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POPULATION STRUCTURE, GROWTH, AND PRODUCTION OF THE WEDGE CLAM *DONAX HANLEYANUS* (BIVALVIA: DONACIDAE) FROM NORTHERN ARGENTINEAN BEACHES

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ABSTRACT *Donax hanleyanus* Philippi, 1847 (Bivalvia: Donacidae) dominates fine to coarse sandy beach communities of the northern Argentinean Atlantic coast. The population biology of this intertidal wedge clam was studied by determining population structure, growth and production at the three locations Santa Teresita, Mar de las Pampas (both from December 2005 to December 2006) and Faro Querandí (from March 2005 to December 2006). Von Bertalanffy growth functions were established from length-frequency distributions using an asymptotic length (L_∞) of 44 mm and the growth constants (K) of 0.46 and 0.47 y^{-1} respectively of Mar de las Pampas and Faro Querandí. Compared with growth studies four decades ago, *D. hanleyanus* today is growing more slowly, but is reaching a higher maximum length. Longevity is estimated to be approximately five years. The present study confirms that the overall growth performance index is habitat-specific, grouping Donacidae into tropical/subtropical, temperate and upwelling species. The intertidal biomass of *D. hanleyanus* ranged between 0.04 and 1.32 g ash-free dry mass (*AFDM*) $m^{-2}yr^{-1}$. Individual production revealed the highest value at 30 mm length (0.16 g *AFDM* $m^{-2}yr^{-1}$) and annual production ranged between 0.08 and 0.99 g *AFDM* $m^{-2}yr^{-1}$, resulting in renewal rate values ($P/\bar{B}$) between 0.82 and 2.16. The $P/\bar{B}$ ratios of *D. hanleyanus* populations increased with decreasing latitude from temperate to tropical regions. Only at Santa Teresita *D. hanleyanus* was found living with the sympatric yellow clam *Mesodesma mactroides*. A significant negative correlation between abundances of both surf clams suggests that abundance peaks of *D. hanleyanus* are related with population crashes of *M. mactroides*. Spatial differences in abundance are significantly related to sand texture as confirmed by nonmetrical multidimensional scaling, but not to sea surface temperature. However, the decrease of *D. hanleyanus* seems to be principally related to human activities.

KEY WORDS: wedge clam, *Donax hanleyanus*, population dynamics, growth performance indices, grain size analysis, human impact

INTRODUCTION

Exposed sandy beaches are some of the most dynamic environments in the world. Their invertebrate populations and communities are usually considered to be regulated mainly by beach morphodynamics depending on physical parameters such as wave energy, wind velocity, tide forces, and sand grain size. On a worldwide basis, Donacidae (super family Tellinacea) form by far the most diverse group inhabiting such highly dynamic environments including the genera *Egeria*, *Iphigenia* and *Donax*, with the latter being composed of 64 species (Pearse et al. 1942, Ansell 1983, Brown & McLachlan 1990, Wilson 1999). In some cases, they dominate the macrozoobenthic communities in number and biomass, which is also the case for the *Donax* populations studied (>95%: McLachlan et al. 1981, Arntz & Fahrbach 1991, Ieno & Bastida 1998).

Donax hanleyanus, also known as the wedge clam and in Argentina as ‘‘berberecho’’, can be found along the South American Atlantic coast from tropical (17°S Caravelas, Brazil) to temperate regions (37°S Punta Mogotes in Mar del Plata, province of Buenos Aires) (Penchaszadeh & Olivier 1975, Narchi 1978, Cardoso & Veloso 2003). This intertidal suspension-feeder represents the only *Donax* species occurring throughout the Argentinean sublittoral (Penchaszadeh & Olivier 1975). As is characteristic of donacids, this bivalve has adapted to live in exposed swash zones characterized by a fair amount of wave action aerating the sediment. This keeps organic detritus in suspension and allows for tidal migration (Mori 1938, Ansell & Trevallion 1969, Penchaszadeh & Olivier 1975, Narchi 1978, Ansell 1983). Although fossils of *D. hanleyanus* have been recorded in South America since the Querandinense period of marine transgression in the early Holocene (von Ihering 1907), live specimens of *D. hanleyanus* were reported from the Argentinean coast no earlier than 1960 (Penchaszadeh & Olivier 1975), from Brazil in 1949 (Lange de Morretes) and from Uruguay in 1951 (Barattini). Planktonic larvae of *D. hanleyanus* have been shown to cut across the Río de la Plata with favorable ocean currents and settled on sandy beaches south of this estuary (Penchaszadeh & Olivier 1975).

Although several *Donax* clams are targeted by artisanal fisheries (McLachlan et al. 1996) and *D. hanleyanus* is edible (Veloso et al. 1953, Penchaszadeh & Olivier 1975), this species is not commercially exploited in Argentina. However, like most donacids *D. hanleyanus* plays an important role in the food web by linking benthic with planktonic ecosystems (Wade 1967, McLachlan et al. 1981, McLachlan & Lewin 1981, McDermott 1983, DeLancey 1989, Heymans & McLachlan 1996, Soares et al. 1997). This wedge clam is the main primary consumer in soft bottom communities and is in turn subject to predation by a wide variety of invertebrates, fish, birds, and mammals (Penchaszadeh & Olivier 1975, Peterson et al. 2000, Salas et al. 2001). Only a few studies on *D. hanleyanus* from Argentinean shores are published dealing with ecological aspects (Penchaszadeh & Olivier 1975), beach morphodynamics and their influence on wedge clam's abundance (Marcomini

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et al. 2002), anthropogenic influences (Dadon et al. 2001) and siphon regeneration (Luzzatto & Penchaszadeh 2001), however, none of the studies investigated the population dynamics.

Therefore the aim of this study is to (1) analyze the population structure of *D. hanleyanus*, (2) estimate its growth and production parameters, (3) compare these results with values of other *Donax* species, (4) examine the possible influences of sand grain size and sea surface temperature on abundance, (5) discuss the effect of mass tourism, and (6) reveal the relationship between *Mesodesma mactroides* and *D. hanleyanus* abundances.

MATERIAL AND METHODS

Study Area

The population structure of the intertidal wedge clam *D. hanleyanus* was studied during alternate spring tides at three beaches (1) Santa Teresita (36°32′S, 56°41′W), which is heavily influenced by mass tourism during the summer season (>1000 tourists 100 m^{-1} coastline, pers. observ. and local tourist office "Secretaría de Turismo, Mar del Tuyú," Argentina), (2) Mar de las Pampas (37°19′S, 57°00′W), which is marginally influenced by humans (<10 tourists 100 m^{-1} coastline, pers. observ.), and (3) Faro Querandí, which is unaffected by humans (<0.01 angler 100 m^{-1} coastline, pers. observ.) and naturally protected (37°29′S, 57°07′W). All three open ocean beaches are located in the Province of Buenos Aires, Argentina (Fig. 1A) and flow continuously into one another with a north-south shoreline orientation, which is stable on a long term basis (Marcomini & López 1993).

Abiotic Factors and Anthropogenic Impacts

According to McLachlan's (1980) rating scale for exposure and Short and Wright's (1983) classifications of beach types, Santa Teresita is sheltered/dissipative, Mar de las Pampas exposed/intermediate, and Faro Querandí exposed/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 ± SE) varies between 11°C ± 0.14°C in winter and 23°C ± 0.21°C in summer (Fig. 2). 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 2.26 φ, 1.43 φ and 1.05 φ, 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 290 km long and up to 220 km wide estuary of the Río de la Plata. Mean salinity ranges between 31 and 34. All three beaches are well drained and oxygenated.

To characterize the physical attributes of the *Donax* belt, particle size analyses from the studied areas were carried out by sampling sediments with a plastic corer of 3.5 cm diameter to a depth of 10 cm. Sand samples were washed with freshwater overnight to remove salt and then dried at 70°C. Subsequently, any shell fragments were extracted and the remaining part of the samples was analyzed 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

