



# Population structure, growth and production of the surf clam *Donax serra* (Bivalvia, Donacidae) on two Namibian sandy beaches

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## Abstract

Population structure, growth and production of the surf clam *Donax serra* (Bivalvia, Donacidae), inhabiting highly exposed sandy beaches of Namibia, were investigated between November 1997 and December 1999. From length–frequency distribution and tagging–recapture data, a von Bertalanffy growth function with an asymptotic length ( $L_{\infty}$ ) of 82 mm and a growth constant ( $K$ ) of  $0.274 \text{ yr}^{-1}$  was established. Regarding growth performance of Donacidae, *D. serra* fits in a group of species inhabiting cold temperate and upwelling regions. The intertidal biomass of the studied population ranged between 141 and 546 g ash-free dry mass (AFDM)  $\text{m}^{-2} \text{ yr}^{-1}$ . Individual production was maximal at 56.5 mm shell length ( $0.83 \text{ g AFDM ind.}^{-1} \text{ yr}^{-1}$ ), and annual production ranged between 167 and 637 g AFDM  $\text{m}^{-2} \text{ yr}^{-1}$ , resulting in productivity values ( $P/\bar{B}$ ) between 1.167 and  $1.589 \text{ yr}^{-1}$ . These data underline the importance of *D. serra* for the beach/surf ecosystem. Further, the findings of this study are crucial to support future aquaculture or exploitation activities and management.

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## 1. Introduction

Bivalves of the family Donacidae inhabit exposed intertidal sandy beaches and form worldwide, by far, the largest group living in such highly dynamic environments (for review, see Ansell, 1983). Members of the genus *Donax* are commonly the main primary consumers in soft bottom communities, while they are in turn subject to predation by a wide variety of invertebrates, fish, birds and mammals (e.g. Luzzatto & Penchaszadeh, 2001; Peterson, Hickerson, & Johnson, 2000; Salas, Tirado, & Manjon-Cabeza, 2001). Moreover, these clams are important recreational and commercial resources in many countries (McLachlan et al., 1996). Although the abundance is limited by their specialisation to coastal high-energy habitats, *Donax* species show a

strong adaptive radiation with tidal migration as a common feature. Notwithstanding Ansell's (1983) assertion that donacids are restricted to distinct zoogeographical domains, some species inhabit regions with an overlap of subtropical and temperate zones. Only 5% of the 64 species are found in cold temperate areas ( $>5^{\circ}\text{C}$ ; Bally, 1986), with lowest species diversity on the West Coast of Africa (Ansell, 1983).

The largest-sized donacid *Donax serra* (Röding, 1798) inhabits the macrozoobenthic community of extended exposed sandy beaches along the Namibian coast and forms dense beds (Donn & Cockcroft, 1989; McLachlan, 1996). As the surf clam *D. serra* feeds on phytoplankton and detritus and is consumed by birds, fish and crabs, it is an important trophic link in surf zone food webs (McLachlan et al., 1996; McLachlan, Wooldridge, Schramm, & Kühn, 1980; Rossouw, 1985; J. Laudien, unpublished data). Furthermore, it is exploited for angling bait, and is of potential value for human consumption. Sims-Castley and Hosking (submitted for publication) calculated a possible price range of

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US\$6.50–60.00 per kg for export markets. Despite its significant ecological role and potential commercial value, few aspects of the population dynamics of the cold temperate Namibian stocks have been investigated, e.g. the reproductive biology (Laudien, Brey, & Arntz, 2001). Growth rates and population structure were studied elsewhere in southern Africa (Donn, 1986; Schoeman, 1994; de Villiers, 1975), but these results cannot simply be transferred to Namibian populations, since it was reported that populations from the south-east and West Coast of southern Africa differ in behaviour and morphometrics (Donn, 1990; Laudien, Flint, van der Bank, & Brey, 2003; Soares, Callahan, & de Ruyck, 1998). Further, genetic differentiation exists between Namibian subpopulations (Laudien et al., 2003). Thus, knowledge of growth parameters and production are essential for the understanding of the ecology and productivity of *D. serra* inhabiting sandy bottoms of the central Benguela upwelling region.

Further, it is crucial to support future aquaculture or exploitation activities and management.

## 2. Material and methods

### 2.1. Study site and sampling

*Donax serra* were collected during alternate spring tides from two Namibian sandy beaches (Fig. 1), Langstrand (22°47'S, 14°33'E) and Paaltjies IV (22°59'S, 14°24'E). According to McLachlan's (1980) rating scale for exposure, Paaltjies IV can be characterised as very exposed and reflective (15.5, mean slope 1/24) and Langstrand as exposed and of an intermediate type (13, mean slope 1/10), being partly recessed behind the sand peninsula Pelican Point (Fig. 1). Both are open ocean beaches receiving continuous wave action. The area is subject to subequal semidiurnal tides, with a

