Aspects of the biology, ecology and seasonal fluctuations in biochemical composition of *Donax serra* in the East Cape

A. McLachlan and N. Hanekom
Department of Zoology, University of Port Elizabeth, Port Elizabeth

Donax serra Röding (Pelecypoda) is a large sand mussel which forms vast populations on some East Cape shores. It is most abundant on exposed beaches where the sand is not too coarse and phytoplankton production is high. Adults occupy a zone just above the mean level of spring tide. Spat settle subtidally and move upshore as they grow. Growth is initially rapid, to about 32 mm at one year and 48 mm at two years. Thereafter growth is very slow and most adult productions goes into reproduction, with a small summer spawning and a large winter spawning each year. Somatic production is low, as large adults totally dominate the population and have low growth and low mortality. Reproductive production is relatively high and P/B values of 0,2 and 0,5 are suggested for growth and reproduction. *D. serra* was found to be very tolerant of fluctuating salinities for up to four days and should be able to penetrate river mouths, but is limited by restricted swash action. Total dry-tissue mass, energy and biochemical constituents showed some seasonal fluctuations related mainly to the reproductive cycle. Carbohydrate appears to be a more important energy reserve than lipids.

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Donax serra Röding (Pelecypoda) is 'n groot sandmossel met hoë bevolkingsdigtheid op sommige Oos-Kaapse strande. Dit is volop op oop strande waar die sand nie te grof is nie en waar fitoplanktonproduksie hoog is. Tydens springgetye kom die volwassenes voor in 'n sone net bokant die gemiddelde getyvlak. Klein mosseltjies vestig in die subgetysone en beweeg teen die strand op namate hulle groei. Groei is aanvanklik vinnig, tot 32 mm na een jaar en 48 mm na twee jaar, maar daarna baie stadig en die grootste deel van volwasse produksie word aangewend vir voortplanting wat manifesteer in 'n jaarlikse klein somer en 'n groot winter kuitskieting. Somatiese produksie is laag omdat die bevolking heeltemal gedomineer word deur groot volwassenes met lae groei en mortaliteit. Voortplantingsproduktiwiteit is relatief hoog en P/B waardes van 0,2 en 0,5 word voorgestel vir groei en reproduksie. *D. serra* kan lae soutgehaltes vir tot vier dae goed verduur en sou riviermondings kon binnedring indien die gebrek aan golfaksie verspreiding nie beperk het nie. Totale droë-weefselmassa, energie en biochemiese bestanddele het seisoenale variasies getoon, wat hoofsaaklik aan die reproduksiesiklus gekoppel is. Koolhidrate blyk 'n meer belangrike energie-reserve as vette te wees.

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A. McLachlan* and N. Hanekom
Department of Zoology, University of Port Elizabeth,
P.O. Box 1600, Port Elizabeth 6000, South Africa
*To whom all correspondence should be addressed

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Wedge clams of the genus *Donax* are typical inhabitants of sandy beaches in both tropical and temperate zones. Two aspects of their ecology in these dynamic environments have attracted the attention of marine biologists for some decades, namely the vast populations that can develop (Nayar 1954; Coe 1955; Loesch 1957; Edgren 1959; Wade 1964; Smith 1971; Ansell *et al.* 1972a, b; De Villiers 1973, 1975; McLusky *et al.* 1975; Moueza & Chessel 1976) and the characteristic tidal migratory behaviour of many species (Mori 1938, 1950; Turner & Belding 1957; Wade 1967; Ansell & Trevallion 1969; Ansell & Trueman 1973; Trueman 1971; McLachlan *et al.* 1979).

Two species of *Donax, D. sordidus* Hanley and the sand mussel *D. serra* Röding, occur on East Cape sandy beaches (McLachlan 1977a, b, *In press*). The former is small and undergoes tidal migration, while *D. serra* is the largest species in the genus (De Villiers 1975) and only exhibits a semilunar pattern of movement up and down the intertidal zone (McLachlan *et al.* 1979). *D. serra* developes vast populations on South African shores (De Villiers 1975; McLachlan 1977b) where biomass values as high as 7 468 g ash-free dry mass per metre shore have been recorded. Despite the great importance of this species in the ecology of South African sandy beaches and its collection for bait and food, the only published studies are those of De Villiers on reproduction (1973) and growth (1975). As aspects of the ecology of *D. serra* differ considerably between East Cape and west coast shores, where De Villiers worked, further study in the former area is long overdue.

This paper describes the general distribution of *D. serra* in the East Cape, its population structure, growth, production, aspects of biology and seasonal changes in biochemical composition.

Methods

Surveys

Nine beaches were examined during spring low tides. Intertidal profiles were determined using graded poles and a tape measure. Wave action was rated on an arbitrary scale from one to five in order of increasing exposure. Sand-cores 20 cm deep were taken at LWS, MTL and HWS and analyzed for particle-size by dry sieving (Morgans 1956). At

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the top and bottom of the zone occupied by *D. serra* 30 cm sand-cores were taken and the upper and lower 15 cm sections analyzed for moisture content by drying at 105 °C for 48 hours and noting the mass loss. The whole intertidal zone from LWS to HWS was sampled for *D. serra* every 2,5 m by excavating two 0,25 m^2 areas to 30 cm depth and passing all the sand through a screen of 4 mm mesh.

Population monitoring

Transect sampling was done every two months at Maitland River beach from November 1973 to November 1974. All individuals were measured to 1 mm greatest antero-posterior shell-length with sliding callipers. The vertical distribution of animals in the sand was investigated in the main *D. serra* zone on the same beach. The top 7 cm of sand from a series of quadrats was removed and sieved and then the 8–15 cm layer was treated similarly until 800 animals had been collected and measured. Sizes of individuals from the two depths were compared statistically using a t-test.

In addition to the above sampling, Kings Beach and Maitland River beach were sampled from MTL to below LWS at six-weekly intervals during 1976/7/8 using a dredge with 1,5 mm mesh. This was successful in shallow water, collecting individuals smaller than 10 mm, and proved valuable as the transect sampling seldom recovered animals smaller than 10–12 mm.

Length, breadth and mass relationships

Five hundred shells from Maitland River beach were measured. The greatest antero-posterior length and greatest dorso-ventral breadth were determined to the nearest 0,5 mm and a linear regression calculated. This allows comparison with De Villiers' (1975) work which is mainly expressed in terms of shell breadth. The length/mass relationship was determined for 27 size-batches of five animals of the same length by measuring all shells and then drying the tissues at 105 °C for 24 h after removal of the shells. Organic matter in the shells, determined by acid digestion of the calcium carbonate, made up 0,8–4,5% of the total organic matter and was added to the dry mass. This was highest in small individuals. This was done during October 1974 and the results expressed as a linear regression after $\log_{10}$ transformation.

Production

Production by growth (P_G) and mortality (P_M) for each age class during 1973/4 was calculated as described by Crisp (1971) and mean or steady state production ($\bar{P}$) and $\bar{P}/\bar{B}$ ratios calculated.