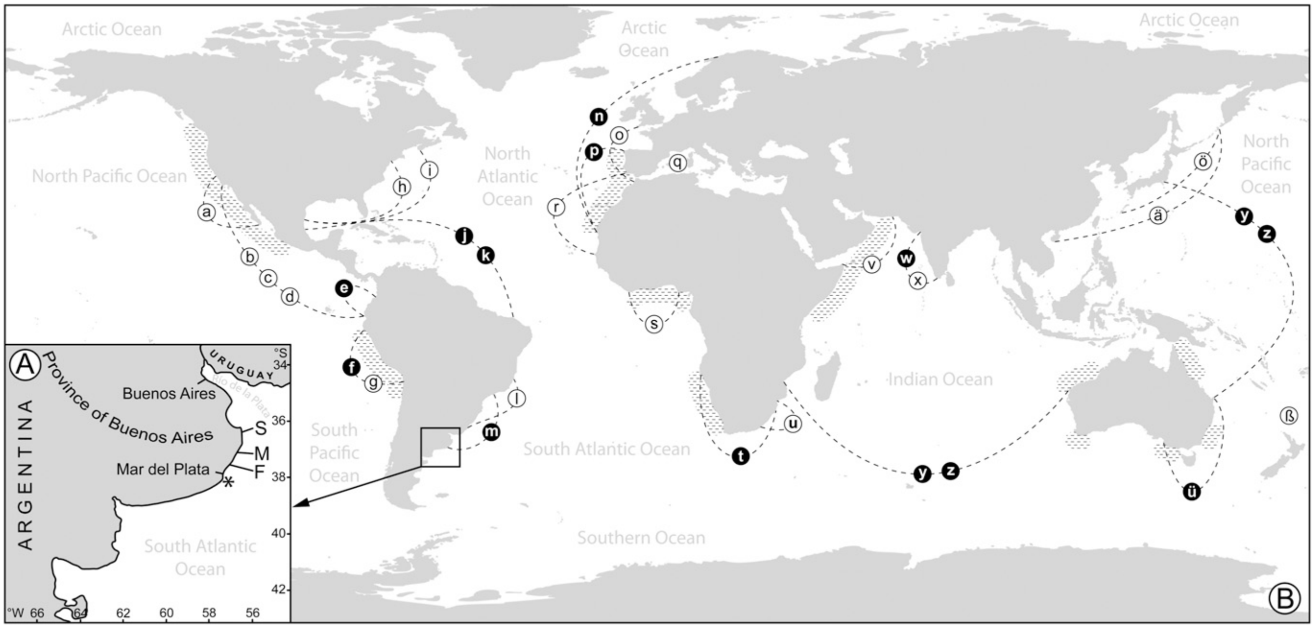

Figure 1. Map of the three study sites at the Argentinean Atlantic coast (A): Santa Teresita (S), Mar de las Pampas (M) and Faro Querandí (F). * Indicate the southern most distribution of *D. hanleyanus* at Punta Mogotes, south of Mar del Plata. Geographical distribution of 30 selected donacids with known scientific information, of which 14 *Donax* species are marked with black dots (for sources of white letters, see Table 3) used for growth in this study (B). Major coastal upwelling areas are dotted. Map modified and extended after Laudien (2002): a: *D. gouldii*, b: *D. carinatus*, c: *D. panamensis*, d: *D. punctatostriatus*, e: *D. dentifer*, f: *D. marincovichi*, g: *D. obesulus*, h: *D. fosser*, i: *D. variabilis*, j: *D. denticulatus*, k: *D. striatus*, l: *D. gemmula*, m: *D. hanleyanus*, n: *D. vittatus*, o: *D. variegatus*, p: *D. trunculus*, q: *D. semistriatus*, r: *D. venustus*, s: *D. oweni*, t: *D. serra*, u: *D. sordidus*, v: *D. townsendi*, w: *D. incarnatus*, x: *D. spiculum*, y: *D. cuneatus*, z: *D. faba*, ä: *D. kiusiuensis*, ö: *D. semigranosus*, ü: *D. deltoides*, β: *D. pallidus*.

TABLE 1.

Characterization of physical and biological attributes of the three studied localities at 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)[1]	2.26/0.21	1.43/0.37	1.05/0.48
Median grain size (phi)[1]	2.28	1.39	0.99
Sorting[1,2,3]	Good (0.36)	Moderate (0.68)	Moderate (0.51)
Skewness[1,2]	–0.11	+0.07	–0.11
Textural group[5]	Fine	Medium	Coarse
Mean slope of intertidal (%)	1/43	1/16	1/14
Exposure[4]	Sheltered	Exposed	Exposed
Morphodyn. type[5]	Dissipative	Intermediate	Reflective
Dean parameter (Ω)[6*]	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

[1] After Flemming and Thum (1978) and after Flemming and Ziegler (1995)
[2] After Inman (1952)
[3] After McLachlan and Brown (2006)
[4] After McLachlan (1980)
[5] After Short and Wright (1983)
[6] After Dean (1973)
* Calculated for specific seasonal *SST* from 9°C to 25°C

Gibbs et al. (1971), which is applicable to smooth glass spheres only to calculate settling velocities. All textural parameters presented in this study were calculated using the percentile statistics of Inman (1952), whereas sediments were classified according to the Wentworth scale (1922).

Wave height was estimated 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 ($n = 50$). The morphodynamic state of each site studied was described by the Dean parameter (Ω) (Dean 1973):

$$\Omega = H_b \frac{100}{WT}, \tag{1}$$

which is based on mean wave height H_b (m) divided by wave period T (s) and sand fall velocity W (m s^{-1}). 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 and McLachlan (1991). Salinity (Optech portable refractometer, model RSM) as well as the *SST* 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 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.

Data of tourists visiting the coast of Buenos Aires were provided by the local tourist office (Secretaría de Turismo, Mar del Tuyú, Argentina).

Sampling and Laboratory Procedures

Quantitative sampling of *D. hanleyanus* 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) from a series of stations (4 m intervals). The latter were located along three transects separated by 20 m intervals and located perpendicular to the shoreline from the spring tide high water mark to the spring tide low water mark. At each station, three replicated sand samples (40 × 40 cm) were excavated to 35 cm depth using a 0.16 m^2 steel corer, and thereafter sieved individually on a 1-mm mesh. Maximum anterior-posterior shell length (*apSL*) of the retained wedge clams was measured to the nearest 0.1 mm with a digital vernier calliper (Mitutoyo, model 500–161U) to obtain monthly length-frequency distributions. For biomass analysis monthly subsamples of 35 randomly taken specimens from each of the three locations were stored in 70% ethanol. Thereafter soft tissues were removed to estimate shell-free wet mass (*SFWM*) by weighing after blotting on filter paper. Subsequently, samples were dried to a constant mass at 70°C, weighed again to determine shell-free dry mass (*SFDM*) and finally ignited in a muffle furnace at 550°C for 5 h to estimate ash-free dry mass (*AFDM*).

Growth, Growth Performance and Life Span

A series of 25 length-frequency distributions provided the basic information for growth estimates. A von Bertalanffy growth function (*VBGF*) (von Bertalanffy 1938) was fitted to the data using the electronic length-frequency analysis 'ELEFAN I' routine of the FISAT II program package (Gayanilo Jr. et al. 2005). Because of the pronounced seasonal changes in temperature (Fig. 2A), the modified version of the

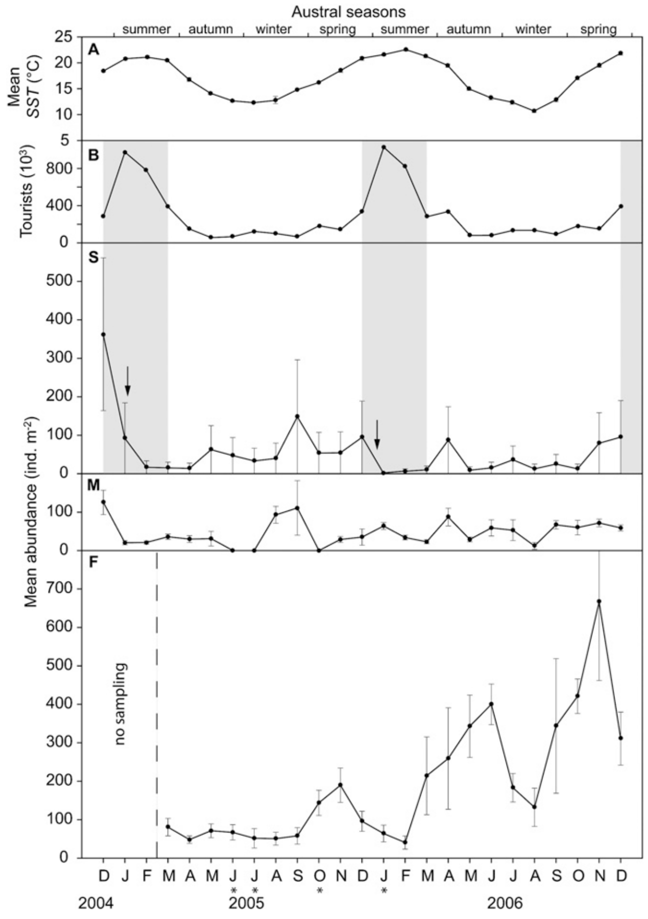

Figure 2. Monthly mean abundance of *D. hanleyanus* at Santa Teresita (S), Mar de las Pampas (M) (from December 2004 to December 2006, respectively) and at Faro Querandí (F) (from March 2005 to December 2006) in relationship to monthly mean *SST* (A) and visiting tourists at the coast of the Province Buenos Aires (B). **D. hanleyanus* was not abundant in June, July and October 2005 at Mar de las Pampas, and also not in January 2006 at Santa Teresita. *Error bars*: standard error (SE). *Grey areas*: high tourist season. *Arrows*: indicate significantly decreases of the *Donax* population during high tourist season. Data set is published in Herrmann et al. (2008).

VBGF was used, which incorporates seasonal oscillation in growth:

$$L_t = L_\infty\left[1 - e^{\left[-K(t-t_0)+\left(\frac{KC}{2\pi}\right)\sin 2\pi(t-ts)-\left(\frac{KC}{2\pi}\right)\sin 2\pi(t_0-ts)\right]}\right], \quad (2)$$

where L_t is the *apSL* (mm) at time *t*, L_∞ the asymptotic maximum shell length, *K* is the curvature parameter, *C* is a constant, which defines the degree of seasonal oscillation (ranging from 0, which defines continuous non oscillating growth, to 1, when growth comes to a complete halt at the "winter point" (*WP*)), t_0 is the theoretical age at zero length and t_s is the initial point of oscillation in relation to $t = 0$ and the *WP*. The different subroutines of ELEFAN (*K*-scan, response surface analysis) were used to identify the *VBGF* that best fits the monthly size-frequency data, using the *Rn* value as a criterion of fit.