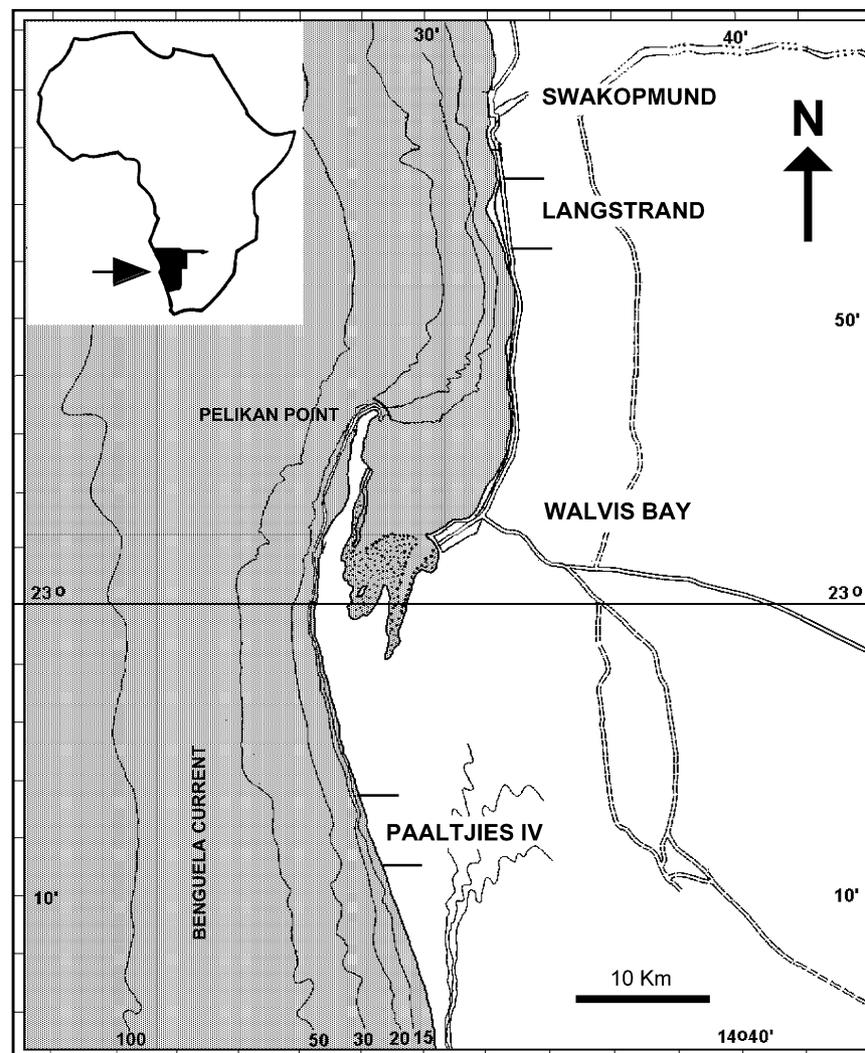


Fig. 1. Map of the study sites 'Langstrand' and 'Paaltjies IV'.

maximum tide range of 2 m; spring tides average 1.4 m and neap tides 0.7 m. The sea surface temperature varies between 11 °C in winter and 23 °C in summer. Both beaches are composed of well-sorted medium sand, with mean particle diameters ranging at Langstrand between 254 µm (low shore) and 291 µm (mid-shore) and at Paaltjies IV, between 398 µm (low shore) and 255 µm (mid-shore), respectively. There is no freshwater seepage at either beach, thus salinity is 35. Both beaches are well drained and oxygenated. McLachlan (1985) gives a summary including additional features of both beaches.

*Donax serra* were sampled quantitatively at monthly intervals (Langstrand: November 1997 to November 1999; Paaltjies IV: November 1997 to December 1999) from a series of stations (2 m intervals) along a transect transverse to the shoreline, from the spring tide high water mark to the subtidal of 1 m water depth. At each station, three replicates of a 0.16 m<sup>2</sup> sand sample were excavated to 35 cm depth using a stirring box, and the sand was sieved on a 1-mm screen. All surf clams were transferred to the laboratory immediately for further investigation. The anterior–posterior length of each individual was measured to the lower 0.1 mm with vernier callipers. In total, 13,298 clams were measured at Langstrand and 16,305 at Paaltjies IV. Parameters of the relationship between length and mass of *D. serra* were estimated by regression analysis

$$M = aL^b \quad (1)$$

where *M* is the ash-free dry mass, AFDM (g), obtained by ignition of soft tissue at 550 °C for 7 h, *L* the shell length (mm) and *a* and *b* are the constants. AFDM was determined for 400 specimens of all size classes between January and December 1998. For comparisons, all published values were converted to AFDM according to Brey, Rumohr, and Ankar (1988).

## 2.2. Growth

### 2.2.1. External and internal shell marks

Dark lines at the anterior end of the valves of *Donax serra* (Fig. 2) were counted macroscopically. Microstructural shell deposits commonly reflect tidal, daily or seasonal growth increments and vary consistently in width according to exposure time and temperature (e.g. Gaspar, Ferreira, & Monteiro, 1999; Richardson, 1989). Therefore, internal shell marks may be suitable for growth analyses. Twenty embedded right valves (between 56 and 82 mm; resin: Metset, Type SW, Buehler 95-B130007) were analysed according to Richardson, Crisp and Runham (1979). Plane sections along the axis of maximum growth were prepared and thereafter grounded on wet grinding paper (P120 followed by P1200). Sections were polished (Mecapol 200 with Meraprex 3 µm; PRESI, France) and etched in 0.5%

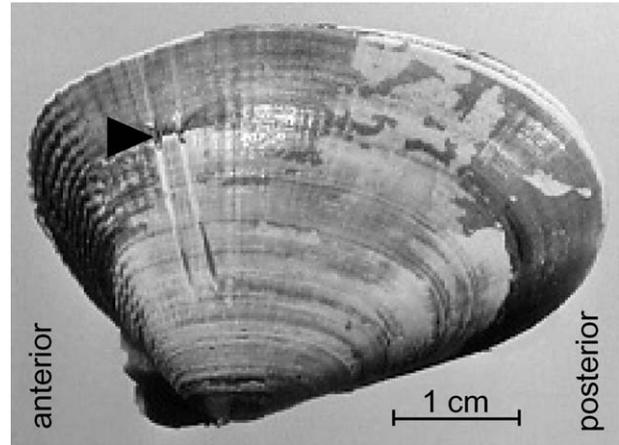


Fig. 2. Right valve of *Donax serra* recovered on 13 June 1999, 6 months after marking and release. The notch marks (arrow) and growth thereafter show clearly at the valve margin. Estimated growth was 17.6 mm. Additionally, typical dark lines at the anterior edge of the valve can be observed.