Salinity tolerances

A simple experiment was performed to estimate lethal effects of low salinities which might occur during heavy rains or if animals penetrated river mouths. Individuals in the 53–57 mm length-range were collected during September 1974 and kept in seawater (35°/oo) for eight hours. Five were then placed in each of seven duplicate sets of glass dishes with 800 ml of a series of dilutions of seawater from 35 to 0°/oo. Salinities were regularly monitored with a hand refractometer to within 1°/oo. Temperature took on the normal laboratory fluctuations of 18–20 °C and the photoperiod was 14 h light. As the dishes were shallow no artificial aeration was used. Dead animals were removed immediately. Animals' reactions were observed and the percentage mortality noted at regular intervals for four days. At this stage, although none had died, control animals began to show uncontrolled gaping. The death criterion was gaping of the valves together with an inability to withdraw the foot or siphon.

Reproduction

Reproduction in *D. serra* in the East Cape will be described in detail by Van der Horst in a subsequent paper. During this study some index of reproductive season was required and a rough gonad index evaluated as follows. The shell, siphons, mantle and adductor muscles of 30 animals in the size-range 54–56 mm (collected during each population sampling at Maitland River beach) were removed and the remaining visceral mass and foot blotted and weighed to the nearest 0,1 mg. The gonads were dissected free and weighed to the nearest 0,1 mg. The gonad index was then calculated as this gonad mass as a percentage of the body mass.

Biochemical composition

Biochemical analyses were only performed on the 55 mm size-class as preliminary work had shown that this was representative of all adult groups, i.e. individuals 45–65 mm long. Fourteen individuals were collected at Maitland River beach every second month during the population surveys. They were removed from their shells, pooled, homogenized, frozen and freeze-dried. The dry tissue was then weighed, milled in a hammer mill and stored in a desiccator. Energy values were determined using an adiabatic bomb calorimeter, nitrogen was estimated by the micro-kjeldahl method and converted to protein by multiplication by 6,25 (Crisp 1971). The Labconco goldfish fat extraction unit was used for determination of lipid, and ashing at 550 °C for three hours gave the ash content. Carbohydrate was determined by difference.

Results and Discussion

Surveys

The positions of the beaches investigated, together with population sizes and wind and wave roses, are illustrated diagrammatically in Fig. 1. As swells approach this area from the south and south-west, and winds blow predominantly from the west and south-west, it is clear that Maitland River and Oyster Bay receive the heaviest wave action and both were given exposure ratings of five in terms of wave action. Kings Beach and Sea Vista are the most sheltered, behind the headlands of Cape Receife and Cape St. Francis respectively, and both had ratings of one. Bluewater Bay and Paradise Beach had ratings of two, Kabeljous River a rating of three and Sundays River and Gamtoos River ratings of four.

With the exception of Oyster Bay, which supports a sparse population despite being very exposed, these beaches tend to support larger *D. serra* populations the more exposed they become. On the more exposed beaches, however, waves usually break first on offshore bars so that their full force is seldom experienced in the intertidal zone. Large populations also tend to develop east of river mouths and Coe (1955) has suggested that rivers are a source of particulate food to *Donax* species. However, Paradise Beach and Bluewater Bay, which are both washed by currents pas-

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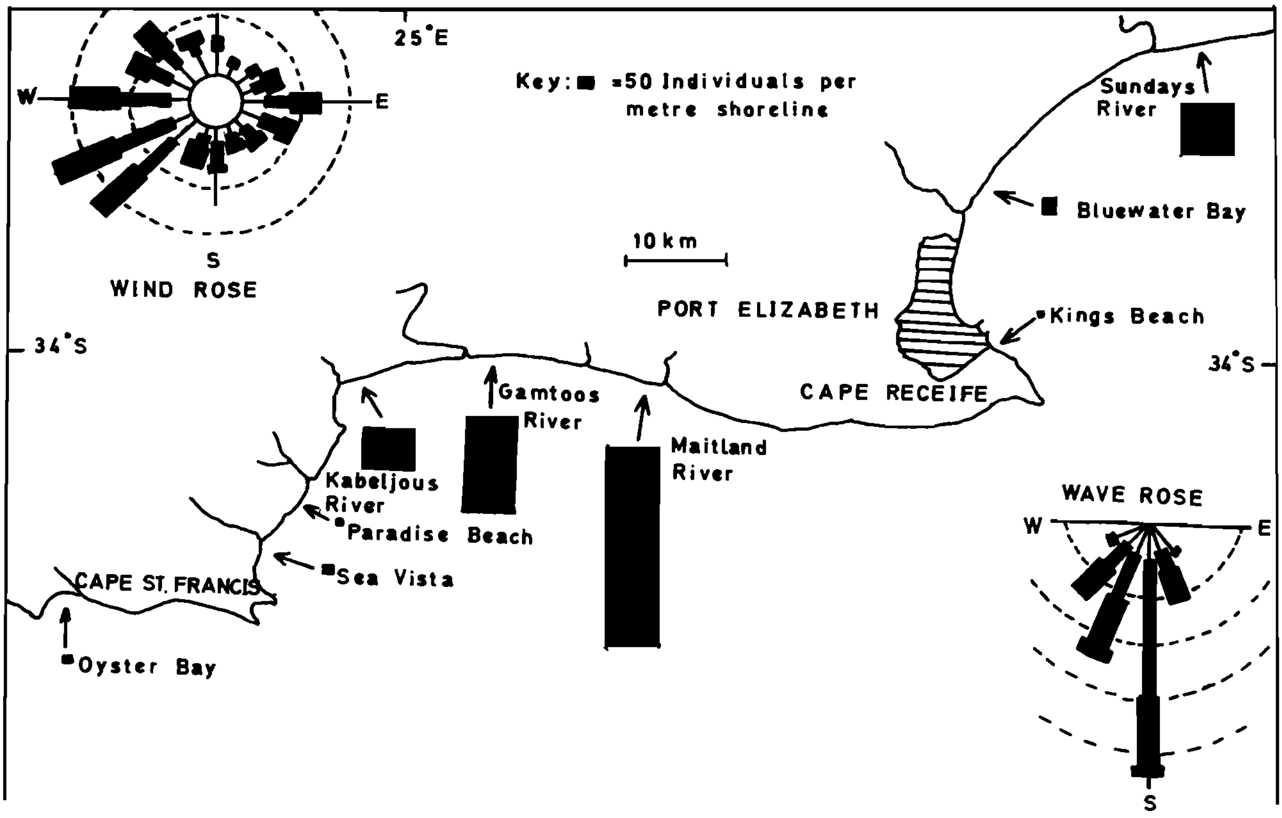

Fig. 1 Map of the study area with wind and wave roses compiled from data recorded at the H.F. Verwoerd airport and Cape St. Francis lighthouse respectively. Wind rose arcs represent 5% frequency intervals while wave rose arcs represent 10% intervals. Thickness proportional to wind speed and wave height respectively. Population sizes of *D. serra* are indicated.

sing river mouths relative to the clockwise inshore currents, have small populations. Observations on numerous occasions have verified that the two richest stretches, *viz.* from the Kabeljous River to Maitland River and east of the Sundays River, regularly have large phytoplankton blooms which come in through the surf as green-brown patches often thousands of square metres in extent and resembling oil slicks. There can be little doubt that the large quantities of organic froth and living microplants which reach the intertidal zone in these areas are one of the reasons for the vast populations there.