Because of the absence of adult individuals at Santa Teresita, it was not possible to apply a *VBGF* (Gayanilo Jr. et al. 2005). Thus the monthly length-frequency distributions of Santa Teresita were converting to size-at-age data (*SAD*) and thereafter fitted to a general von Bertalanffy growth function (*gVBGF*) (Gulland & Holt 1959) applying Microsoft Excel's SOLVER routine (Brey 2001). Differences in growth among sites were checked by variance analysis of the residuals of the *gVBGF*.

To compare growth performance the growth index phi prime (φ') was used:

$$\phi' = 2\ \log_{10}(L_\infty) + \log_{10} K. \quad (3)$$

This criterion was chosen because the negative correlation between *K* and L_∞ invalidates direct comparisons between individual parameters (Pauly & Munro 1984). Finally the overall growth performance index:

$$OGP = \log(K[L_\infty]^3), \quad (4)$$

which represents growth rate at the point of inflexion of the size-growth curve (Pauly 1979), was calculated to compare growth of *D. hanleyanus* with other *Donax* species.

The theoretical life span $t_{\max}$ (equal to relative age, because the larval period of this species is unknown, $t = 0$) of *D. hanleyanus* was estimated by the inverse von Bertalanffy growth equation (Taylor 1958):

$$t\max = \frac{[\ln L_{95\%} - \ln(L_\infty - L_{95\%})]}{K}, \quad (5)$$

where $L_{95\%}$ represents 95% of the maximum shell length recorded during field sampling.

Biomass and Production

To compare biomass of *D. hanleyanus* with values of other *Donax* species, all published values were converted to *AFDM* (according to Brey et al. 1988), based on the empirically determined conversion factor of 0.186 (*SFWM* to *AFDM* for preserved *D. hanleyanus*). Parameters of the relationship between length and ash-free dry mass (*AFDM*) of *D. hanleyanus* were estimated by regression analysis

$$M = aL^b, \quad (6)$$

where *M* is the *AFDM* (g), *L* is the shell length of the size class (mm), and *a* and *b* are constants. *AFDM* was determined for 400 specimens covering all size classes between December 2004 and December 2006.

Total annual production was calculated for *D. hanleyanus* belts at Santa Teresita, Mar de las Pampas (January–December 2005 and January–December 2006) and Faro Querandí (March–December 2005 and January–December 2006) by the mass specific growth rate method (Crisp 1984, Brey 2001). The latter requires information from size-mass relationships and the size-frequency distribution obtained from all pooled samples and the *VBGF*:

$$P = \sum N_i M_i G_i (\text{g } AFDM \text{ m}^{-2}\text{yr}^{-1}), \quad (7)$$

where N_i is the average number of animals (number per m^2) and M_i is the mean individual *AFDM* in length class *i*, and G_i is the mass-specific growth rate:

$$G_i = bK\left[\left(\frac{L_\infty}{L_i}\right) - 1\right](\text{yr}^{-1}), \quad (8)$$

where *b* is the exponent of the size-mass relation, *K*, L_∞ are *VBGF* parameters and L_i is the mean size in class *i*.

Mean annual biomass was estimated by:

$$\bar{B} = \sum N_i M_i \ (\text{g } AFDM \ \text{m}^{-2}), \tag{9}$$

and annual renewal rates (P/B ratios) of the *D. hanleyanus* populations were calculated from annual total production P and annual mean biomass $\bar{B}$.

Statistical Analysis

Spatial and temporal differences of the population abundance (one-way ANOVA) as well the influence of *SST* and anthropogenic factors on the population abundance (Spearman's rank order correlation) were analyzed using the statistical package SPSS version 17.0 (SPSS 2008). Differences were considered significant at a level of $\alpha = 5\%$ (Zar 1999). The relationship between monthly mean abundance and mean grain size was analyzed through a nonmetric multidimensional scaling (nMDS), using square root transformed data and calculated Bray-Curtis similarities (PRIMER 2007) as used by several authors (e.g., Rumohr & Karakassis 1999, Jaramillo et al. 2001, Sousa et al. 2008). Correlation analysis was used to assess the relationships between renewal rate ($P/\bar{B}$ ratios) and latitude of *D. hanleyanus* compared with those of several *Donax* species from other areas. The relation between the population abundance of *D. hanleyanus* and *M. mactroides* was estimated by linear regression analysis.

RESULTS

Abiotic Factors and Anthropogenic Impacts

Results of grain size and sand fall velocity analyses, as well as the associated parameters are summarized in Table 1. The nMDS analysis, based on monthly mean abundance data, identified two main areas of distinct granulometry: mean grain size 1.43 and 2.26 ϕ (at Mar de las Pampas and Santa Teresita, respectively, Figure 3A), and mean grain size 1.05 phi (at Faro Querandí, Figure 3B). The stress factor of 0.08 indicates an excellent representation with no prospect of misinterpretation (Clarke & Warwick 2001).

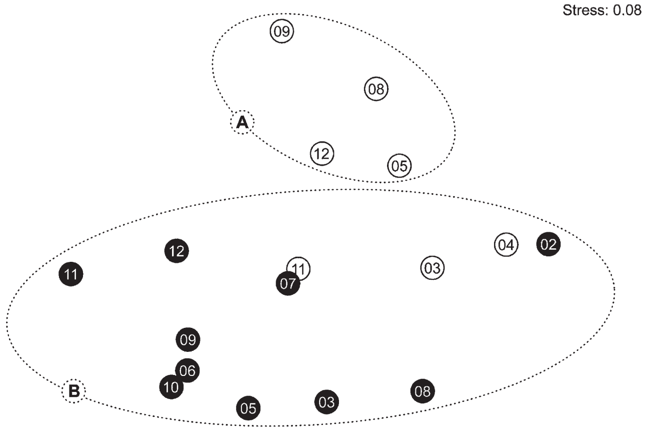

Figure 3. Resulting from square root transformed data and calculated Bray-Curtis similarity of 78% (PRIMER 2007) the nMDS diagram identifies two main areas of distinct granulometry, which is based on monthly mean abundance data (months in circles) in 2005 (○) and in 2006 (●): A: mean grain size 1.43–2.26 φ (Mar de las Pampas and Santa Teresita, respectively), B: mean grain size 1.05 phi (Faro Querandí).

Mean annual *SST* (mean ± SE) was 17.6°C ± 0.17°C, with lowest temperatures of 9.8°C and 9.1°C in austral winter (June 2005 and July 2006, respectively), and highest values of 24.8°C and 24.5°C in austral summer (December 2005 and February 2006, respectively) (Fig. 2A). *SST* was not correlated with the abundance of *D. hanleyanus* at all three sampling sites (Spearman's rank order correlation: Santa Teresita $r_s = -0.013$, $P > 0.05$, $n = 25$; Mar de las Pampas $r_s = 0.122$, $P > 0.05$, $n = 25$; Faro Querandí $r_s = 0.077$, $P > 0.05$, $n = 22$). However, at Santa Teresita the number of visiting tourists (>1,000 tourists 100 m^{-1} coastline, pers. observ. and local tourist office "Secretaría de Turismo, Mar del Tuyú," Argentina) was significantly correlated with the decrease of the wedge clam population during the summer months of both years (Spearman's rank order correlation, $r_s = -0.829$, $P < 0.05$, $n = 6$). At Mar de las Pampas (<10 tourists 100 m^{-1} coastline, pers. observ.) this correlation was not found (Spearman's rank order correlation, $r_s = -0.371$, $P > 0.05$, $n = 6$), and at Faro Querandí no tourist effect was apparent (<0.01 angler 100 m^{-1} coastline, pers. observ.).

Population Structure

During the study period of 25 mo, 21,405 *D. hanleyanus* were collected and measured: in the first year at Santa Teresita 4,230 ind., at Mar de las Pampas 1,545 ind. (December 2004-November 2005) and at Faro Querandí 3,911 ind. (March 2005–November 2005). During the second year 2,183 ind. were measured at Santa Teresita, 1,452 ind. at Mar de las Pampas and 8,524 ind. at Faro Querandí (December 2005–December 2006). The smallest recorded individual had an *apSL* of 3 mm at Santa Teresita and 4 mm at Mar de las Pampas and Faro Querandí. The largest individual measured 35 mm, 36 mm, and 40 mm respectively.

Mean annual *D. hanleyanus* abundance (mean ± SE) was 78 ± 42 ind. m^{-2} (2005) and 40 ± 15 ind. m^{-2} (2006) at Santa Teresita, 55 ± 23 ind. m^{-2} (2005) and 50 ± 12 ind. m^{-2} (2006) at Mar de las Pampas, and 84 ± 22 ind. m^{-2} (2005) and 267 ± 77 ind. m^{-2} (2006) at Faro Querandí. Maximal abundance was recorded in spring (2,475 ind. m^{-2} at Santa Teresita in December 2004, 531 ind. m^{-2} at Mar de las Pampas in December 2004, and 950 ind. m^{-2} at Faro Querandí in November 2006).