DE-CAL™ (National Diagnostics, Atlanta, GA) for 1 min. Acetate peel replicas were prepared according to Richardson et al. (1979) and examined under a transmitted light microscope (e.g. Gaspar et al., 1999; Richardson, 1989).

### 2.2.2. Tagging–recapture experiments

Individuals (7215) of *Donax serra* covering the whole size range were collected at Paaltjies IV on three consecutive new moon spring tides in December 1998, January and February 1999. The animals were transported to the laboratory while burrowed in wet sand. Two carborundum discs, 0.7 mm thick, spaced 2 mm apart and mounted in the mandrel of an electric grinder, were used to produce distinct parallel, shallow grooves from the ventral margin up onto the valve surface (e.g. Ropes, 1984; Ropes & Merrill, 1970). The marked clams were released at Paaltjies IV within a rectangular area (7 × 5 m). Each individual was put into a 15 cm deep hole and covered with sediment in order to prevent the clams being carried away by the strong swash. The recapture length and the length at the time of release reflected in a disturbance ring following the notch marks (Fig. 2) were measured. The obtained size increments were used for the estimation of growth parameters (see the subsequent discussion).

### 2.2.3. Length–frequency distribution and analyses

A series of 25 (Langstrand) and 24 (Paaltjies IV) length–frequency distributions (2 mm size classes, monthly) were determined. Electronic length–frequency analysis (ELEFAN; Gayanilo, Soriano, & Pauly, 1989; Pauly & David, 1981) was not applicable in the present analysis, as it is currently not capable of simultaneously estimating more than one annual growth curve (e.g. Schoeman, personal communication). Cohorts were identified visually, and mean individual length in each

identified cohort was computed by the weighted average

$$L_{\text{mean}_{c,t}} = \frac{(L_{j-1}N_j) + (L_jN_j) + (L_{j+1}N_{j+1})}{N_{j-1} + N_j + N_{j+1}} \quad (2)$$

where  $N_j$  and  $L_j$  are the number of specimens and mid-length of size class  $j$ , respectively,  $j$  the size class with the highest number of individuals and  $c$  and  $t$  are the indices of cohort and month, respectively.

Growth was described by the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938)

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (3)$$

where  $L_t$  is the length at age  $t$ ,  $L_\infty$  the asymptotic length (mm),  $t$  the age (yr) and  $t_0$  is the age at zero length. A rearranged form of the VBGF

$$L_2 = L_1 + (L_\infty - L_1)(1 - e^{-K(t_2-t_1)}) \quad (4)$$

was fitted to size-increment data (length  $L_1$  at  $t_1$  and  $L_2$  at  $t_2$ ) obtained from length–frequency and tagging–recapture data using the non-linear Newton algorithm.

Non-linear functions are sensitive to missing data at either end of the distribution (Pauly, 1983; Wetherall, Polovina, & Ralson, 1987). As the Langstrand population is exploited and the centre of adult individual distribution is subtidal, larger animals are poorly represented and our samples and data lack size-increment data referring to larger individuals. Therefore, the parameter  $L_\infty$  was not determined iteratively, but set to 82 mm according to the maximum length observed.

### 2.3. Production

Total annual production (January–December 1998 and January–December 1999) was calculated for the intertidal *Donax serra* belt of both beaches by the mass-specific growth rate method (Brey, 2001; Crisp, 1984) from the size–mass relation, the size–frequency distribution obtained from all pooled samples and the VBGF

$$P = \sum N_i M_i G_i \quad (\text{g AFDM m}^{-2} \text{yr}^{-1}) \quad (5)$$

$N_i$  and  $M_i$  are the average number of animals (number per  $\text{m}^2$ ) and mean individual AFDM in length class  $i$ , respectively, and  $G_i$  is the mass-specific growth rate

$$G_i = bK((L_\infty/L_i) - 1) \quad (\text{yr}^{-1}) \quad (6)$$

where  $b$  is the exponent of the size–mass relation,  $K$ ,  $L_\infty$  are VBGF parameters and  $L_i$  is the mean size in class  $i$ .

Mean annual biomass was computed by

$$\bar{B} = \sum N_i M_i \quad (\text{g AFDM m}^{-2}) \quad (7)$$

and annual  $P/\bar{B}$  ratios of the *Donax serra* populations were calculated from annual total production  $P$  and annual mean biomass  $\bar{B}$ .

## 3. Results

### 3.1. Growth

#### 3.1.1. External and internal shell marks

The number of macroscopic shell marks at the anterior end of the valves was linearly correlated with shell length ( $y = 0.5x + 4.6$ ,  $r^2 = 0.93$ ,  $n = 30$ ). The analyses of microgrowth structures revealed a fine meandric growth line pattern in the outer of three shell layers (outer prismatic, middle crossed lamellar and inner homogeneous/complex crossed lamellar layer) (Fig. 3). The microstructural deposit pattern was neither detectable as discreet increments throughout the shell nor did it show consistent cycles as to be expected from tidal, lunar or annual rhythms.

