Growth and reproduction of two molluscs from an exposed sandy beach

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Populations of a gastropod, *Bullia rhodostoma*, and a bivalve, *Donax sordidus*, were monitored quantitatively over one year on an exposed sandy beach which supports a rich macrofauna. *B. rhodostoma* had a single reproductive season with copulation in early summer. Growth was slow and is described by a Von Bertalanffy growth curve. The annual mortality rate was very low, – 0,34. Production was estimated and a $\bar{P}/\bar{B}$ ratio of 0,94 obtained. A minimum estimate for production by reproduction gave a P_R/B of 0,06. The average calorific value was 19,34 kJg $^{-1}$. *D. sordidus* appeared to have two spawning seasons and settlements in late winter and late summer. Growth was rapid and mortality moderate – 0,72. Steady state $\bar{P}/\bar{B}$ was estimated to be 1,78. The mean calorific value was 18,84 kJg $^{-1}$. All of these values for both species are compared to those obtained on a nearby sheltered beach which has a poor macrofauna.
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Bevolkings van 'n spesie van Gastropoda, *Bullia rhodostoma*, en een van die Pelecypoda, *Donax sordidus*, was kwantitatief oor 'n periode van een jaar op 'n oop strand waar 'n ryk makrofauna voorkom, gemonster. *B. rhodostoma* het 'n broeiperiode wat in die somer voorkom. Groei was stadig en word beskryf deur 'n Von Bertalanffy groeikurwe. Jaarlikse mortaliteit was baie laag, – 0,34. Produksie was bereken en 'n gemiddelde $\bar{P}/\bar{B}$ van 0,94 verkry. 'n Minimum waarde vir produksie deur reproduksie het 'n P_R/B van 0,06 gegee. Die gemiddelde energiewaarde was 19,34 kJg $^{-1}$. *D. sordidus* het twee onduidelike kuitskietseisoene getoon met neerlegging in die laat winter en laat somer. Groei was vinnig en mortaliteit matig – 0,72. Die gemiddelde $\bar{P}/\bar{B}$ was 1,78 en die gemiddelde energiewaarde 18,84 kJg $^{-1}$. Al hierdie parameters vir albei spesies word vergelyk met dié verkry van 'n meer beskutte strand waar minder makrofauna voorkom.
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In two earlier papers growth and production of *Bullia rhodostoma* Reeve and *Donax sordidus* Hanley were described for an open sandy beach in Algoa Bay (McLachlan, Cooper & Van der Horst 1979; McLachlan 1979). The aim of the present work was to do a comparative study on these two species on another beach, Maitland River beach, which experiences much greater wave action, has a richer food supply and supports considerably higher biomass values (McLachlan 1977). Both species are important on East Cape beaches, exhibit tidal migratory behaviour (McLachlan, Wooldridge & Van der Horst 1979) and attain a greater size on Maitland River beach than on any other beach in the area. It was thought that this greater size may be a result of different growth rates and that production may thus also differ from other beaches.

Materials and Methods

Maitland River beach is a very exposed, south-facing sandy beach which has already been described (McLachlan 1977). It usually has a gentle slope (1/30 – 1/40) and medium quartz sand with extensive dunes above the drift line. There is a broad surf zone with waves first breaking 200 – 500 m from the shore. The presence of vast macrofaunal populations suggests that large quantities of available food in the form of carrion and phytoplankton and particulate matter are supplied to this beach. During offshore easterly winds upwelling can sometimes occur and water temperatures as low as 10 °C can then be recorded in summer.

Sampling was carried out approximately every six weeks from July 1977 to July 1978 using a dredge 0,5 m wide with 1,5 mm mesh. A series of hauls each 10 m long and cutting to 5 cm in the sand were staggered so as to cover the shore from ELWS to just above the mean tide level. The total area so sampled varied between 20 and 60 m² on different occasions. All individuals collected were measured to the nearest 1 mm greatest shell-length using sliding callipers.

Animals were also collected for determination of length/mass relationships and calorific contents. After removal of shells animals were dried for 24 h at 90 °C. This was done in preference to treating shells with hydrochloric acid and collecting the organic remains together with the tissues on glass-fibre filter paper (McLachlan, Cooper & Van der Horst 1979) as the latter method is considered less accurate due to variability in mass of the filter paper. For determination of energy contents, tissue from a number of animals was pooled to make pills for combustion in an adiabatic bomb calorimeter.

From the shell length measurements size/frequency histograms were constructed and year classes separated using probability paper (Cassie 1954). A Von Bertalanffy growth curve was computed for *B. rhodostoma* using a Ford-Walford plot to estimate constants L_∞ and K (Crisp 1971). The age-specific mortality rate was calculated from the slope of the survivorship curve *l*n (numbers) against age (Crisp 1971).