The population abundance at Santa Teresita and Mar de las Pampas did not varied significantly between the studied years (ANOVA, $F_{1,22} = 2.427$, $P > 0.05$; $F_{1,22} = 2.209$, $P > 0.05$, respectively), but was significantly lower in 2005 compared with 2006 at Faro Querandí (ANOVA, $F_{1,22} = 11.891$, $P < 0.05$). In all three beaches, population abundance differed significantly between months (Santa Teresita: $F_{11,13} = 1.171$, $P > 0.05$; Mar de las Pampas: $F_{11,13} = 0.681$, $P > 0.05$; and Faro Querandí: $F_{11,10} = 0.542$, $P > 0.05$; ANOVA respectively). Monthly mean abundance was significantly higher in the reflective beach, Faro Querandí (ANOVA with Scheffé-procedure *post hoc* test, $F_{2,69} = 14.675$, $P < 0.05$). The highest abundance of *D. hanleyanus* was recorded mainly in spring (at Santa Teresita [mean ± SE] 361 ± 149 ind. m^{-2} in December 2004 and 95 ± 27 ind. m^{-2} in December 2006, at Mar de las Pampas 125 ± 32 ind. m^{-2} in December 2004 and 111 ± 71 ind. m^{-2} in September 2005 and at Faro Querandí 190 ± 45 ind. m^{-2} in November 2005, and 667 ± 205 ind. m^{-2} in November 2006) (Fig. 2S, M, F). During the present study we did not find any evidence of migration of *D. hanleyanus* although the abundance may vary drastically at a given location (Fig. 2). Additional random sampling south and east of the transects did not reveal higher abundance compared with the monthly stations. Further random sampling in the highly dynamic wave breaking zone, taken with a diver-operated corer (Rumohr & Arntz 1982), confirmed that clams did not migrate into the surf zone.

The length-frequency distribution of *D. hanleyanus* of Santa Teresita, Mar de las Pampas and Faro Querandí showed distinct cohorts. One single new cohort was observed during both years (April 2005 and March 2006) at Santa Teresita. Cohorts were tracked up to 10 months reaching approximately 20 mm *apSL* before the cohort disappeared and new recruits were recorded (Fig. 4S). In March 2006 a new cohort was detected along with two additional cohorts at Mar de las Pampas and could be followed until the end of the study in December 2006 (Fig. 4M). Adult individuals co-occurring in two (February 2005 until March 2006) and three cohorts (April 2006 to October 2006) were found at Faro Querandí (Fig. 4F).

Growth and Life Span

The maximum sized valve of 44 mm was found at Faro Querandí. This length was used as a fixed L_∞ value to calculate a seasonal *VBGF* with a growth constant $K = 0.47$ at Mar de las Pampas and $K = 0.48$ at Faro Querandí (Fig. 4M, F). Estimates of growth indicated moderate seasonal oscillations ($C = 0.8$), with slowest growth rates occurring in austral autumn ($WP = 0.45 \sim$ mid-May). At Santa Teresita adult individuals were not abundant which prevented the reliable calculation of a *VBGF* with FISAT (Gayanilo Jr. et al. 2005). Thus monthly length-frequency distributions of Santa Teresita were converted to *SAD* and fitted to a g*VBGF*. Variance Analysis of the residuals ($P > 0.05$) revealed that growth parameters of Santa Teresita deviated strongly from those of populations inhabiting the beaches of Mar de las Pampas and Faro Querandí. Because of the lack of larger size classes and the resulting methodological bias, we decided to only compare growth parameters from the two latter populations.

The calculated life span ($t_{\max}$) was 4.96 y (Mar de las Pampas) and 5.18 y (Faro Querandí) (Table 2).

Biomass and Production

The observed relationship between length and calculated *AFDM* of *D. hanleyanus* $M_{(\mathrm{AFDM})} = (4.27 \cdot 10^{-6}) \bullet L_{(\mathrm{mm})}^{3.19}$ ($n = 2233$, $r^2 = 0.98$) was used for production estimates.

Within the *Donax* belt these abundance values represent an average annual biomass $\bar{B}$ of 0.21 g *AFDM* $\mathrm{m}^{-2}\,\mathrm{yr}^{-1}$ (2005) and

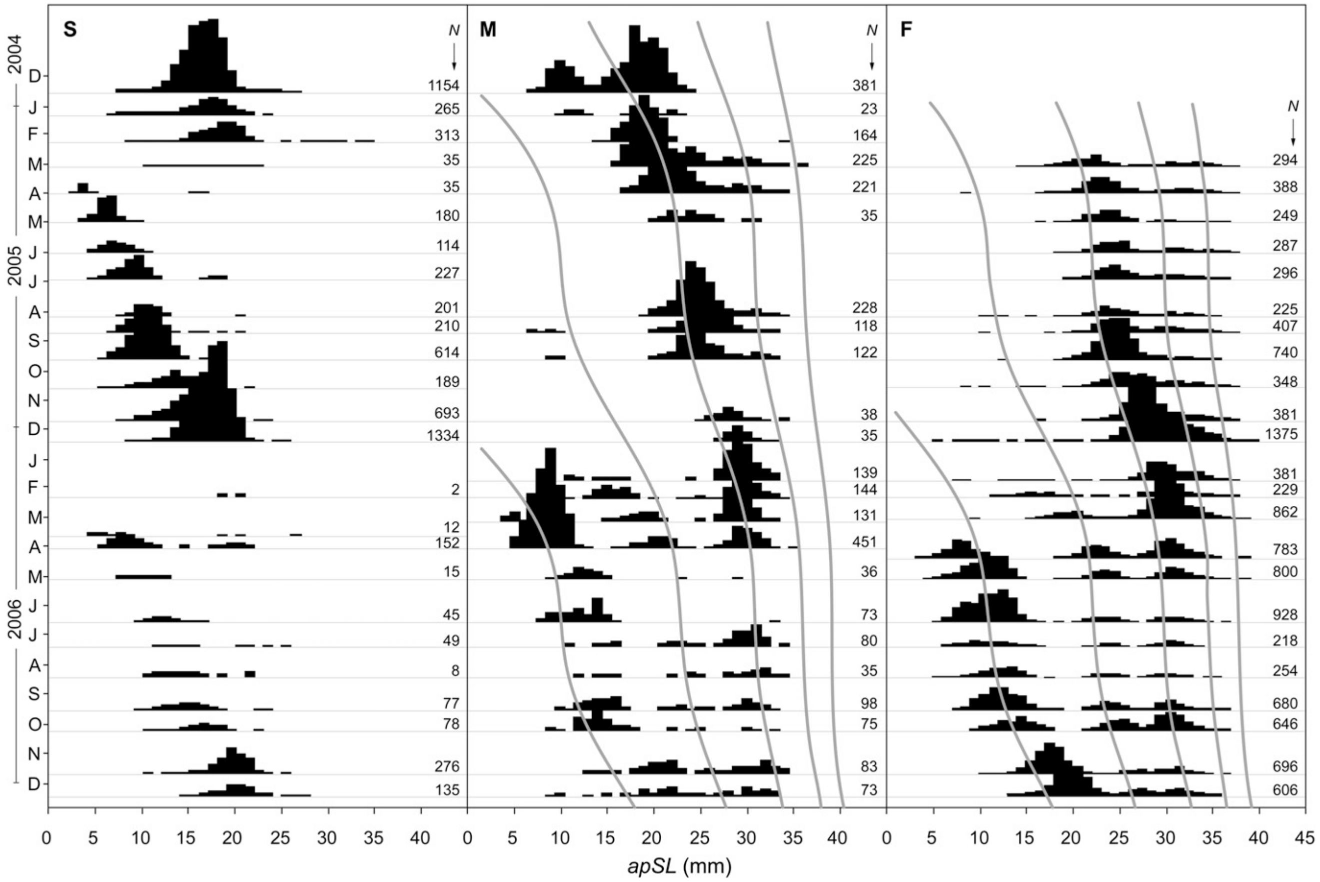

Figure 4. Growth curves (grey lines) of *D. hanleyanus* estimated with the FISAT program from monthly length-frequency data (black histograms) for the periods of December 2004 to December 2006 (M: Mar de las Pampas) and of March 2005 to December 2006 (F: Faro Querandí). Electronic length-frequency analysis was not applicable at Santa Teresita (S) because of the absence of adult individuals. Shaded parts of the histograms indicate peaks in each sample. Data set is published in Herrmann et al. (2008).

TABLE 2.