#### 3.1.2. Length–frequency distribution and tagging–recapture data

New cohorts were detected at Langstrand in December 1997, September 1998, May 1999 and August 1999. In 1997, two additional cohorts were evident: September/October (extrapolated) and around April (D. Louw, unpublished data). At Paaltjies IV, one single new cohort was observed during both years in March. Defined cohorts could be tracked up to 13 months resulting in 72 size-increment data pairs (Langstrand 45 pairs, Paaltjies IV 27 pairs; Fig. 4). During the first year of life, a mean length of 35 mm was reached at both beaches. Only 11 (0.15%) of the 7215 marked *Donax serra* were recaptured. A common VBGF with a growth constant  $K = 0.274 \text{ yr}^{-1}$  and fixed  $L_\infty = 82 \text{ mm}$  was fitted to the combined data set ( $r^2 = 0.97$ ; Fig. 5), as the comparison of residuals from size-increment and tagging–recapture data of both populations and among each other revealed no significant differences.

### 3.2. Biomass and production

Mean annual clam abundance at Langstrand was  $96.4 \text{ ind. m}^{-2}$  (1998) and  $95.5 \text{ ind. m}^{-2}$  (1999) and at

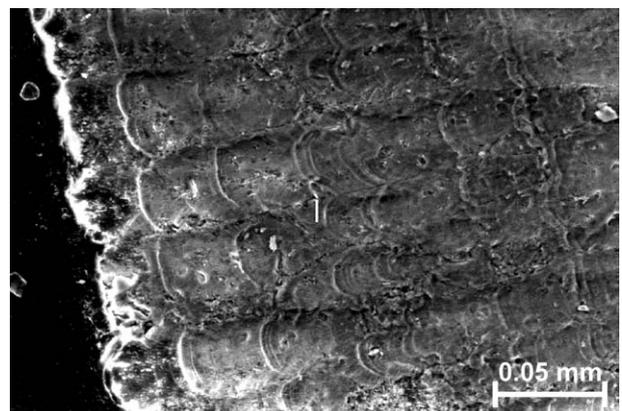


Fig. 3. REM picture of a sectioned valve showing microgrowth bands.

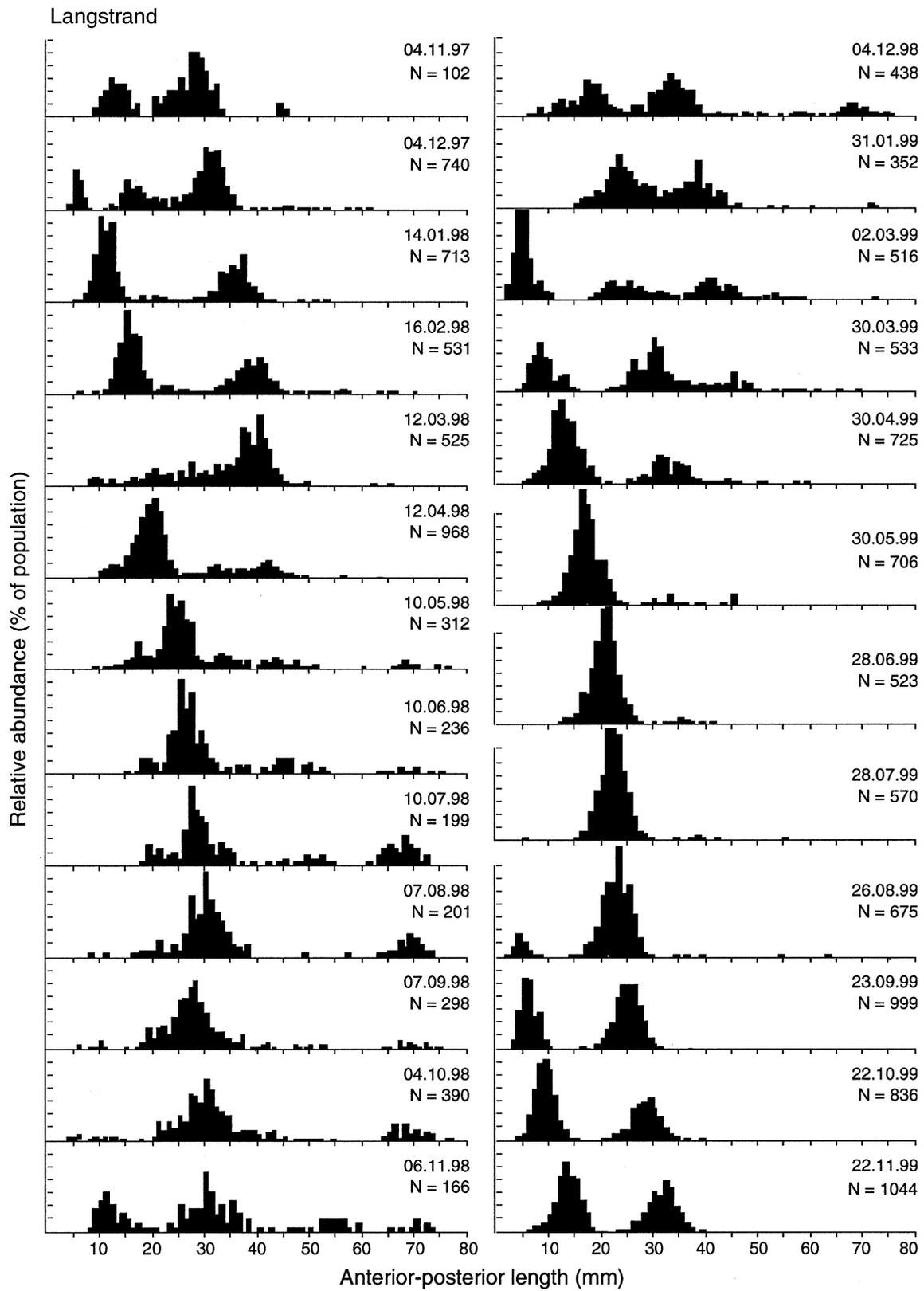


Fig. 4. Monthly length–frequency distribution of *Donax serra* collected (a) at Langstrand (November 1997 to November 1999) and (b) at Paaltjies (November 1997 to December 1999, except April 1999). Each scale unit on the y-axis is equivalent to 2% of population.

