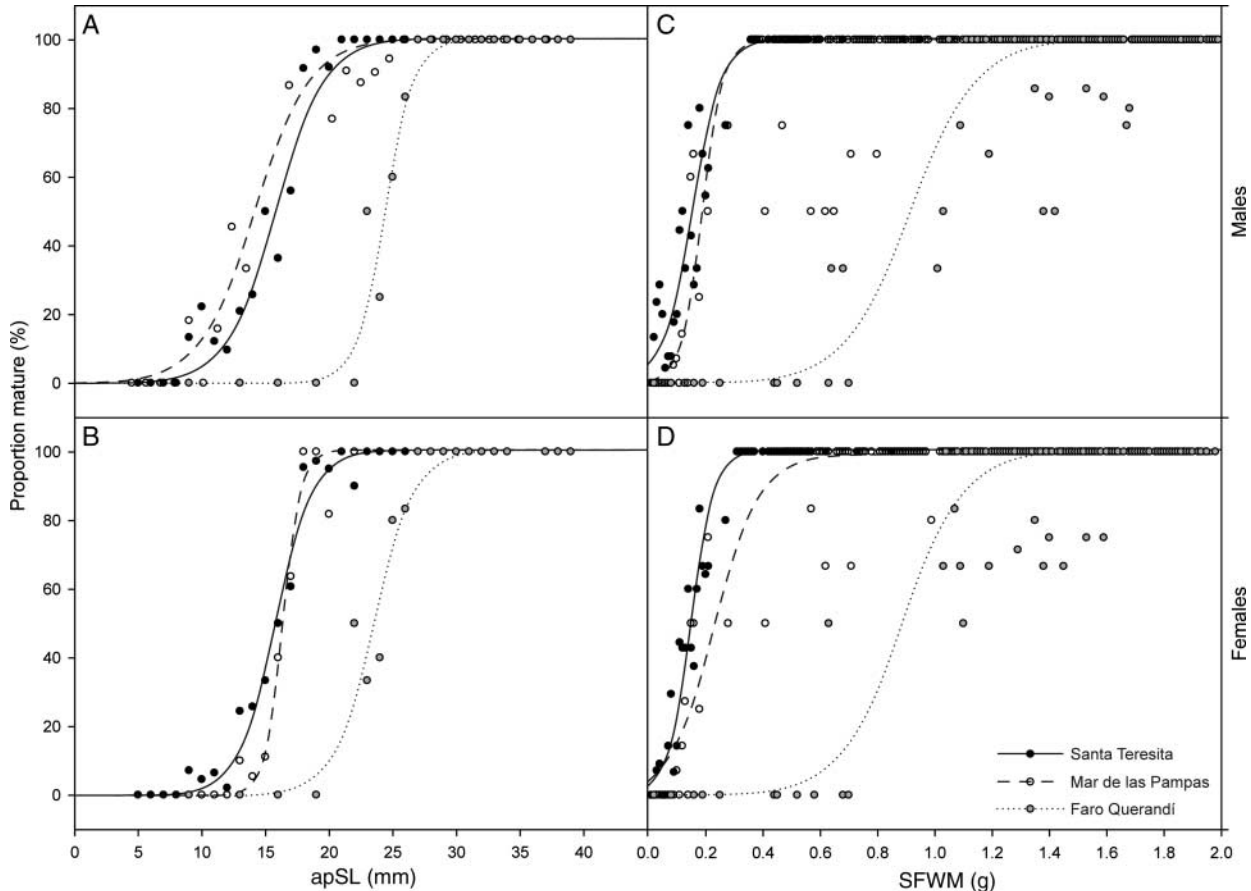

Figure 6. Logistic function (Eq. 4) indicating size (apSL) and biomass (SFWM) at sexual maturity in male (**A**, **C**) and female (**B**, **D**) *Donax hanleyanus*, fitted by non-linear regression, showing sex-specific differences. Statistical results are provided in Table 5.

Table 5. Parameters (a, b and x_0) estimated values and associated statistics relating to size (apSL) and biomass (SFWM) at sexual maturity function (Eq. 3) and size of 50% population maturity (apSL$_{50\%}$) and biomass of 50% population maturity (SFWM$_{50\%}$), respectively (Eq. 5).