Beach profiles (Fig. 2) indicate gradients between $^1/_{11}$ and

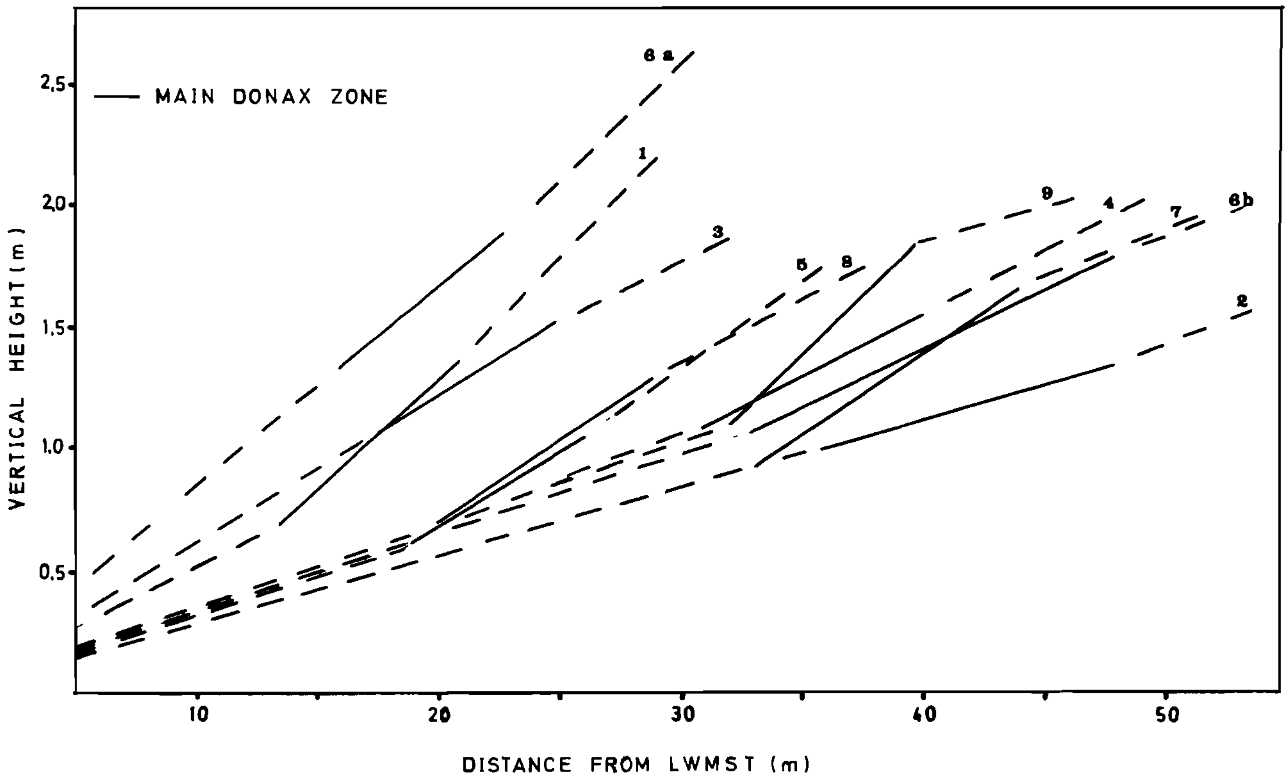

Fig. 2 Beach slopes with the *D. serra* zone indicated by a solid line. 1 = Oyster Bay, June 1974; 2 = Sea Vista, July 1974; 3 = Paradise Beach, June 1974; 4 = Kabeljous River, May 1974; 5 = Gamtoos River, May 1974; 6 = Maitland River, (a) Sept. 1974, (b) March 1974; 7 = Kings Beach, Sept. 1974; 8 = Bluewater Bay, Sept. 1974; 9 = Sundays River, April 1974.

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Table 1 Median particle diameters in mm, phi quartile deviations and phi quartile skewness values for sands collected from three tide-levels on nine beaches

Beach	Md (mm) LWS	 MTL	 HWS	QDφ LWS	 MTL	 HWS	Skφ LWS	 MTL	 HWS
Kings Beach	0,194	0,211	0,190	0,39	0,46	0,37	0,01	−0,02	+0,03
Sea Vista	0,225	0,210	0,210	0,48	0,35	0,35	0,0	−0,07	0,07
Bluewater Bay	0,213	0,196	0,189	0,30	0,29	0,04	−0,06	0,02	0,02
Paradise Beach	0,300	0,312	0,225	0,64	0,76	0,48	−0,08	−0,13	−0,01
Kabeljous River	0,312	0,246	0,207	0,34	0,49	0,51	−0,04	0,00	−0,02
Sundays River	0,299	0,255	0,199	0,48	0,50	0,35	0,05	0,01	0,02
Gamtoos River	0,263	0,300	0,325	0,36	0,48	0,60	0,20	0,06	−0,17
Maitland River	0,353	0,350	0,335	0,31	0,32	0,34	−0,01	0,00	−0,01
Oyster Bay	0,350	0,330	0,309	0,44	0,47	0,46	0,07	0,06	0,00

$^1/_{34}$ with an average around $^1/_{20}$. Slope varies with sea conditions and on Maitland River beach a range from $^1/_{12}$ to $^1/_{30}$ was recorded. There was no clear relationship between slope and degree of exposure or between slope and population size. Brown (1971) has discussed the variable slopes of Cape beaches and pointed out that slope is not related to degree of exposure.

Results of the substrate analyses (Table 1) show a close correlation between substrate grade and exposure as has often been found (Eltringham 1971; Eleftheriou & Nicholson 1975; McLachlan 1977a, b). The finest substrate, on Kings Beach, ranged between medians of 190 μm and 211 μm while that on Maitland River beach fell between 335 μm and 353 μm. These values are similar to those recorded before in the East Cape (McLachlan 1977a, b) and confirm that even on very exposed shores coarse sands are never found in this area. Oyster Bay and Paradise Beach did, however, have high proportions (> 10%) of shell grit coarser than 500 μm and poor faunas. Sands from these beaches were also less well sorted (high quartile deviation (QDφ)) than most of the others. This makes the substrate less compact and hinders burrowing. A high proportion of coarse material thus appears to be unfavourable for *D. serra* populations in this area.

Moisture content of the sands (Table 2) was highest in finest sands which have higher porosities and lower permeabilities or drainage rates than coarser sands (Hulings & Gray 1971). The maximum values, 21−30%, came from Kings Beach and the minimum, 5−22%, from Oyster Bay. As low values were recorded at the top of the rich *Donax* zone on Maitland River beach it appears that a considerable degree of desiccation of the sand can be tolerated by *D. serra* during low tide.

Table 2 Moisture content (%) of the surface and subsurface 15 cm layers of sand at the upper and lower borders of *D. serra* zone

Beach	Top of *Donax* zone Depth of sample 0-15 cm	 15-30 cm	Bottom of *Donax* zone Depth of sample 0-15 cm	 15-30 cm
King Beach	21	25	26	30
Sea Vista	19	21	24	23
Bluewater Bay	18	19	20	20
Paradise Beach	7	7	12	17
Kabeljous River	19	20	20	21
Sundays River	9	18	18	20
Gamtoos River	9	18	20	20
Maitland River	7	14	19	18
Oyster Bay	5	9	22	22

No attempt was made to measure organic content of these sands as the values are too low for all suitable methods (Brown 1971; McLachlan 1977c). Tensile strength of the sand was estimated with a simple penetrometer, but values were scattered and there was no clear pattern in the readings.