***D. hanleyanus* von Bertalanffy growth parameters: L_∞ = asymptotic length (mm), K = curvature parameter (y^{-1}), C = constant for the amplitude of seasonal oscillation of growth, WP = point of lowest growth rate (y), Rn = goodness-of-fit index, $L_{95\%}$ = length (mm) representing 95% of maximum shell length that was used to estimate t_{max} = life span (y), ϕa = standard growth index (according to Pauly & Munro 1984).**

Localities	L_∞	K	C	WP	R_n	$L_{95\%}$	t_{max}	ϕ'
Mar de las Pampas	44	0.47	0.80	0.45	0.202	40.11	4.96	2.96
Faro Querandí	44	0.48	0.80	0.45	0.350	40.62	5.18	2.97

0.04 g $AFDM$ m^{-2} yr^{-1} (2006) at Santa Teresita, of 0.17 g $AFDM$ m^{-2} yr^{-1} (both, 2005 and 2006) at Mar de las Pampas and of 1.32 g $AFDM$ m^{-2} yr^{-1} (2005) and 0.96 g $AFDM$ m^{-2} yr^{-1} (2006) at Faro Querandí (Fig. 5B-G). Individual production increased to its highest value at 30 mm length (0.16 g $AFDM$ m^{-2} yr^{-1}) and decreased thereafter (Fig. 5A). The distribution of total annual production P and the abundance among the size classes are illustrated in Figure 5B-G. Annual production ranged between 0.08 and 0.99 g $AFDM$ m^{-2} yr^{-1}, depending on beach and year, and $P/\bar{B}$ ratios were between 0.82 and 2.16.

DISCUSSION

Abiotic Factors

A clear spatial pattern of *D. hanleyanus* inhabiting dissipative to reflective beaches was revealed from monthly mean abundance data. Mean grain size of sediments is dependent on currents, the mean slope, the exposure and thus the morphodynamic type of the beach (McLachlan & Brown 2006). Therefore mean grain size integrates over the latter parameters and is therefore a suitable factor to be analyzed for physical effects on beach organisms. The nMDS analysis distinguishing two main sites (Fig. 3), A: the first area (Santa Teresita and Mar de las Pampas) is characterized by a fine to medium textural group and smaller grain size (210–370 μm, dissipative to intermediate beach morphology), and B: a second one (Faro Querandí, reflective beach morphology) by larger grain size (480 μm) and a coarse textural group (Table 1). Thus, differences in the abundance of *D. hanleyanus* (Fig. 2) may be related to the compactness of the sand: the more compacted the sand, the more difficult for adult clams to burrow and consequently they can be washed away. This hypothesis is supported by Trueman (1971) stating that *Donax* is only secure against the drag of the waves when the shell is oriented with the current and at least two thirds of the shell is buried. In conformity with our work, Penchaszadeh and Olivier (1975) already stated in the 1970s that sediment characteristics are principle factors for the distribution of *D. hanleyanus*. In accordance, Alexander et al. (1993), McLachlan et al. (1995) and Nel et al. (2001) also described substrate-sensitivity of *Donax* species, although the clams are able to penetrate into sediments with a wide spectrum of grain sizes. In addition, Guillou and Bayed (1991) observed higher abundance of *D. trunculus* in sediments with larger mean grain sizes (from 190–230 μm) and minimum abundance in sediments with smaller mean grain size (≤160 μm).

Anthropogenic Impacts

Sandy beaches such as Santa Teresita are prime sites for human recreation: especially during the holiday season, short intense anthropogenic disturbances can affect organisms at

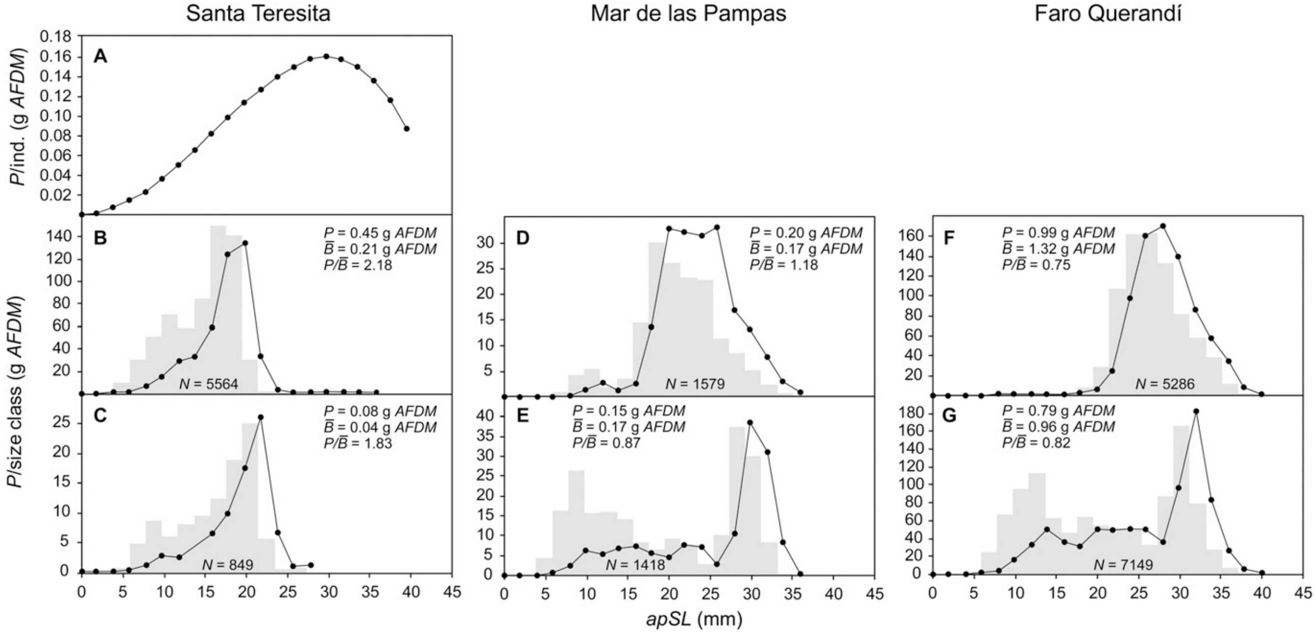

Figure 5. Distribution of annual somatic individual (A) and population production at Santa Teresita for 2005 (B) and 2006 (C), at Mar de las Pampas for 2005 (D) and 2006 (E) and at Faro Querandí for 2005 (F) and 2006 (G). Additionally the mean abundance (grey area = 100%) for the different length classes of *D. hanleyanus* is provided. Data set is published in Herrmann et al. (2008).

TABLE 3.

***D. hanleyanus* (mL, m2) in comparison with several other *Donax* species and their variation in growth performance using the von Bertalanffy growth parameter *K* (y^{-1}) and L_∞ (mm) as well as the standard growth index ϕ' and the *OGP*. Climate areas (Ca) are: tropical/subtropical (A), temperate (B) and upwelling (C) species. Code letters (L.) are equivalent to Figure 1B. Datasets are published in Herrmann et al. (2008).**

L.	Species	Country	Area	Lat.	Long.	Ca	*K*	L_∞	ϕ'	*OGP*	Source
m1	*D. hanleyanus*^{2}	Argentina	Mar de las Pampas	37°19′S	57° 00′W	B	0.47	44.00	2.96	4.60	Present study
m2	*D. hanleyanus*^{2}	Argentina	Faro Querandí	37°29′S	57° 07′W	B	0.48	44.00	2.97	4.61	Present study
m3	*D. hanleyanus*^{2}	Argentina	Villa Gesell	37°16′S	56° 59′W	B	1.18	33.50	3.12	4.65	Penchaszadeh and Olivier (1975)
m4	*D. hanleyanus*^{2}	Uruguay	Barra del Chuz	33°40′S	53° 29′W	B	0.80	33.00	2.94	4.46	Defeo (1996)
m5	*D. hanleyanus*^{2}	Brazil	Arroio Teixeira	29°38′S	49° 56′W	B	0.09	28.82	1.90	3.36	Gil and Thomé (2000)
m6	*D. hanleyanus*^{2}	Brazil	Marambaia	23°03′S	43° 34′W	B	0.80	26.40	2.75	4.17	Cardoso and Veloso (2003)
m7	*D. hanleyanus*^{2}	Brazil	Marambaia	23°03′S	43° 34′W	B	0.90	28.50	2.86	4.32	Cardoso and Veloso (2003)
j1	*D. denticulatus*^{2}	Venezuela	Araya Península	10°38′N	64° 16′W	A	0.43	18.50	2.17	3.43	Vélez et al. (1985)
j2	*D. denticulatus*^{2}	Venezuela	Playa Brava	—	—	A	1.48	31.47	3.17	4.66	García et al. (2003)
j3	*D. denticulatus*^{2}	Venezuela	La Guardia	11°00′N	64° 00′W	A	1.79	30.02	3.21	4.69	Marcano et al. (2003)
e1	*D. dentifer*^{2}	Costa Rica	Playa Garza, Puntarenas	—	—	A	0.30	46.00	2.80	4.19	Palacios et al. (1983)
e2	*D. dentifer*^{2}	Colombia	Bahía Málaga	4°05′N	77° 16′W	A	0.62	29.30	2.73	4.19	Riascos and Urban (2002)
y1	*D. cuneatus*^{2}	India	Palk Bay	9°17′N	79° 05′E	A	0.06	22.87	1.48	2.84	Nayar (1955)
y2	*D. cuneatus*^{2,5}	India	Miriya Bay, Ratnagiri	17°N	53°E	A	0.04	33.02	1.67	3.19	Talikhedkar et al. (1976)
z	*D. faba*^{2,5}	India	Gulf of Mannar	—	—	A	0.10	26.15	1.84	3.25	Alagarswami (1966)
k1	*D. striatus*^{2}	Venezuela	Tucucas, Txori	—	—	A	0.29	20.20	2.07	3.37	McLachlan et al. (1996)
k2	*D. striatus*^{2}	Brazil	Futuro Beach, Fortaleza	03°42′S	38° 27′W	A	1.16	25.10	2.86	4.26	Rocha-Barreira de Almeida et al. (2002)
w1	*D. incarnatus*^{2,5}	India	Shertallai	9°42′N	76° 20′E	A	0.09	29.04	1.86	3.33	Ansell (1972)
w2	*D. incarnatus*^{2,5}	India	Cochin	10°00′N	76° 12′E	A	0.09	25.13	1.76	3.16	Ansell (1972)
w3	*D. incarnatus*^{2,5}	India	Goa	15°22′N	73° 52′E	A	0.09	20.06	1.55	2.85	Nair et al. (1978)
w4	*D. incarnatus*^{2}	India	Panambur	12°27′N	74° 48′E	A	0.16	30.94	2.19	3.68	Thippeswamy and Joseph (1991)
f1	*D. marincovichi*^{2}	Peru	Santa Maria del Mar	12°20′S	76° 50′W	C	1.00	46.00	3.33	4.99	Arntz et al. (1987) → *before El Niño*
f2	*D. marincovichi*^{2}	Peru	Santa Maria del Mar	12°20′S	76° 50′W	C	1.17	35.00	3.16	4.70	Arntz et al. (1987) → *during El Niño*
f3	*D. marincovichi*^{2}	Peru	Santa Maria del Mar	12°20′S	76° 50′W	C	0.70	42.00	3.09	4.71	Arntz et al. (1987) → *after El Niño*
n1	*D. vittatus*^{2}	France	St. Trojan	45°50′N	1° 20′W	B	0.61	33.15	2.83	4.35	Ansell and Lagardère (1980)
n2	*D. vittatus*^{2}	France	St. Trojan	45°50′N	1° 20′W	B	1.32	29.76	3.07	4.54	Ansell and Lagardère (1980)