	Males						Females					
	Santa Teresita		Mar de las Pampas		Faro Querandí		Santa Teresita		Mar las Pampas		Faro Querandí	
	apSL	SFWM	apSL	SFWM	apSL	SFWM	apSL	SFWM	apSL	SFWM	apSL	SFWM
a	102.96 (3.32)*	101.62 (1.39)*	97.66 (1.92)*	97.94 (0.73)*	101.03 (2.45)*	98.84 (0.75)*	100.61 (2.09)*	100.63 (1.04)*	99.41 (1.23)*	99.12 (0.66)*	101.74 (2.52)*	98.62 (0.80)*
b	1.95 (0.27)*	0.05 (0.01)*	1.93 (0.24)*	0.03 (0.01)*	1.14 (0.20)*	0.12 (0.01)*	1.49 (0.16)*	0.04 (0.00)*	0.72 (0.09)*	0.08 (0.01)*	1.61 (0.23)*	0.11 (0.01)*
x_0	15.81 (0.32)*	0.15 (0.01)*	17.57 (0.27)*	0.19 (0.01)*	24.40 (0.23)*	0.92 (0.01)*	15.77 (0.19)*	0.15 (0.00)*	16.37 (0.11)*	0.24 (0.01)*	23.54 (0.27)*	0.89 (0.01)*
50%	15.69	0.15	17.66	0.19	24.38	0.92	15.75	0.15	16.38	0.25	23.49	0.89
R^2	0.97	0.91	0.97	0.86	0.97	0.89	0.99	0.96	0.99	0.92	0.97	0.90
DW	1.64	1.62	2.49	1.99	2.32	1.84	2.11	1.73	2.39	1.99	2.43	2.18

Values are mean ± SE, mean size at first maturity in millimetres (apSL) and biomass at first maturity in grams (SFWM), Durbin–Watson statistic (DW).

*$P < 0.05$.

hanleyanus populating three morphodynamically distinct beaches. However, in contrast to the 13-month data set of Delgado & Defeo (2007), which documented the reproductive cycle of Uruguayan *D. hanleyanus* from two sandy beaches and supported the HHH, the present study does not confirm all predictions of this hypothesis for the reproductive cycle of the species in Argentina.

Consistency with predictions of the HHH: In accordance with the HHH, the settlement period of *D. hanleyanus* recruits was extended and recruits were more abundant at the dissipative beach compared to either the intermediate or reflective beach. Although there have been several previous studies on the reproduction biology of *Donax* species (Argentinean *D. hanleyanus*: Penchaszadeh & Olivier, 1975; Peruvian *D. marincovichi*: Huaraz & Ishiyama, 1980; Portuguese *D. trunculus*: Gaspar *et al.*, 1999; Spanish *D. semistriatus* and *D. venustus*: Tirado & Salas, 1999; Brazilian *D. hanleyanus*: Gil & Thomé, 2004), data on recruitment at beaches with different morphodynamics are scarce and inconsistent. The present results are in keeping with those of Delgado & Defeo's (2007) conclusions regarding recruitment in the Uruguayan *D. hanleyanus* population, in that both abundance of recruits and recruitment period are greater at a dissipative beach. The results of the current study suggest a shorter recruitment season for *D. hanleyanus* in reflective beach populations and so coincide with a prediction of the HHH. However, recruits of *Donax* do not always show the same pattern. For instance, Laudien, Brey & Arntz (2001) observed a longer period of recruitment in Namibian *D. serra* at a reflective beach than a dissipative one, a finding that directly contradicts the predictions of the HHH.