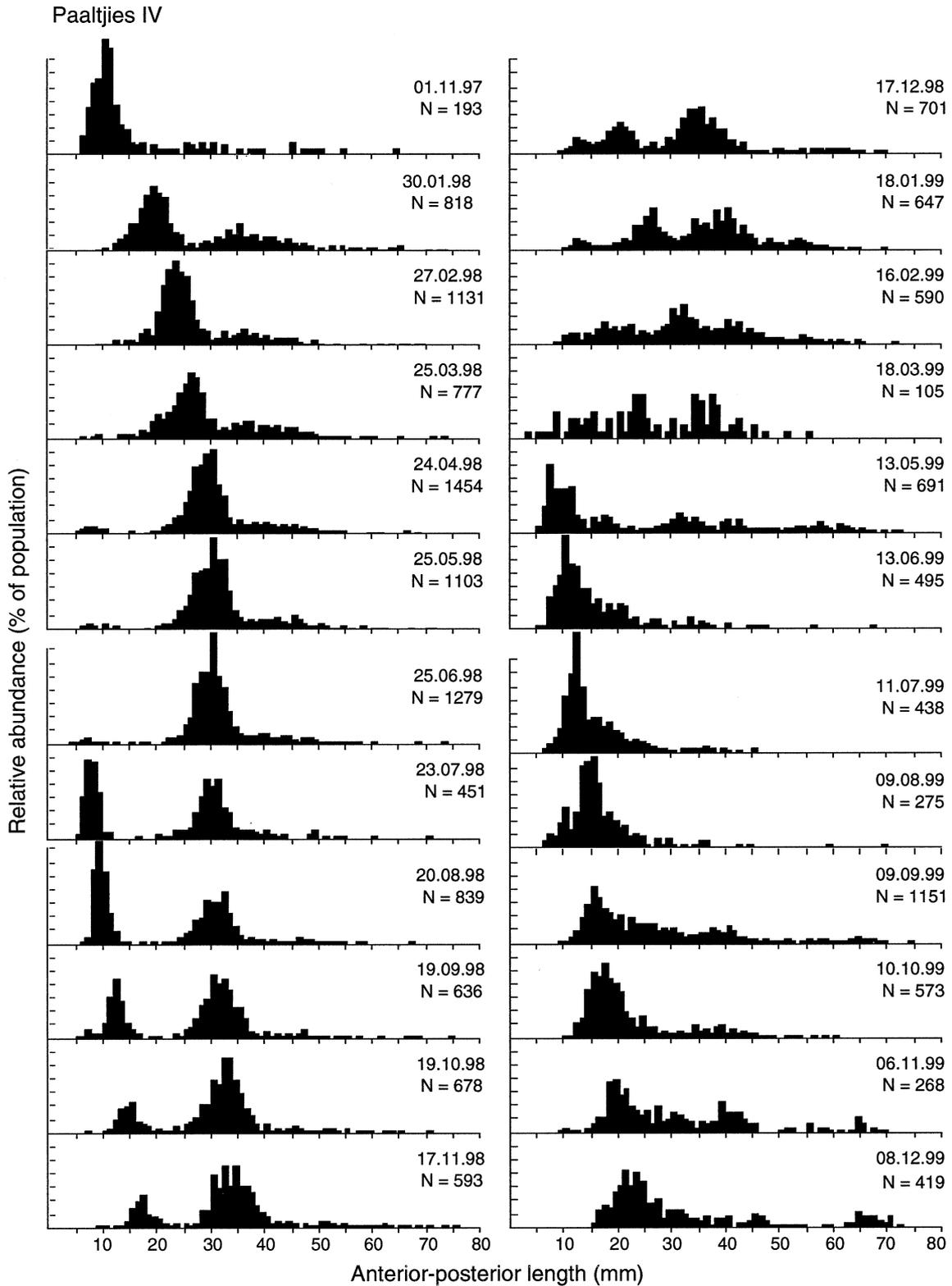


Fig. 4 (continued)

Paaltjies IV, 141.4 ind.m<sup>-2</sup> (1998) and 54.9 ind.m<sup>-2</sup> (1999), respectively. This represents a mean annual biomass  $\bar{B}$  at Langstrand of 288.8 g AFDM m<sup>-2</sup> (1998)

and 171.9 g AFDM m<sup>-2</sup> (1999) and at Paaltjies IV of 545.9 g AFDM m<sup>-2</sup> (1998) and 141.2 g AFDM m<sup>-2</sup> yr<sup>-1</sup> (1999) (Fig. 6b–e).

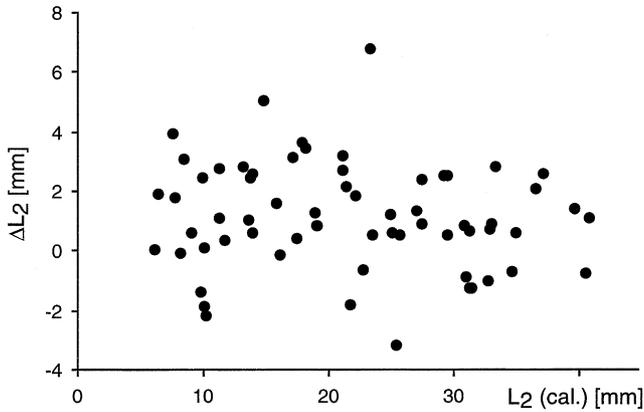


Fig. 5. Residuals of best-fitting von Bertalanffy growth curve of *Donax serra*;  $\Delta L_2 = L_2$  (measured) –  $L_2$  (calculated).