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TABLE 3.
continued

L.	Species	Country	Area	Lat.	Long.	Ca	*K*	L_∞	ϕ'	*OGP*	Source
n3	*D. vittatus*^{2}	France	St. Trojan	45°50′N	1°20′W	B	1.01	35.90	3.11	4.67	Ansell and Lagardère (1980)
n4	*D. vittatus*^{2}	France	Vertbois	45°50′N	1°20′W	B	1.06	31.28	3.02	4.51	Ansell and Lagardère (1980)
n5	*D. vittatus*^{2,4}	France	Bay of Douarnenez	48°05′N	4°18′W	B	0.68	38.00	2.99	4.57	Guillou and Le Moal (1980)
p1	*D. trunculus*^{2,4}	France	Vertbois	45°50′N	1°20′W	B	0.45	43.48	2.93	4.57	Ansell and Lagardère (1980)
p2	*D. trunculus*^{2,4}	France	Vertbois	45°50′N	1°20′W	B	0.70	36.33	2.97	4.53	Ansell and Lagardère (1980)
p3	*D. trunculus*^{2,4}	France	Vertbois	45°50′N	1°20′W	B	0.79	35.55	3.00	4.55	Ansell and Lagardère (1980)
p4	*D. trunculus*^{2,4}	France	Vertbois	45°50′N	1°20′W	B	0.68	32.25	2.85	4.36	Ansell and Lagardère (1980)
p5	*D. trunculus*^{2,4}	France	Vertbois	45°50′N	1°20′W	B	0.70	38.22	3.01	4.59	Ansell and Lagardère (1980)
p6	*D. trunculus*^{2,4}	France	St. Trojan	45°50′N	1°20′W	B	0.72	38.41	3.02	4.61	Ansell and Lagardère (1980)
p7	*D. trunculus*^{2,4}	France	St. Trojan	45°50′N	1°20′W	B	0.74	39.78	3.07	4.67	Ansell and Lagardère (1980)
p8	*D. trunculus*^{2,4}	France	St. Trojan	45°50′N	1°20′W	B	0.77	39.70	3.09	4.68	Ansell and Lagardère (1980)
p9	*D. trunculus*^{2}	France	Bay of Douarnenez	48°05′N	4°18′W	B	0.38	48.90	2.96	4.65	Guillou and Le Moal (1980)
p10	*D. trunculus*^{2}	France	Camarque	43°27′N	4°26′W	B	0.96	35.99	3.09	4.65	Bodoy (1982)
p11	*D. trunculus*^{2}	Spain	Atlantic	—	—	B	0.97	43.80	3.27	4.91	Fernández et al. (1984)
p12	*D. trunculus*^{2}	Spain	Atlantic, El Barquero	—	—	B	0.55	52.84	3.19	4.91	Mazé and Laborda (1988)
p13	*D. trunculus*^{2}	Spain	Mediterano, Callera	—	—	B	0.58	46.00	3.09	4.75	Ramon et al. (1995)
p14	*D. trunculus*^{3}	Spain	Mediterano, Callera	—	—	B	0.71	41.80	3.09	4.71	Ramon et al. (1995)
p15	*D. trunculus*^{2}	Portugal	Faro	36°57′N	7°53′W	B	0.58	47.30	3.11	4.79	Gaspar et al. (1999)
p16	*D. trunculus*^{2}	Italy	Apulia	41°55′N	15°26′E	B	0.30	47.56	2.83	4.51	Zeichen et al. (2002)
ü1	*D. deltoides*^{2}	Australia	Goolwa	—	—	B	0.86	59.00	3.48	5.25	King (1985)
ü2	*D. deltoides*^{2}	Australia	New South Wales	36°S	151°E	B	1.59	56.00	3.70	5.45	Laudien et al. (2003)
t1	*D. serra*^{2}	South Africa	Elands Bay	32°19′S	18°21′E	C	0.28	82.00	3.28	5.19	de Villiers (1975)
t2	*D. serra*^{2}	South Africa	Elands Bay	32°19′S	18°21′E	C	0.43	75.00	3.39	5.26	de Villiers (1975)
t3	*D. serra*^{2}	South Africa	Melkbosstrand	33°42′S	18°26′E	C	0.28	82.00	3.27	5.18	de Villiers (1975)
t4	*D. serra*^{2}	South Africa	Melkbosstrand	33°42′S	18°26′E	C	0.32	78.00	3.29	5.19	de Villiers (1975)
t5	*D. serra*^{2}	South Africa	Elands Bay	32°19′S	18°21′E	C	0.46	79.00	3.46	5.36	Laudien et al. (2003)
t6	*D. serra*^{2}	South Africa	Koeberg	33°40′S	18°25′E	C	0.47	85.00	3.53	5.46	Laudien et al. (2003)
t7	*D. serra*^{2}	South Africa	St Francis Bay	33°59′S	25°20′E	C	0.60	76.00	3.54	5.42	Laudien et al. (2003)

Continued on next page

TABLE 3.

continued

L.	Species	Country	Area	Lat.	Long.	Ca	*K*	*L*∞	*ϕ′*	*OGP*	Source
t8	*D. serra*[2]	South Africa	St Francis Bay	33°57′S	25°04′E	C	0.65	67.00	3.47	5.29	Laudien et al. (2003)
t9	*D. serra*[2]	South Africa	Langestrand	22°47′S	14°33′E	C	0.27	82.00	3.27	5.18	Laudien et al. (2003)
t10	*D. serra*[2]	South Africa	Paaltjies	22°59′S	14°24′E	C	0.47	78.00	3.46	5.32	Laudien et al. (2003)

[1] Maximum length.
[2] Age estimated from length-frequency distributions.
[3] Age estimated from hyaline growth rings.
[4] Age estimated from external growth rings.
[5] Values calculated on monthly basis from raw data reported by the authors.

several biological scales, ranging from biogeochemistry and physiology up to the community level. Chandrasekara and Frid (1996) reported that human trampling changes the saltmarsh benthic fauna of the English coast. Schlacher and Thompson (2008) described a modification of the physical environment of two Australian sandy beaches and van der Merwe and van der Merwe (1991) found a negative effect on two intertidal *Donax* species in South Africa, both caused by off-road driving. In a Dutch intertidal mudflat, trampling affected the abundance and population dynamics of the clam *Macoma balthica* and the cockle *Cerastoderma edule* (Rossi et al. 2007). The authors assume that footsteps directly kill or bury specimens, provoking asphyxia. On Argentinean shores it is evident that human activities and urbanization in coastal areas affect the presence and abundance of *D. hanleyanus* (Marcomini et al. 2002). Some authors (Bastida et al. 1996, Dadon 2005) assume that human activities are probably one of the main factors interfering with the recovery of bivalve populations. The abrupt decrease of the *D. hanleyanus* population during summer especially at Santa Teresita (arrows in Fig. 2S) is significantly related to mass tourism. Up to one million tourists (Secretaría de Turismo, Mar del Tuyú, Argentina) visit the coast of Buenos Aires during each holiday season (Fig. 2B) and disturb the intertidal zone by intensive trampling. Therefore we argue that anthropogenic impact is one of the main causes of strong reductions in *D. hanleyanus* abundance at Santa Teresita. Further research should therefore focus on human activities as an important abundance oppressing factor.