Contrasts to predictions of the HHH: The 'spawning' stage of the clams was more restricted in the dissipative beach population than in those from the beaches exhibiting intermediate and reflective morphodynamics. Furthermore, the proportion of specimens in the sexual rest stage varied from beach to beach. While at the reflective and intermediate beach gonads of indistinguishable sex appeared in low percentages from autumn to spring, large numbers of specimens in the sexual rest stage were only found twice (early autumn 2005 and late summer 2006) at the dissipative beach. Comparable size classes were present at all three beaches at the same time (Herrmann, 2009). Additionally, RSA was lower at the dissipative and intermediate beaches than at the reflective one. Further evidence for an extended reproductive cycle at the reflective beach, contrary to the predictions of the HHH, was derived from monthly oocyte size–frequency distributions. Modal oocyte values indicate two spawning events per year at the dissipative and intermediate beaches and continuous gamete releases at the reflective beach. Size and biomass at first maturity of both sexes were lower at the dissipative beach, suggesting an abrupt transition from sexual rest to reproductive activity at this site. Monthly mean abundance of *D. hanleyanus* was significantly higher at the reflective beach (ANOVA, $F_{2,69} = 14.675$, $P < 0.05$), compared to the dissipative and intermediate locations (Herrmann *et al.*, 2008b, 2009a), which is also counter to the predictions of the HHH. Consequently, the present study supports the results of previous investigators documenting increases in abundance of isopods (*E. braziliensis*: Defeo *et al.*, 1997; Defeo & Martínez, 2003), amphipods (*P. brasiliensis*: Gómez & Defeo, 1999; *A. brasiliensis*: Defeo & Gómez, 2005) and decapods (*E. brasiliensis*: Defeo *et al.*, 2001) at Uruguayan reflective beaches.

Table 6. Annual reproductive events of *Donax hanleyanus* from Argentinean (AR), Uruguayan (UY) and Brazilian (BR) beaches of different morphodynamic types (M): dissipative (D), intermediate (I) and reflective (R). **A**, spawning events (grey) indicated by classifying gonad tissue into different gametogenic stages; **B,** spawning events (grey) derived from oocyte measurements.

	J	F	M	A	M	J	J	A	S	O	N	D	Beach	M	Source
A													Santa Teresita (AR)	D	Present study
													Mar de las Pampas (AR)	I	Present study
													Faro Querandí (AR)	R	Present study
													Arachania (UY)	R	Delgado & Defeo (2007)
													Barra del Chuy (UY)	D	Delgado & Defeo (2007)
													Arroio Teixeira (BR)	D	Gil & Thomé (2004)
B													Santa Teresita (AR)	D	Present study
													Mar de las Pampas (AR)	I	Present study
													Faro Querandí (AR)	R	Present study
													Villa Gesell (AR)	I	Penchaszadeh & Olivier (1975)

Comparison of the reproductive biology among the three beaches

Gametogenic cycle: The histological examination of *D. hanleyanus* gonads suggests several reproductive events per year (Fig. 2), with an underlying seasonality, confirmed by a significant correlation with SST at all three beaches. Gonad classifications revealed two annual spawning events at the dissipative beach (spring and summer) and the intermediate beach (spring and summer–autumn) and a continuous gamete release over the year at the reflective beach (Table 6A). These are in line with the results of Delgado & Defeo (2007) and Gil & Thomé (2004), who observed two spawning events at dissipative beaches and continuous spawning at reflective sites in Uruguay and Brazil respectively. However, spawning events can be determined more exactly by oocyte measurements (e.g. Penchaszadeh & Olivier, 1975; Sarkis, Couturier & Cogswell, 2006; Morriconi, Lomovasky & Calvo, 2007). Modal values of the oocyte size–frequency distributions (Fig. 4) indicate two spawning events at the dissipative beach (September and December), and three each at the intermediate beach (February, August and December) and the reflective beach (January, April–July and September), with a more extended period at the latter (Table 6B). Similarly, four decades ago Penchaszadeh & Olivier (1975) detected two spawning events (January–February and August–September) of *D. hanleyanus* by measuring oocyte sizes at Villa Gesell, 10 km north of the intermediate beach, Mar de las Pampas. In agreement with previous investigations on the reproductive biology of *D. hanleyanus* (Penchaszadeh & Olivier, 1975; Gil & Thomé, 2004; Delgado & Defeo, 2007), the present study confirms that there is no period of complete gonadal inactivity in this species. The same is true in the Peruvian *D. marincovichi* (Huaraz & Ishiyama, 1980) and the Namibian *D. serra* (Laudien et al., 2001), but not in the Portuguese *D. trunculus* (Gaspar et al., 1999) and the Spanish *D. venustus* and *D. semistriatus* (Tirado & Salas, 1999). The discrepancy may be caused by the significant differences in seasonal ranges in SST range routinely experienced by different species (Urban & Campos, 1994; Sasaki, Ota & Saeki, 1997; Laudien et al., 2001). However, SST is not the only parameter influencing the reproductive cycle of suspension feeders (Sastry, 1968, 1979; Giese, 1974). Changes in phytoplankton biomass and species composition are also key factors. Thus, the increase of chlorophyll *a* concentrations in the Buenos Aires shelf region observed during winter and summer by Carreto et al. (1995), with a main peak in spring and a secondary peak in autumn, corresponds convincingly with the dominance of ripe and spawning stages of *D. hanleyanus* (Fig. 3). This suggests that phytoplankton abundance may also have a direct impact on the reproductive cycle of *D. hanleyanus*.