Distribution within the intertidal zone

The typical intertidal distribution pattern during spring low tides at Maitland River beach is shown in Fig. 3. The population is centred just above the mean tide level (McLachlan 1977a). During neaps this zone moves down to the LWN level (McLachlan *et al.* 1979). The distribution of size classes within the *D. serra* zone is shown in Fig. 4. From a length of about 20 mm the animals enter the adult zone while smaller individuals occur lower on the shore. Stratified sampling on Maitland River beach and Kings

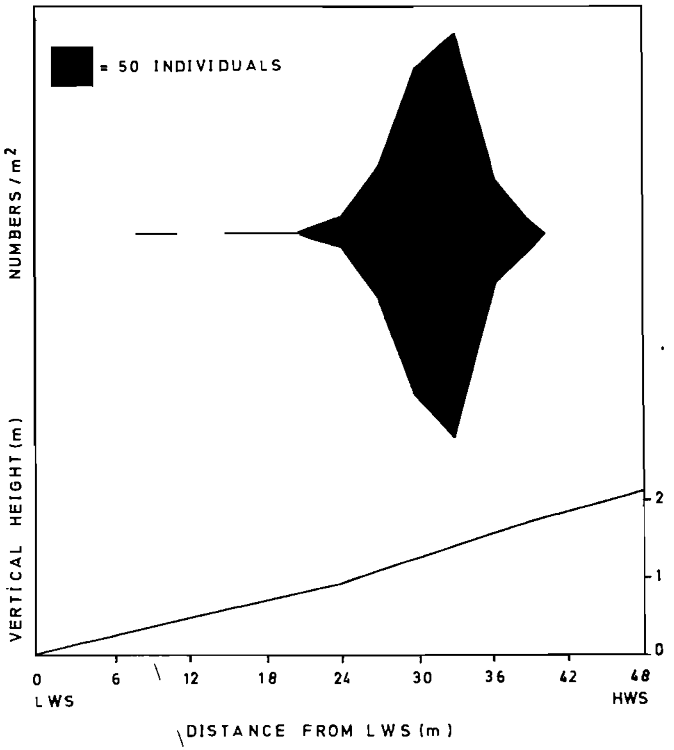

Fig. 3 Zonation of *D. serra* individuals larger than 10 mm within the intertidal of Maitland River beach during a spring tide.

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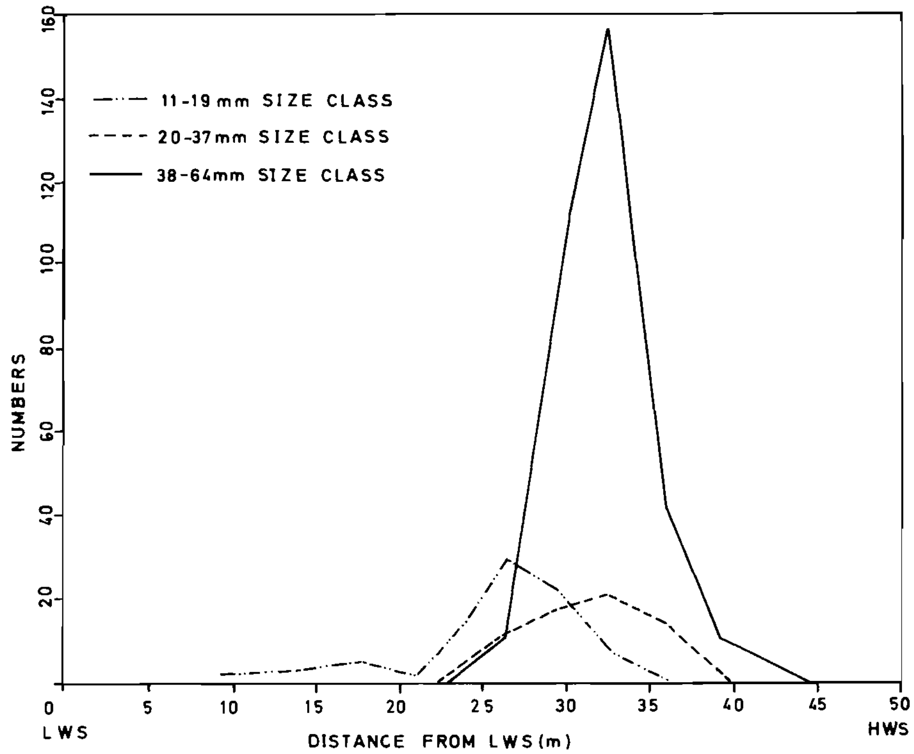

Fig. 4 Zonation of size classes of *D. serra* within the Maitland River intertidal during a spring tide.

Beach with a dredge (Table 3) during November 1977 revealed a similar pattern with individuals smaller than 15 mm length being most abundant at and below LWS. This size class zonation is opposite to that recorded for *D. serra* on the west coast (De Villiers 1975) and for *D. denticulatus* (Wade 1967) where small individuals occurred highest on the shore and the adults were found at and below LWS.

Table 3 Numbers 5 m^{-2} and mean sizes of small (< 15 mm) *D. serra* collected by dredge at a series of levels on the shore at Kings Beach and Maitland River beach

	Kings Beach		Maitland River	
Level	Nos.	$\bar{L}$ mm	Nos.	$\bar{L}$ mm
LWS 1	20	7,2	6	8,0
2	6	7,6	–	–
3	5	7,0	1	12,0
4	1	9,0	–	–
MTL 5	4	6,5	2	12,5
6	2	8,5	–	–

Vertical distribution in the sediment during low tide (Fig. 5) follows the obvious pattern where larger individuals with longer siphons occupy a deeper position. The differences between the sizes in the two depth-ranges was significant ($p < 0,05$).

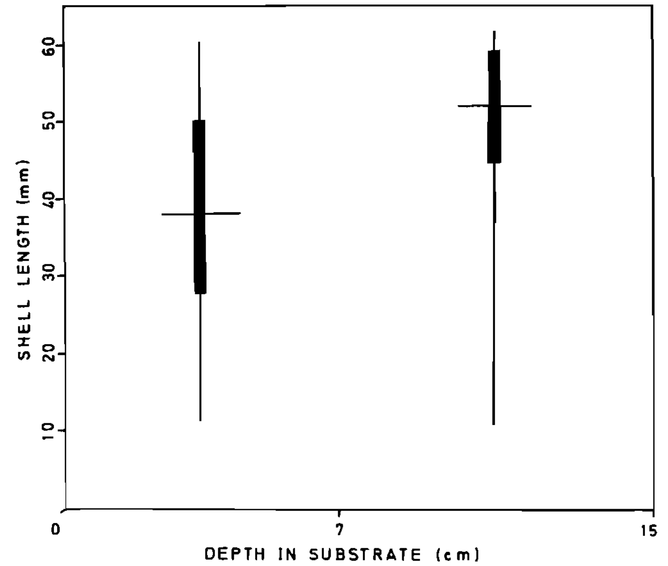

Fig. 5 Mean, standard deviation, and range of shell-lengths of *D. serra* collected from two depths, 0-7 cm and 7-15 cm, in the sand.