The observed relationship between length and AFDM of *Donax serra*  $y = 4 \times 10^{-6}x^{3.2576}$  ( $r^2 = 0.96$ ,  $n = 965$ ) was used for production estimates. Individual production increased to its highest value at 56.5 mm length ( $0.83 \text{ g AFDM ind.}^{-1} \text{ yr}^{-1}$ ) and decreased thereafter (Fig. 6a). The distribution of total annual production  $P$  and the abundance among the size classes are illustrated in Fig. 6b–e. Annual production ranged between 167 and 637 g AFDM  $\text{m}^{-2} \text{ yr}^{-1}$ , depending on beach and year, and  $P/\bar{B}$  ratios were between 1.2 and 1.6. In order to convert AFDM to wet mass (WM), the empirical relationship  $\text{WM} = 13.318 \text{ AFDM}$  ( $n = 400$ ) can be used.

#### 4. Discussion

##### 4.1. Growth data and growth

The analyses of macroscopic lines at the anterior end of the *Donax serra* valve (Fig. 2) revealed that these structures are linearly correlated with shell length. Previous studies (McLachlan & Hanekom, 1979; Schoeman, personal communication; de Villiers, 1975) are consistent with our findings that growth of *D. serra* follows a non-linear growth function. Thus, the external stripe pattern is not likely to reflect a temporal pattern.

Microgrowth analyses of Namibian *Donax serra* are unsuitable for estimate growth. The amplitudes of cyclic growth patterns as observed in Donacidae inhabiting sheltered environments (Nayar, 1955; Ramón & Richardson, 1992; Wade, 1968) are too small to be detected in the random pattern caused by disturbance events (e.g. continuous strong wave action) for donacids inhabiting exposed habitats. Consequently, uninterpretable microgrowth patterns have been reported for surf zone *Donax trunculus* (Gaspar et al., 1999; Ramón, Abelló, & Richardson, 1995) and *Donax variabilis* (Wilson, 1999). The microgrowth pattern of upwelling donacids is only usable when a prominent disturbance ring can be detected, which follows a strong event (e.g. Benguela Niño, river run-off) and is reflected in the shell structure of all individuals within the population (de Villiers, 1975).

The low recapture rate of 0.15% in the tagging–recapture experiment is most likely due to natural

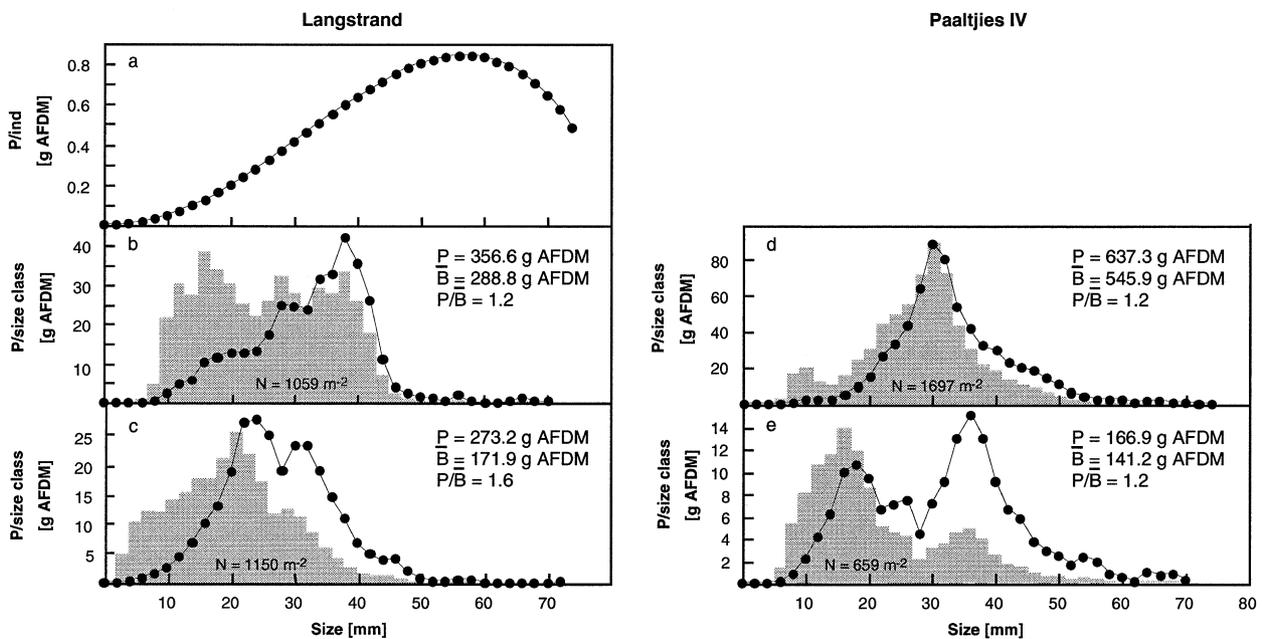


Fig. 6. Distribution of annual somatic individual (a) and population production at Langstrand for 1998 (b) and 1999 (c) and at Paaltjies IV for 1998 (d) and 1999 (e). Additionally, the mean abundance (grey area = 100%) for different length classes of *Donax serra* is included.

alongshore migration. All marked animals were found in flow direction of the Benguela current up to 450 m north of the release area. A pilot study with tagged *Donax serra* revealed as well a significant daily long-shore migration (Dugan & McLachlan, 1999; J. Laudien, unpublished data).