Growth

The von Bertalanffy growth constant *K* varied insignificantly between 0.47 yr^{-1} (Mar de las Pampas) and 0.48 yr^{-1} (Faro Querandí). During the first two years of life, differences of growth parameters become obvious by comparing the present values (Table 3, values m1, m2) with those of Penchaszadeh and Olivier (1975) (Table 3, value m3). Forty years ago populations of *D. hanleyanus* grew faster within the first two years ($K = 1.18$) compared with those presently studied ($K = 0.48$), but reached a smaller maximal length (33.5 mm) (presently 44.0 mm). This difference in growth may be caused by a relaxed competition with the co-occurring *M. mactroides* population (Table 3, Fig. 8, see later). Thus, growth of *D. hanleyanus* apparently depends on this competition. Other studies have also demonstrated abundance-dependent growth for various bivalves (Broom 1982, Peterson 1982, Peterson & Black 1987, Peterson & Black 1988, Peterson & Beal 1989, Jensen 1993, Defeo & de Alava 1995, Weinberg 1998, Talman & Keough 2001).

Non-linear growth functions, such as the *VBGF*, are difficult to compare, whereas several authors (e.g., Pauly 1979, Munro & Pauly 1983, Moreau et al. 1986) demonstrated the suitability of the *OGP* index for inter and intraspecific comparisons. The *OGP* of the *D. hanleyanus* studied (4.60 at Mar de las Pampas and 4.61 at Faro Querandí) conforms well, with values calculated from data sets of the same species from the Brazilian (4.17 and 4.32: Cardoso & Veloso 2003), Uruguayan (4.46: Defeo 1996) and Argentinean coast (4.65: Penchaszadeh & Olivier 1975). *OGP* values (Fig. 6) from Uruguay (m4) and Brazil (m5–m7) are conspicuously lower than those from Argentina (m1-m3), which may be caused by the lower mean *SST*. This trend provides support to the latitudinal gradient hypothesis (*LGH*)

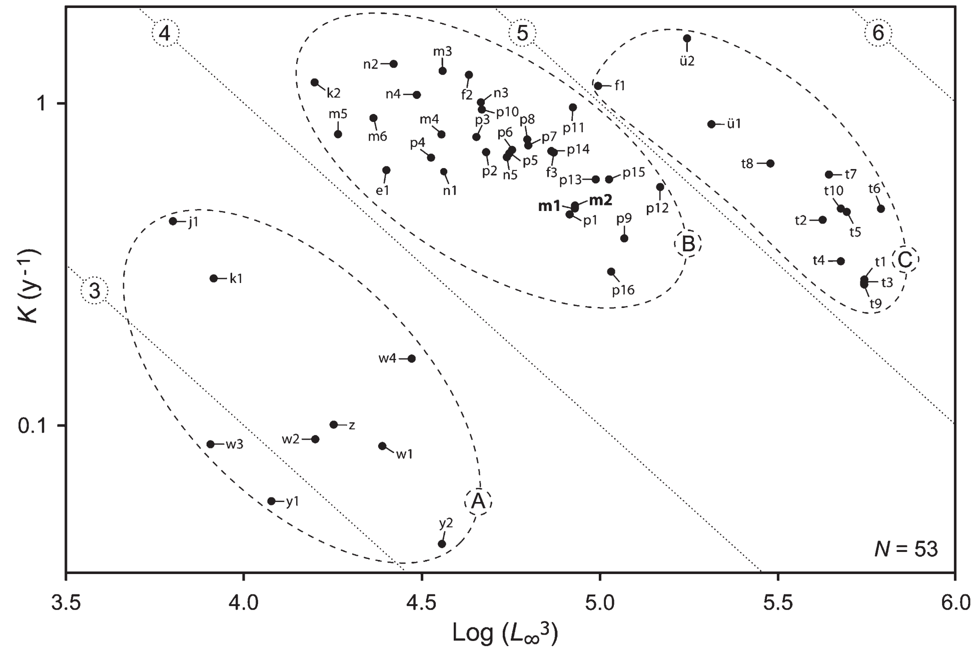

Figure 6. Auximetric grid (extended and corrected from Laudien et al. 2003) comparing *OGP* of the Argentinean *D. hanleyanus* (m1 and m2) with several Donacidae from other areas. Plot indicates three groups (dashed lines): tropical/subtropical (A), temperate (B) and upwelling species (C). Diagonal dotted lines indicate equal values of *OGP* (numbers in circles). For keys and data sources see Table 3; for the distribution of the plotted *Donax* species see Fig. 1B. Stitches at data points in the grid are not representing any value; they only serve as help for labeling. Data set is published in Herrmann et al. (2008).

postulated by Defeo and Cardoso (2002), which predicts a positive correlation between body size of species and latitude. Thus, subtropical beaches exhibit higher growth and mortality rates and shorter life spans than temperate beaches. However, the *LGH* cannot be generalized for invertebrates, because there are different, sometimes opposing, results for different taxa (cf. Schilder 1956, Jones & Simons 1983, Henmi 1993, Barnes & Arnold 2001, Hausdorf 2003, Clarke et al. 2004). The present data compilation from several studies confirmed the hypothesis of Laudien et al. (2003) that the *OGP* is habitat-specific (Fig. 6): species populating tropical/subtropical regions show the lowest *OGP* (2.84–3.68, group A), temperate species have intermittent *OGP* (4.17–4.91, group B), whereas species of upwelling areas show the highest *OGP* (5.06–5.65, group C). Even the effect of climate anomalies may be detected with the help of the auximetric grid, as indicated by the upwelling surf clam *D. marincovichi* sampled in Peru during and shortly after an El Niño event 1982 and1983 (Fig. 6, values f2, f3) in comparison with the population sampled during normal upwelling years (Fig. 6, value f1) (Arntz et al. 1987). With an *OGP* of 3.36, calculated from Gil and Thomé (2000), the Brazilian *D. hanleyanus* seems to be an exception (Fig. 6, value m5). Whereas all other computed *OGP* values for *D. hanleyanus* show that this is a temperate species, population parameters of the latter study classify this species as tropical/subtropical.

A few *OGP* values calculated from tropical/subtropical regions deflect from the model of the auximetric grid (Fig. 6), namely the growth performance of *D. dentifer* (e1: Palacios et al. 1983, e2: Riascos & Urban 2002), *D. denticulatus* (j2: García et al. 2003, j3: Marcano et al. 2003), and *D. striatus* (k2: Rocha-Barreira de Almeida et al. 2002), classifying these species as temperate. Sparre and Venema (1997) state that growth estimates, based only on length-frequency data, may not always be useful for tropical species with several recruitment events through the year.

Life Span

Most *Donax* species have a relatively short life span of 1–2 y (McLachlan 1979, Ansell 1983). Whereas Penchaszadeh and Olivier (1975) estimated a longevity of *D. hanleyanus* from the Argentinean coast of three years with a maximal length of 33 mm, the recent study indicates an even longer life span of approximately five years (maximal length of 44 mm) for the same species and region. In contrast to our estimation, Cardoso and Veloso (2003) noted for Brazilian *D. hanleyanus* only 1.5 y as the maximal life period. Similarly shorter maximal life spans were reported for various *Donax* species from temperate areas, such as *D. vittatus* (3.5 y) from the French coast (Ansell & Lagardère 1980) or *D. deltoides* (3.5 y) from South Australia (for data source see at Laudien et al. 2003). The recent value is however in accordance with *D. trunculus* from France (6 y, Guillou & Le Moal 1980, Guillou 1982) and *D. serra* (>5 y, de Villiers 1975) from South Africa. Lower values of longevity were reported for tropical/subtropical *Donax* species, *D. faba* and *D. cuneatus* from India probably does not reach 3 y (McLachlan et al. 1996) and *D. striatus* (McLachlan et al. 1996) and *D. denticulatus* (Vélez et al. 1985) from Venezuela have a life span of only approximately 1.5 y. The analysis suggests a longer life span of temperate *Donax* species compared with tropical/subtropical *Donax* species (climate areas of *Donax* species are compared in Table 3 and Figure 6).

Biomass and Production

The intertidal biomass of the *D. hanleyanus* population ranged between 0.04 and 1.32 g *AFDM* m^{-2} yr^{-1} (Fig. 5). These

TABLE 4.

Secondary production (P, g $AFDM$ $m^{-2}y^{-1}$), biomass ($\bar{B}$, g $AFDM$ m^{-2}) and renewal rate ($P/\bar{B}$) of *D. hanleyanus* at Santa Teresita (m1, m2), Mar del las Pampas (m3, m4) and Faro Querandí (m5, m6) between 2005 and 2006 in comparison with several *Donax* species from different geographical regions. Table modified from (Cardoso & Veloso 2003). Code letters (L.) are equivalent to Figure 1B and were used for visualizing the relationship between the production-to-biomass ($P/\bar{B}$) ratio and latitude in Figure 7. Datasets are published in Herrmann et al. (2008).