Population structure and growth

Size frequency histograms are given for the Maitland River population during 1973/4 in Fig. 6. As the bulk of the population is made up of large adults, earlier age classes are difficult to interpret. Further, the method of sampling missed individuals smaller than about 12 mm. By separating individuals greater than 43 mm shell-length in the histograms the structure of the younger part of the population becomes somewhat clearer. Although some specimens of 65 mm were recorded, individuals over 62 mm were very rare and have thus been included in the last size class. Some 0 + and 1 + age classes can be distinguished with the aid of probability paper (Cassie 1954). It is assumed that there are two spawning seasons with peak spat settlements in mid April (summer spawning) and mid September (winter spawning) (see under Reproduction). On this basis mean lengths of age classes in Fig. 6 are plotted against their estimated ages in Fig. 7. The curves so obtained are then combined in Fig. 8. This suggests that summer and winter classes have different growth-rates until an age of about 1,5 years. The difficulty in distinguishing exact size classes in this population make precise growth curves for these two classes unreliable but a combined mean growth curve

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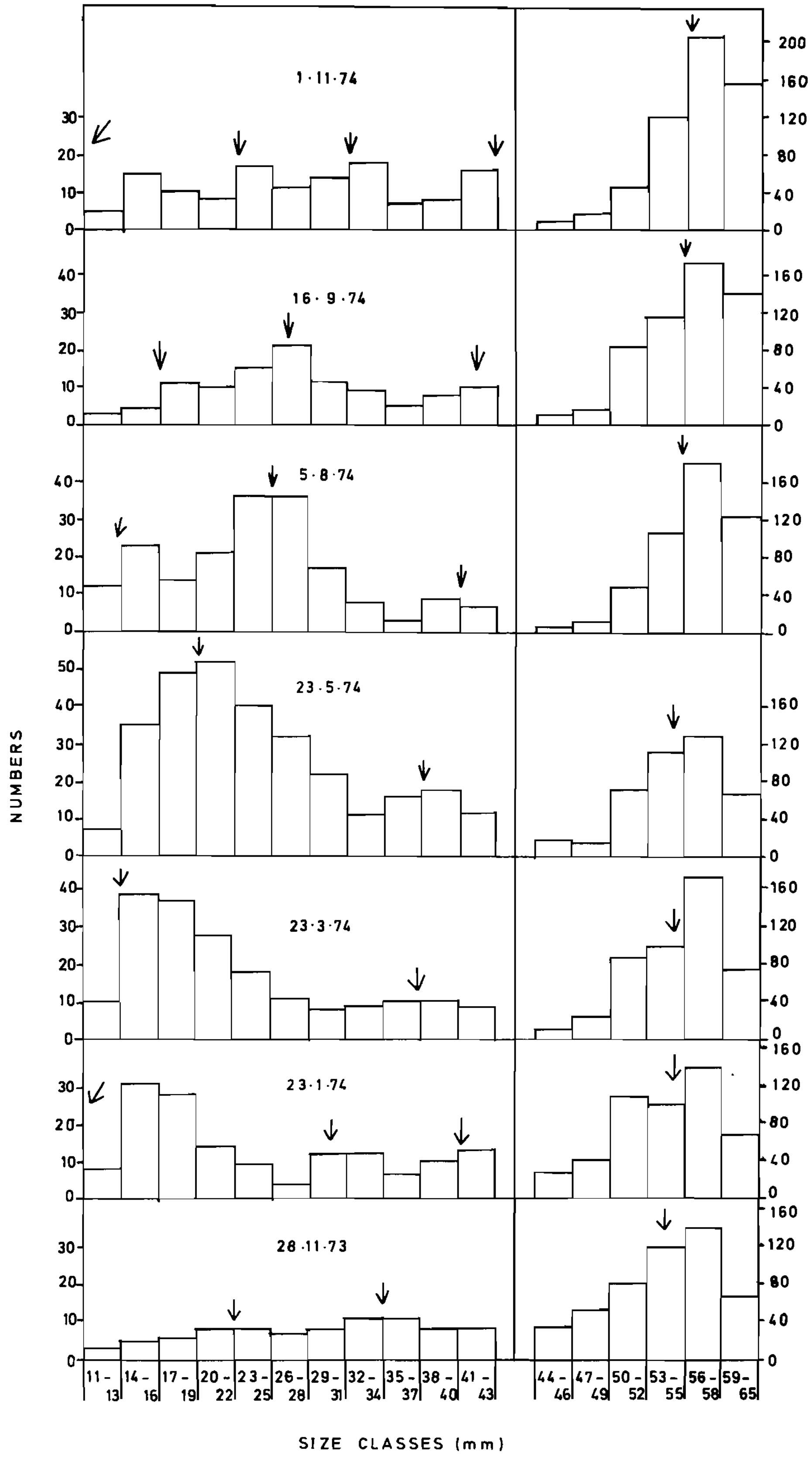

Fig. 6 Size frequency histograms of *D. serra* larger than 10 mm from Maitland River beach during 1973/4. Included in each histogram is the sampling date and arrows indicate mean lengths of age classes.

(Fig. 8) may be taken as a reasonable average for the population. While summer-spawned individuals grow to about 36,5 mm at one year and winter-spawned individuals to about 27,5 mm the average value is about 32 mm and 48 mm at two years. Length at three years is about 55 mm.

Results of dredging for small individuals on Maitland River and Kings beaches are shown in Fig. 9. The dredge only samples to 5 cm in the sand and misses most individuals larger than 15–20 mm. Dredge results have thus only been plotted for animals up to 20 mm. Results are somewhat patchy but may be interpreted as follows. At Maitland River one class (0 + *b*) was present at 10–20 mm from July to November 1977 when the winter (0 + *a*) class appeared around 4–5 mm. This class (0 + *a*) grew to about

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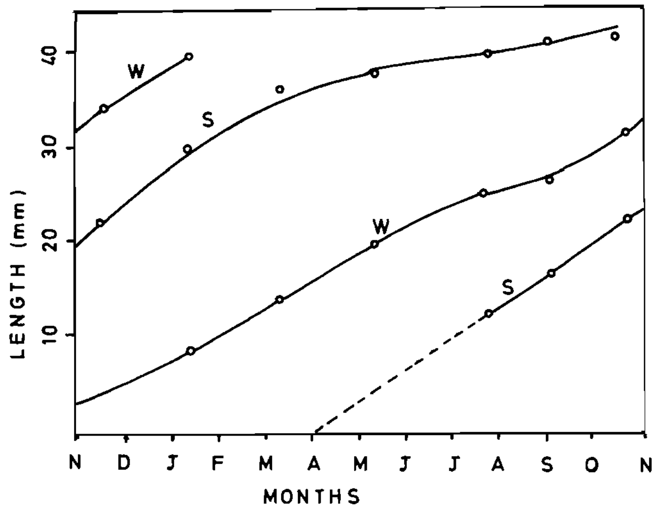

Fig. 7 Growth curves for four age classes of *D. serra* on Maitland River beach during 1973/4. W = winter spawned individuals; S = summer spawned individuals.

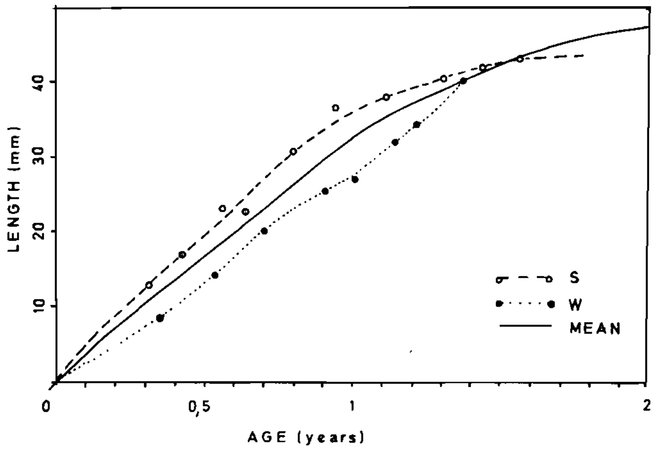

Fig. 8 Combined growth curves for summer and winter spawned individuals as well as a mean growth curve for *D. serra* on Maitland River beach.