Non-linear growth functions are difficult to compare, whereas several authors (e.g. Moreau, Bambino, & Pauly, 1986; Munro & Pauly, 1983; Pauly, 1979) demonstrated the suitability of composite indices for overall growth performance (OGP) for inter- and intraspecific comparisons. The index  $P$  is proportional to the maximum rate of body mass increase during lifetime, i.e. the mass increase at the inflexion point of the VBGF, since few values of maximum body mass can be found in the literature and maximal mass is proportional to  $L_\infty$ . The  $P$  was calculated by

$$P = \log(K[L_\infty]^3) \quad (8)$$

OGP of Namibian *Donax serra* ( $P = 4.7$ ) corresponds well with values calculated from a data set of de Villiers (1975) for two West Coast populations (Elands Bay:  $P = 4.7$ ; Melkbosstrand:  $P = 4.7$ ) (Fig. 7). Our values are also in line with  $P$  values computed from data of Schoeman (1997) for a southeast coast population (Maitlands:  $P = 4.7$ – $5.2$ ). A compilation of donacid OGP data indicated that OGP is habitat-specific (Fig. 7): species inhabiting tropical/subtropical regions show lowest OGP (2.5–3.3, group A), temperate species have intermittent OGP (3.7–4.3, group B), while species of upwelling regions show the highest OGP (4.7–5.2, group C). Growth of suspension feeding bivalves is related to food availability (Jensen, 1992, 1993; Nair, Dalal, & Ansari, 1978; Nakaoka, 1992; Peterson, 1982; Sastre, 1984; Wade, 1968), which can get limited at exposed sandy beaches (Defeo, Ortiz, & Castilla, 1992; Lima, Brazeiro, & Defeo, 2000). Consequently, the high (Jarman & Carter, 1981; Walsh, 1981) and year-round (Schulz, 1982; Weeks & Shillington, 1994) primary production in upwelling areas might be the major cause for the observed higher OGP of upwelling donacids.

Another reason may be the narrower annual temperature range of permanent coastal upwelling areas (about 10 °C) compared with boreal regions (about 30 °C), which facilitates settlement of stenothermic species (e.g. Guillou & Bayed, 1991). There is evidence that costs of mitochondrial maintenance are lower in stenothermal than in eurythermal species (Pörtner, van Dijk, Hardewig, & Sommer, 2000). Therefore, low temperature variations might favour growth performance of upwelling donacids.

#### 4.2. Biomass and production

*Donax serra* was the only bivalve inhabiting the studied Namibian beaches. The intertidal biomass of the pop-

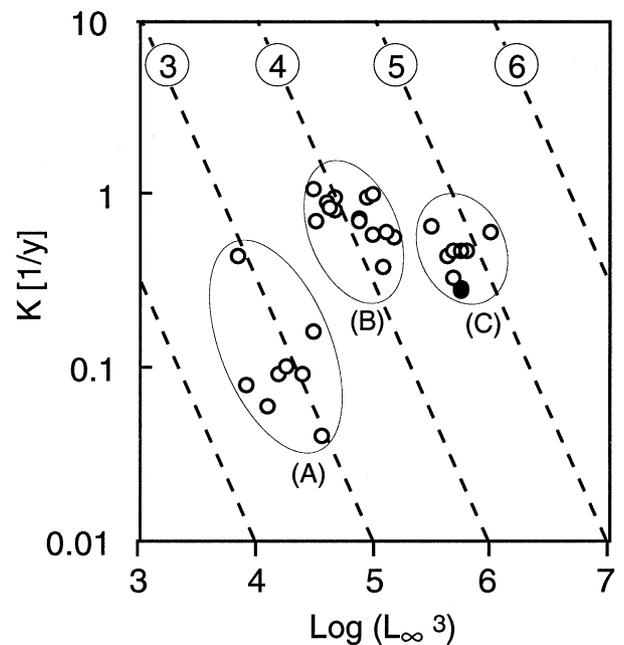


Fig. 7. Auximetric grid (according to Pauly, 1979) comparing OGP index  $P = \log(K[L_\infty]^3)$  of several Donacidae (○) with Namibian *Donax serra* (●). Plot indicates three groups (a) tropical/subtropical, (b) temperate and (c) upwelling species. Diagonal lines indicate equal values of  $P$  (numbers in circles). Data: (a) *Donax cuneatus*: Nayar (1955), Talikhedkar, Mane, and Nagabhushanam (1976); *Donax incarnatus*: Ansell, Sivadas, Narayanan, and Trevallion (1972), Nair et al. (1978), Thippeswamy and Mohan Joseph (1991); *Donax faba*: Alagarswami (1966); *Donax denticulatus*: Vélez, Barney, Venables, and Fitzpatrick (1985); (b) *Donax trunculus*: Ansell and Lagardère (1980), Guillou and Le Moal (1980), Bodoy (1982), Fernández, Otero, and de Coö (1984), Mazé and Laborda (1988), Ramón et al. (1995), Voliani, Auteri, Baino, and Silvestri (1997); *Donax vittatus*: Ansell and Lagardère (1980); *Donax hanleyanus*: Defeo (1996); (c) *Donax marincovichii*: Arntz et al. (1987); *D. serra*: de Villiers (1975), Farquhar (1996), Schoeman (1997), present study.