L	Species	P	$\bar{B}$	$P/\bar{B}$	Lat.	Long.	Source
m1	*D. hanleyanus*	0.45	0.21	2.18	36°32′S	56°41′W	Present study (Santa Teresita 2005)
m2	*D. hanleyanus*	0.08	0.04	1.83	36°32′S	56°41′W	Present study (Santa Teresita 2006)
m3	*D. hanleyanus*	0.20	0.17	1.18	37°19′S	57°00′W	Present study (Mar de las Pampas 2005)
m4	*D. hanleyanus*	0.15	0.17	0.87	37°19′S	57°00′W	Present study (Mar de las Pampas 2006)
m5	*D. hanleyanus*	0.99	1.32	0.75	37°29′S	57°07′W	Present study (Faro Querandí 2005)
m6	*D. hanleyanus*	0.79	0.96	0.82	37°29′S	57°07′W	Present study (Faro Querandí 2006)
m7	*D. hanleyanus*	0.76	0.48	1.59	23°03′S	43°34′W	Cardoso and Veloso (2003)
m8	*D. hanleyanus*	3.67	2.53	1.45	23°03′S	43°34′W	Cardoso and Veloso (2003)
t1	*D. serra*	356.60	288.80	1.20	22°47′S	14°33′E	Laudien et al. (2003)
t2	*D. serra*	273.20	171.90	1.60	22°47′S	14°33′E	Laudien et al. (2003)
t3	*D. serra*	637.30	545.90	1.20	22°59′S	14°24′E	Laudien et al. (2003)
t4	*D. serra*	166.90	141.20	1.20	22°59′S	14°24′E	Laudien et al. (2003)
u1	*D. sordidus*[1]	0.38	0.21	1.78	33°57′S	25°40′E	McLachlan and van der Horst (1979)
u2	*D. sordidus*[1]	0.15	0.10	1.56	33°57′S	25°40′E	McLachlan (1979)
u3	*D. sordidus*[1]	0.13	0.12	1.03	33°57′S	25°40′E	McLachlan (1979)
i	*D. variabilis*[1]	1.96	0.26	7.64	33°41′S	78°53′W	Wilson (1999)
j	*D. denticulatus* [1,2]	31.39	—	5.84	10° 8′N	64°16′W	Vélez et al. (1985)
p1	*D. trunculus*[1]	18.98	15.42	1.23	45°50′N	1°20′W	Ansell and Lagardère (1980)
p2	*D. trunculus*[1]	39.99	39.35	1.02	45°50′N	1°20′W	Ansell and Lagardère (1980)
n1	*D. vittatus*[1]	12.33	7.66	1.61	45°50′N	1°20′W	Ansell and Lagardère (1980)
n2	*D. vittatus*[1]	17.33	10.43	1.66	45°50′N	1°20′W	Ansell and Lagardère (1980)
n3	*D. vittatus*[1]	0.60	0.29	2.10	51°41′N	4°28′W	Warwick et al. (1978)
w	*D. incarnatus*[1]	1.08	0.18	5.88	9°42′N	76°20′E	Ansell et al. (1978)
x	*D. spiculum*[1]	0.87	0.08	10.29	9°42′N	76°20′E	Ansell et al. (1978)

[1] Transformed values (g $AFDM$ m^{-2} yr^{-1}) by Ricciardi and Bourget (1998).

[2] Maximum daily value (0.016 g $AFDM$ d^{-1} × 365 days).

values are in accordance with biomass data of *Donax* species from other temperate and tropical/subtropical areas (Ansell et al. 1978, Warwick et al. 1978, McLachlan 1979, McLachlan & van der Horst 1979, Wilson 1999). However, these values are in contrast to biomasses from upwelling systems (Laudien et al. 2003), which can be three orders of magnitude higher than the present values (Table 4). Four decades ago *D. hanleyanus* reached a biomass of 7.5 g $AFDM$ $m^{-2}yr^{-1}$(calculated from Penchaszadeh & Olivier 1975), which is approximately seven times higher than recent values.

Annual intertidal production of *D. hanleyanus* ranged between 0.08 and 0.99 g $AFDM$ $m^{-2}yr^{-1}$ (Table 4, Fig. 5) and is therefore within the span (0.79–3.67 g $AFDM$ $m^{-2}yr^{-1}$) observed by Cardoso and Veloso (2003), but lower than that recorded by Gianuca (1985) (13.56 g $AFDM$ $m^{-2}yr^{-1}$). By comparing production, biomass and renewal rate among different *Donax* species from several geographical regions (Table 4, Fig. 7), it is evident that the renewal rates ($P/\bar{B}$) increase from temperate to tropical regions, which was also observed for several other donacids (Ansell et al. 1978, Kalejta & Hockey 1991, Cardoso & Veloso 2003).

Clam Interaction

Presently *D. hanleyanus* numerically dominates the community at Santa Teresita. The sympatric yellow clam *M. mactroides* has been known to co-occur with *D. hanleyanus* populations since the seventies (Olivier et al. 1971, Penchaszadeh & Olivier 1975). However, *M. mactroides* was only abundant at Santa Teresita (mean annual abundance [mean ± SE] of 47 ± 13 ind.

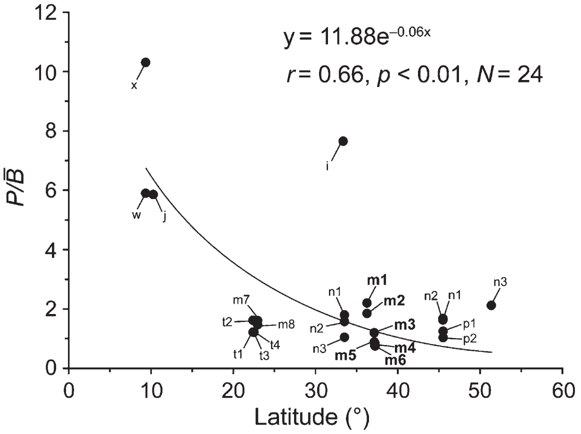

Figure 7. Relationship between the renewal rate ($P/\bar{B}$ ratios) and latitude of *D. hanleyanus* from the present study (m1–m6) in comparison with several *Donax* species. For keys and data sources see Table 4. For the distribution of the mapped *Donax* species see Figure 1B. Data set is published in Herrmann et al. (2008).

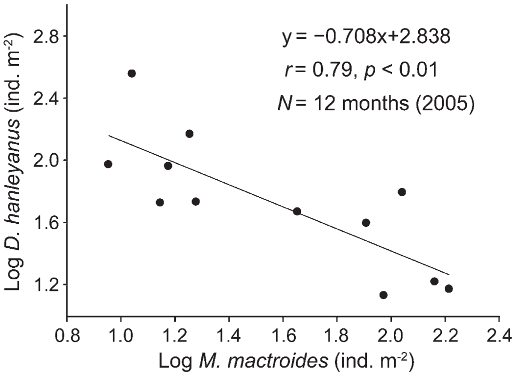

Figure 8. *D. hanleyanus - M. mactroides* linear correlation of the abundance (Log ind. m^{-2}) in 2005 at Santa Teresita. Data set is published in Herrmann et al. (2008).

m^{-2} in 2005 and 29 ±3 ind. m^{-2} in 2006); in Mar de las Pampas and in Faro Querandí no more than single individuals were found during the whole sampling period (Herrmann 2009). In contrast, Olivier et al. (1971) found a mean abundance of 538 ind. m^{-2} in a sampling section including Santa Teresita and 629 ind. m^{-2} in a sampling section including Mar de las Pampas and Faro Querandí in 1968–1970. A significant negative correlation between abundances of these two suspension-feeders (Fig. 8) suggests that abundance peaks of *D. hanleyanus* are related with population crashes of *M. mactroides*. Penchaszadeh and Olivier (1975), Dadon (2005) as well as Defeo and de Alava (1995) observed similar inverse correlations between abundances of *D. hanleyanus* and *M. mactroides* from Argentinean and Uruguayan beaches. In agreement, surf clam populations from the Peruvian Pacific coast revealed the same relations; *D. marincovichi* (formerly called *D. peruvianus*) increased coincidentally with the collapse of *M. donacium* (Penchaszadeh 1971, Tarazona et al. 1985, Arntz et al. 1987). Defeo and de Alava (1995) hypothesized that interspecific competition may be the cause and Olivier et al. (1971) provided evidence by describing overlapping trophic niches of the two clams.

CONCLUSION

In conclusion, lowest abundance of *D. hanleyanus* was observed at intermediate to dissipative beaches (Mar de las Pampas and Santa Teresita) composed of finer sediment. The present results confirm that the abundance of *D. hanleyanus* is influenced by sand grain size. Highest abundance was recorded at the reflective beach Faro Querandí characterized by coarse sediment. Decrease in *D. hanleyanus* abundance during the holiday season at Santa Teresita was significantly related to human trampling (mass tourism). *D. hanleyanus* abundance was negatively correlated with *M. mactroides* abundance, but was not significantly influenced by *SST*. In comparison with a 40-year-old data set, growth of *D. hanleyanus* is now slower, but specimens reach a larger maximal length and have a longer life span. The *OGP* index of *D. hanleyanus* conforms well to values calculated from several *Donax* species of other areas. Thus, as expected, the Argentinean wedge clam *D. hanleyanus* is classified into the temperate group of Donacidae on an auximetric grid. Presently the intertidal biomass of *D. hanleyanus* is seven times lower compared with data from the 1970s. Thus, without a sustainable management the conservation status of *D. hanleyanus* is endangered.

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