10 − 15 + mm by May 1978. In July 1978 the 0 + *a* class had mainly moved beyond 20 mm while some new 0 + *b* (summer) individuals were present at around 12 − 14 mm. On Kings Beach small individuals were taken in almost all samples and new classes appeared at about 6 mm in April 1977 and 7 mm in November 1977, these being the 0 + *b* and 0 + *a* classes.

On the west coast De Villiers (1975) found slower, more sustained growth, his animals reaching 22, 43, 58, 64 and 68 mm at the end of their first five years respectively. Considering the higher water temperatures in the East Cape, growth to 32, 48 and about 55 mm after the first three years appears reasonable, the growth curve climbing faster but levelling off sooner than on the west coast.

Length, breadth and mass regressions

The regressions obtained for October 1974 were: shell breadth (mm) = 0,68 length (mm) − 2,1 ($r = 0{,}999$, $p < 0{,}001$, 498d.f.)

$\log_{10}$ (mass (mg)) = 3,07 $\log_{10}$ (length (mm)) − 2,1 ($r = 0{,}97$, $p < 0{,}01$, 25d.f.)

Production

Estimates of production were made only on the data in Fig. 6 and thus ignore classes less than about 10 mm shell-length. As these smaller classes contribute less than 1% of the total population biomass the resultant error is negligible. Table 4 lists the age classes separated in Fig. 6 and gives their mean lengths, mass values (from the length/

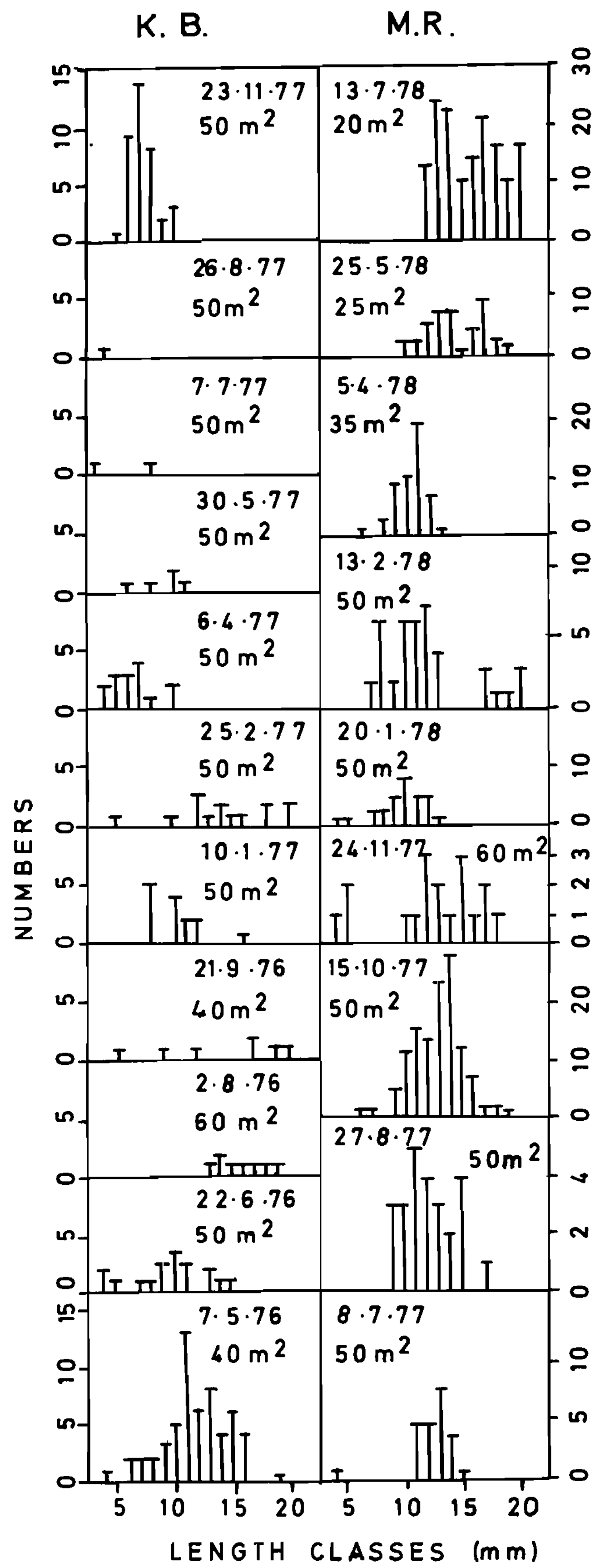

Fig. 9 Size frequency histograms of small (< 20 mm) *D. serra* collected by dredge on Kings Beach and Maitland River beach during 1976-78. Included in the histogram is the date of sampling and the total area sampled.

Table 4 Results of analysis of size frequency histograms of *D. serra* on Maitland River beach during 1973/4. $\bar{L}$=mean length in mm; $\bar{W}$=mean mass in mg; N=numbers per transect

	Age class														
	0+*b*			0+*a*			1+*b*			1+*a*			2+→		
Date	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N
November 1973	–			–			22,5	113	34	34,5	418	46	54,0	1,654	500
January 1974	–			9,0	7	1 000[1]	31,0	301	36	41,0	710	29	54,5	1 701	485
March 1974	–			14,0	26	550[1]	37,0	518	44				→55,0	1 750	474
May 1974	–			20,0	78	239	38,0	562	60				55,0	1 750	403
August 1974	12,5	19	80[2]	25,5	163	137	40,5	684	20				55,5	1 799	483
September 1974	16,5	44	50[2]	27,0	197	64	42,0	764	30				56,0	1 849	535
November 1974	23,0	119	41	32,0	332	39	43,0	822	32				56,0	1 849	559

[1] Values obtained from survivorship curve (Fig. 10).

[2] Double recorded numbers.

mass regression) and numbers per transect (equivalent to numbers per 0,2 m shoreline). At their first appearance smaller individuals of the 0 + *a* class were missed and their numbers during January and March 1974 were thus estimated by back extrapolation of the survivorship curve (Fig. 10). No such survivorship curve could be obtained for the 0 + *b* class and the abundances given for August and September were obtained by doubling recorded numbers, but make little difference to overall biomass or production estimates. After January 1974 the 1 + *a* class could not be separated and was lumped with the 2 + → adults.

Calculated production values are given in Table 5. There was a large increase in biomass (ΔB) during the year and consequently P_G exceeded P_M. Smaller classes with faster growth and high mortality had highest production values, but made up a minor proportion of the population as 2 + → adults accounted for 46% of numbers at 96% of biomass. This adult group had very slow growth and low mortality. Their increase in numbers over the study period was probably due to sampling error and the passage of age-groups through this size-range. This resulted in a highly negative P_M and consequently negative $\bar{P}$. Because of this the overall population $\bar{P}/\bar{B}$ was only 0,1. Obviously large individuals must die and a decrease in their numbers would thus normally be expected, even though this mortality may be considerably lower than for the juveniles. If numbers of the 2 + → class had decreased by only 5% during the study year this would have resulted in an overall $\bar{P}/\bar{B}$ of 0,2. This would still be a very conservative figure and is due to slow growth and low mortality in the adults. The foregoing indicates a very stable population dominated by adults and with low recruitment mainly due to high larval and juvenile mortality.