ulation ranged between 141 and 546 g AFDM  $m^{-2} yr^{-1}$  (Fig. 6). Taking into account the fact that the centre of the adult specimen distribution is likely to be situated in the subtidal (Donn, 1990; Soares et al., 1998), our estimate of intertidal biomass has to be considered conservative regarding the entire population. However, our value is much higher than in *D. serra* at warm temperate (South Africa) beaches (27 g AFDM, McLachlan et al., 1981; 754 g AFDM  $m^{-1}$  beach line, McLachlan & Hanekom, 1979). Schoeman's value of 1731 g shell free dry mass per meter beach line corresponds to 48 g AFDM  $m^{-2} yr^{-1}$  in the *Donax*-belt (30 m belt width, D. Schoeman, personal communication; AFDM = 0.831DM, Brey, 2001). Apparently, the biomass reached by *D. serra* inhabiting the upwelling system distinctly exceeds the range reported for several non-upwelling *Donax* species (0.1–2.0 g AFDM  $m^{-2}$ ; Ansell, McLusky, Stirling, & Trevallion, 1978; Mazé, 1990; McLachlan et al., 1981; McLachlan & van der Horst, 1979; Warwick, George, & Davies, 1978; Wilson, 1999). From the South American Humboldt upwelling system, again higher values are feasible:

70 g AFDM for *Donax marincovichii* (Tarazona, Arntz, Canahuire, Ayala, & Robles, 1985), formerly called *Donax peruvianus*. High biomass was also reported for the surf clam *Mesodesma donacium* (910 g AFDM m<sup>-2</sup>; Arntz, Brey, Tarazona, & Robles, 1987), which is very similar in shape and size to *D. serra* and plays a comparable ecological role in the Humboldt ecosystem.

The annual intertidal production of *Donax serra* ranged between 167 and 637 g AFDM m<sup>-2</sup> yr<sup>-1</sup> at Paaltjies IV and between 273 and 357 g AFDM m<sup>-2</sup> yr<sup>-1</sup> at Langstrand. These values are significantly higher than values of 34–46 g AFDM m<sup>-2</sup> yr<sup>-1</sup>, calculated from habitats without permanent upwelling at the Eastern Cape of South Africa (Schoeman, personal communication) and converted to g AFDM m<sup>-2</sup> yr<sup>-1</sup> (see previous discussion). The presented values also distinctly exceed those of non-upwelling donacids. Ansell et al. (1978) found production values of 2.9 and 3.3 g AFDM m<sup>-2</sup> yr<sup>-1</sup> for tropical (India) *Donax incarnatus* and *Donax spiculum*, respectively. Warm temperate *Donax variabilis* produced 6.0 g AFDM m<sup>-2</sup> yr<sup>-1</sup> (Wilson, 1999), *Donax trunculus* produced between 1.8 and 3.7 g AFDM m<sup>-2</sup> yr<sup>-1</sup> (Mazé, 1990) and production of temperate *Donax vittatus* was 0.7 g AFDM m<sup>-2</sup> yr<sup>-1</sup> (Warwick et al., 1978). To our knowledge, there is currently no information available on production for Donacidae from permanent upwelling areas, but *Mesodesma donacium* from the Humboldt upwelling system has even higher production rates (2400 g AFDM m<sup>-2</sup> yr<sup>-1</sup>; Arntz et al., 1987). Therefore, upwelling habitats seem to favour higher production rates presumably due to year-round food availability, high food quality and low temperature ranges around the optimal temperature, on which clams are adapted (Pörtner et al., 2000).

Production/biomass ( $P/\bar{B}$ ) ratios of *Donax serra* ranged between 1.167 and 1.589 yr<sup>-1</sup>. These values are slightly higher than those of warm temperate South African *D. serra* (0.63–1.06 yr<sup>-1</sup>; Schoeman, personal communication), but correspond to *Donax sordidus* (1.30–1.78 yr<sup>-1</sup>; McLachlan, 1979; McLachlan & van der Horst, 1979) and *Donax trunculus* (1.37–2.26 yr<sup>-1</sup>; Mazé, 1990). As the subtidal adults are not accounted for in our calculation and, additionally, exploitation concentrates on large clams, the size–frequency distribution is biased towards smaller individuals with high somatic productivity ratios (see also Urban & Campos, 1994).

Donacids play different roles in different habitats. On tropical beaches (Venezuela), *Donax denticulatus* dominates benthic biomass, but only accounts for a comparatively low portion (5%) of the total production (Ansell, 1983). In comparison, the combined contribution of Indian *Donax incarnatus* and *Donax spiculum* to macrobenthic production ranged between 56 and 61% (Ansell et al., 1978). In temperate shallow water habitats of the Bristol Channel (UK), *Donax vittatus* only accounts for 0.75% of the benthic biomass; a high mass-specific

production rate, however, ensures that it ranks among the top five secondary producers in the community (Warwick et al., 1978). At the warm temperate South African east coast, *Donax serra* is responsible for 94% of macrobenthic production, while *Donax sordidus* contributes only 2.5% (McLachlan et al., 1981). The role of *D. serra* in the beach/surf zone ecosystems is important, as it significantly contributes to the regeneration of dissolved and particulate organic nitrogen (Cockcroft & McLachlan, 1993). Part of the secondary production by this clam is consumed by crabs, birds and benthos feeding fish (McLachlan et al., 1980, 1996; Rossouw, 1985; J. Laudien, unpublished data), which makes *D. serra* an essential trophic link in the coastal upwelling ecosystem. Along with high abundance and production rate and its use as bait and potential economic value for export markets (Sims-Castley & Hosking, submitted for publication), *D. serra* is apparently a valuable species for aquaculture. Future research should evaluate the possibility to rear *D. serra*. Further, ageing methods, which are independent of variable environmental factors (e.g. isotopic age determination) should be focussed on.

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