Relative spermatozoon abundance: As documented and discussed above, RSA was lower at the dissipative and intermediate beach (spring), than at the reflective one (spring–summer). The measurement of spermatozoon abundance turned out to be a good reflection of male gonadal tissue condition and thus a useful indicator in the investigation of seasonal variations in the gametogenic cycle between beaches with contrasting morphodynamics. This method negates the need for time-consuming microscopical examination of gonads to assign samples to different developmental stages. RSA may be used to analyse the relationships between abiotic and biotic parameters and the gametogenic cycle. Furthermore, RSA may be calibrated species-specifically; counting spermatids per surface area allows estimations of absolute spermatozoon abundance.

Condition index, biomass and recruitment: CI and AFDM are useful tools in describing the reproductive biology of *D. hanleyanus*. Both indicate gonadal mass changes throughout the year, with highest values when gonads are in the mature stage. The results presented here are in line with studies of other surf clams, where the CI was also successfully used to describe changes in the gametogenic cycle (*D. trunculus*: Gaspar et al., 1999; *D. serra*: Laudien et al., 2001; *Mesodesma donacium*: Riascos et al., 2008). Recruitment pattern and abrupt changes in oocyte size appear to indicate a meroplanktonic phase of *c*. 3 months, assuming that collected recruits originated from the studied adult population. Recruitment patterns observed in the present study provide clear evidence that juvenile wedge clams occur only sporadically and recruitment varies between years, agreeing with the findings of other studies (e.g. Arntz et al., 1987; Laudien et al., 2001; Herrmann et al., 2009b). It should be noted that the absence of recruits does not necessarily indicate a lack of spawning activity (Caddy & Defeo, 2003). Environmental conditions may strongly influence recruitment of marine invertebrates (e.g. hydrodynamic processes: Roughgarden, Gaines & Possingham, 1988; food limitation: Olson & Olson, 1989; predators: Sale, 1990), and unfavourable conditions may lead to failure of recruitment at the parent beach.

Size and biomass at sexual maturity: Single individuals of *D. hanleyanus* in the present study matured with an average shell length of 9 mm (and 0.02 g SFWM) and reached gonadal maturity $apSL_{50\%}$ at 16 mm (and 0.15 g $SFWM_{50\%}$). The

present results coincide well with estimates of 40 years ago (15 mm: Penchaszadeh & Olivier, 1975), and with data from the Uruguayan *D. hanleyanus* population (minimal length with gonad development 10 mm, gonad maturity 12 mm; Delgado & Defeo, 2007).

CONCLUSION

In conclusion, the results of the present study obtained from three beaches over 25 months demonstrate that at the population level *Donax hanleyanus* respond systematically to beach morphodynamics in a manner opposite to that predicted by the HHH. The population at the dissipative beach exhibited a greater abundance of recruits and an extended recruitment period, but spawning specimens were greatly outnumbered by those in sexual rest stages. Spawning events were recorded twice each year at the dissipative (early spring and spring–summer) and intermediate beaches (winter and summer), whereas continuous gamete release was noted at the reflective beach. The onset of maturity was observed in single *D. hanleyanus* individuals of *c*. 9 mm apSL and 0.02 g SFWM. 50% of the population attained maturity at 15 mm apSL and 0.15 g SFWM, and 100% were mature at a size of 23–27 mm apSL and 0.4–0.9 g SFWM. Size at first maturity and biomass at first maturity were lower at the dissipative beach, whereas monthly mean abundance of *D. hanleyanus* was higher at the reflective beach. Finally, the current study demonstrated that the 'hypothesis of habitat safety (HHS)', originally postulated by Defeo & Gómez (2005) for supralittoral species, may be extended to intertidal species; the combination of narrow swashes and steep slopes make reflective beaches a safer and more stable environment for supralittoral and intertidal species such as *D. hanleyanus*.

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