Fig. 10 Survivorship curve for 0 + *a* age classes of *D. serra* on Maitland River beach during 1974.

Salinity tolerances

Figure 11 shows that above a salinity of 17,5°/oo no mortality occurred within four days, while in distilled water 50% mortality took 2,25 days. Having a small posterior gape this species must equilibrate rapidly with the medium so that mortality should occur within a few days in lethal salinities. *D. serra* is thus quite tolerant of lowered salinities and could easily cope with any dilution which might occur as a result of rain or seepage during low tide. Penetration of river mouths would seem quite feasible and is confirmed by Macnae's (1957) record of this species 1 km inside the Swartkops River mouth.

Table 5 Production estimates for *D. serra* on Maitland River beach during 1973/4. P_G = production by growth; P_M = production by mortality; $\bar{P}$=mean or steady state production; $\bar{B}$=mean biomass; ΔB=final biomass – initial biomass; $\bar{N}$=mean numbers

	Age class					
	0+*b*	0+*a*	1+*b*	1+*a*	2+→	Total
P_G mg transect^{-1}y^{-1}	6 595	68 589	26 226	10 950	93 800	206 160
P_M mg transect^{-1}y^{-1}	1 689	55 641	3 764	30 178	– 112 791	– 21 529
$\bar{P}$ mg transect^{-1}y^{-1}	4 137	62 115	14 995	20 564	– 9 496	92 315
$\bar{B}$ mg transect^{-1}	1 228	12 547	19 156	5 688	868 351	906 970
ΔB mg transect^{-1}	4 879	12 948	22 462	– 19 228	206 591	227 652
$\bar{N}$ transect^{-1}	24,4	290	37	11	491	1 073
$\bar{P}/\bar{B}$ y^{-1}	3,37	4,95	0,78	3,62	–	0,10

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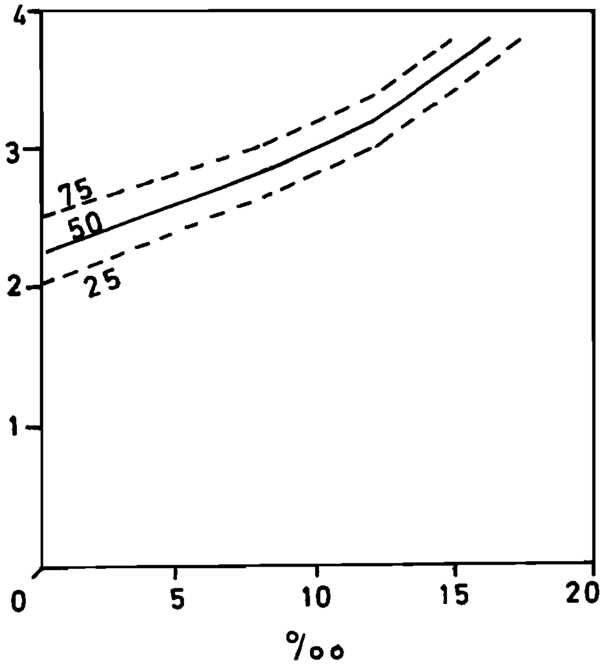

Fig. 11 Curves of 25, 50 and 75% mortality of *D. serra* in various dilutions of seawater for up to four days.

Reproduction

The gonad index is illustrated in Fig. 12 for the period January–November 1974. Two fall-offs indicating spawning are evident during January–April and July–August. Although the summer spawning appears larger than the winter one, the winter age classes were found to be more numerous than the summer ones. This suggests that the full extent of the change in gonad index in winter may not have been recorded and this is verified by Fig. 10 (see later). De Villiers (1973) found two extended spawning seasons, from February to March and May to November, with the latter (corresponding to the winter spawning in the East Cape) being more important.

In *D. serra* East Cape specimens appear to reach sexual maturity between 38 and 49 mm shell length (Hanekom 1975) which is very similar to the 37–54 mm recorded on the west coast (De Villiers 1973). This represents an average of about 44 mm (1,5 years) in the East Cape and 46 mm (two years) on the west coast.

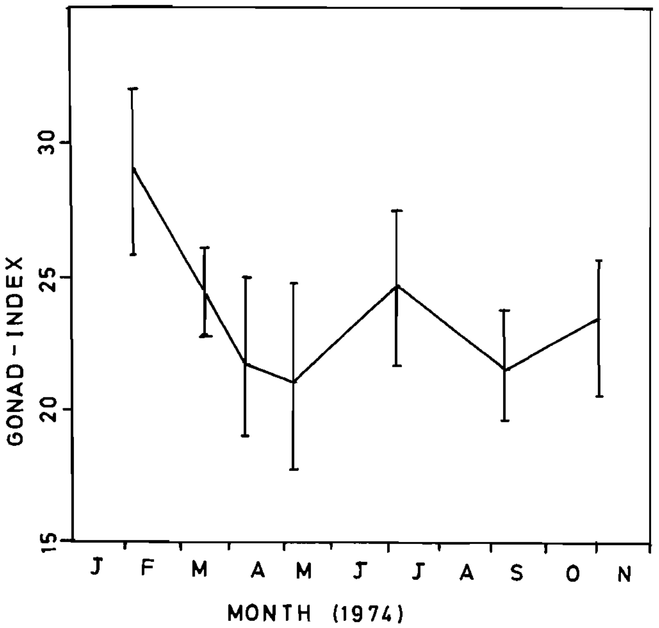

Fig. 12 The mean and standard deviation of the gonad index of *D. serra* during 1974.

A rough estimate of reproductive production (P_R) can be made if it is assumed that each 2+→ individual spawns twice per annum and on each occasion this accounts for 8% drop in gonad index or about 5% of the total dry mass. From Tables 4 and 5 there were on average 491 2+→ individuals with an average mass of 1 769 mg. For this stock P_R may be approximated at 2 × 0,05 × 491 × 1 769 mg transect^{-1}y^{-1} = 86 858 mg transect^{-1}y^{-1} giving a P_R/B of 0,1 for the population. This may be considered an underestimate as will be discussed below under biochemical composition.

Biochemical composition

Results of the analyses are illustrated in Fig. 13. There was a small decline in mass in summer, probably corresponding to spawning, followed by a build-up and then a large drop from June – September. This drop coincides with the estimated winter spawning and the findings of De Villiers (1973) and is also reflected by a drop in energy values from June–August. These data seem to confirm the earlier suggestion of a large winter spawning centered around July–August and a smaller summer spawning around February–March.

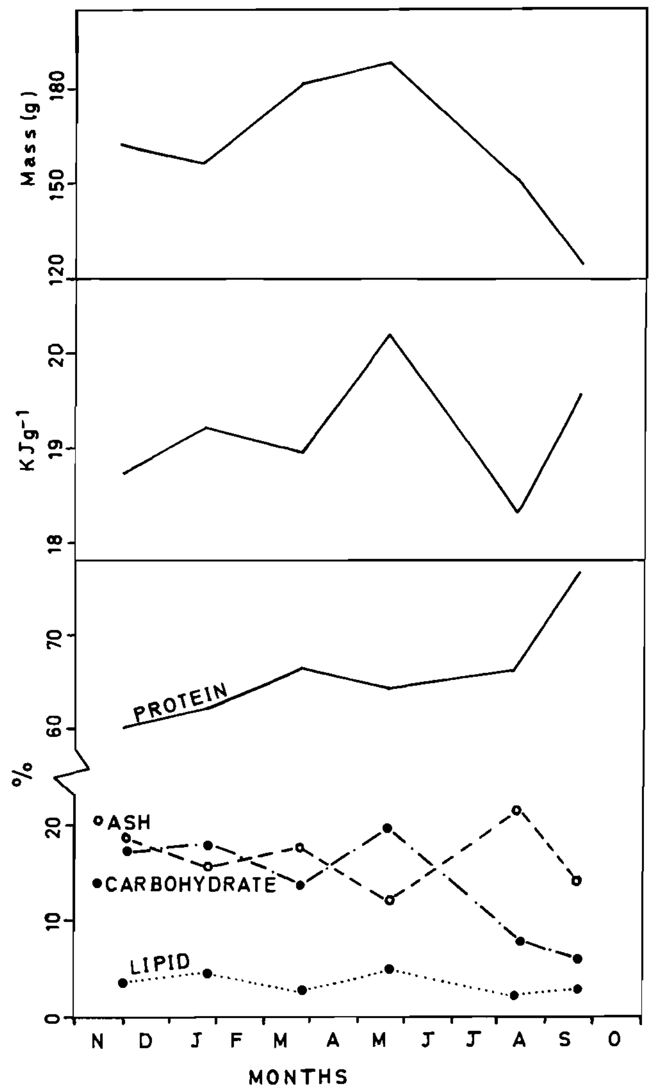

Fig. 13 The seasonal variation in the total dry tissue mass, energy values and biochemical constituents of 55 cm long *D. serra* from Maitland River beach during 1973/4.

Total mass of the standard 55 mm individuals varied between 1 240-1 908 mg during the year with a mean of 1 614 mg and range of 23%. Energy values were $18{,}27-20{,}31\ \mathrm{kJg^{-1}}$ with a mean of $19{,}14\ \mathrm{kJg^{-1}}$. Protein made up 60-77% (mean 66%), Carbohydrate 6-20% (mean 15%), ash 12-22% (mean 17%) and lipid 3-5% (mean 4%). Biochemical composition of various species of *Donax* have been summarized by Ansell *et al.* (1973). Values for *D. serra* reported here are within the recorded range although carbohydrate tends to be high and lipid low. While the temperate species, *D. vittatus,* has regular seasonal changes related to the gonadal cycle and storage and utilization of reserves (Ansell 1972), tropical species such as *D. incarnatus* and *D. spiculum,* show little or no seasonal change except for a mass increase associated with the development of the gonads (Ansell *et al.* 1973). The situation in *D. serra* is closer to that of *D. vittatus,* with fairly distinct seasonal changes which appear to be mainly related to the gonadal cycles. It is noteworthy that in *D. serra* carbohydrate appears to be a more important energy reserve than lipids. This is probably related to its more sedentary habits (Schmidt-Nielsen 1975), large size and lack of the type of tidal migrations found in other species.

Seasonal changes in adults (Fig. 13) indicate a drop in mass of about 6% of the mean after the summer spawning and 50% after the winter spawning. If these mass changes are only due to reproduction and not general changes in condition, then a P_R equal to 56% of the adult biomass or 54% of the population biomass would be expected. This gives a $\bar{P}_R/\bar{B}$ of 0,54. This is a high figure and suggests that growth levels off rapidly after two years and most adult energy goes into spawning. The low estimates based on the gonad index are probably due to the crudeness of this measure.

Conclusions

D. serra is a suspension feeder which sucks in water from the swash zone of these open beaches and subsists mainly on phytoplankton and the organic froth resulting from heavy wave action. Although it appears to prefer open wave-swept beaches where the substrate is not too coarse, the dominant factor affecting population density is available food and large populations only develop where phytoplankton blooms are regularly seen in the surf. Heavy wave action results in a large turnover of water through the surf zone thereby transporting phytoplankton and detritus via the swash to the intertidal zone.

The high position in the intertidal zone occupied by *D. serra* during spring tides has a parallel on New Zealand beaches where Rapson (1952, 1954) studied two species of *Amphidesma.* He found the larger species, *A. ventricosum,* above the mean tide level and the smaller species, *A. subtriangulatum,* towards the low tide levels. These two species thus appear to occupy the same niches as *D. serra* and *D. sordidus* respectively in the East Cape and vast populations also developed in areas of very high phytoplankton production. However, small individuals of *A. ventricosum* were found highest on the shore as for *D. serra* on the west coast.

Day (1969) records *D. serra* from Luderitz to Port Elizabeth, below mean tide level and migrating with the tides. Numerous live *D. serra* have since been collected on the southern Transkei coast, thus extending the range considerably. Further, their spring-tidal position has been shown to be above the mid tide level in the East Cape where they do not undergo normal tidal migration. Semilunar movement up and down the shore has been described elsewhere (McLachlan *et al.* 1979).

D. serra is unique in the genus because of its large size, this probably being the reason for its lack of mobility and tidal migrations and its high position on the shore. Ansell and Trueman (1973) found that maintenance of position on the shore by repeated burrowing in response to erosion and deposition of sand by the waves was more expensive energetically than tidal migration in *Donax.* It is postulated here that because *D. serra* is so large the opposite is the case. Lying deep in the sand, repeated burrowing to maintain position is unnecessary. The large size, however, makes transport by the swash slow, thus requiring a great number of energetically expensive emergences and reburials. During spring tides the mean tide level provides sufficient feeding time but never exposes the animals to the full force of the swash encountered on the lower shore during high tide. During neaps the tide range is halved and a position near the low tide level is safe from excessive deposition or erosion and provides maximum feeding time.

Although this study has not produced accurate growth curves or production figures some estimates have been obtained. Growth is initially rapid but slows considerably after sexual maturity (45 mm) and lengths of about 32 mm, 48 mm and 55 mm are reached at the end of the first three years. After this, growth seems extremely slow with most energy presumably going into reproduction. Lifespan may exceed five years.

Somatic production is low because the population is totally dominated by the adults which are apparently slow-growing and have low mortality rates. Reproductive production is probably relatively high for the same reasons and because spawning occurs twice per annum. Ansell *et al.* (1972b) found very high contributions of reproduction to total production in *D. incarnatus* and *D. spiculum.* Predation on siphons by birds and fish increases production without causing mortality and ongoing work on birds indicates this to amount to about 6 g per metre shoreline per year, a negligible figure in comparison to the biomass. In view of the foregoing, $\bar{P}/\bar{B}$ ratios of 0,2 and 0,5 are proposed for somatic and reproductive production respectively of the Maitland River population.

Predators on East Cape beaches include gulls (*Larus dominicanus*), which break adult *D. serra* shells by dropping them onto the sand from a height of 5 – 8 m, oystercatchers (*Haematopus moquini*), sanderlings (*Calidris alba*) which only nip siphons, elasmobranchs such as sandsharks (*Rhinobatus annulatus*) and duckbill rays (*Myliobatis aquila*), some fish and humans. Juveniles are preyed on mainly by fish and sandsharks and suffer high mortalities.

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