Production was calculated for each year class over the whole year as both growth (P_G) and mortality (P_M), as done previously (McLachlan, Cooper & Van der Horst 1979; McLachlan 1979) and described by Crisp (1971). An attempt was also made to estimate production by reproduction (P_R) in *B. rhodostoma* by using length/mass regressions to estimate the mass differences between ripe and non-ripe individuals.

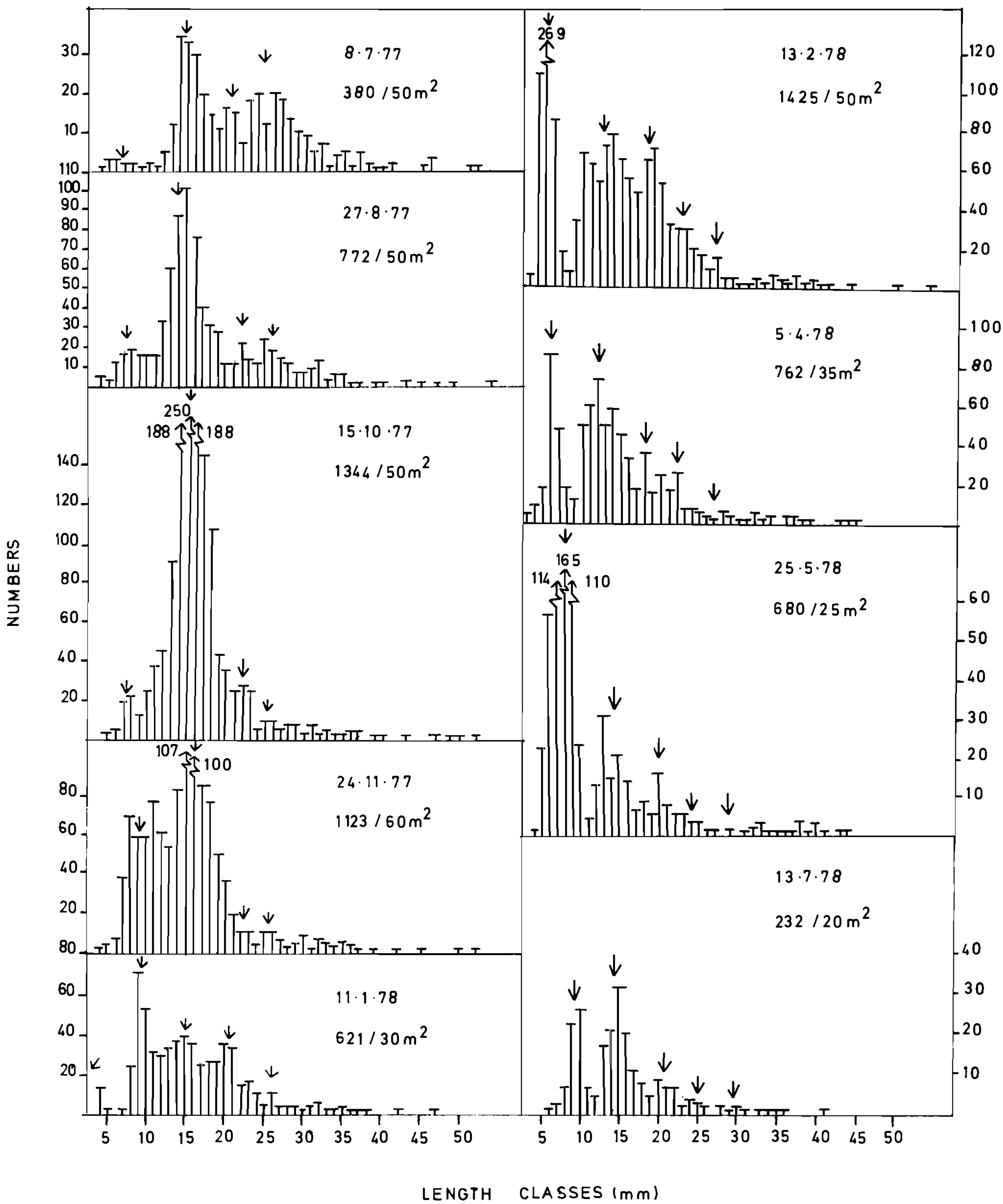

Fig. 1 Size/frequency histograms for *B. rhodostoma* on Maitland River beach at nine sampling times during 1977/8. Included in each histogram is the date of sampling, total numbers collected and total area sampled. Arrows indicate mean lengths for year classes.

Results

Bullia rhodostoma

Growth

Size-frequency histograms are shown in Fig. 1. The largest specimen collected was 55 mm, 15 mm larger than the maximum on Kings Beach (McLachlan, Cooper & Van der Horst 1979). However, individuals over 40 mm were never abundant in the samples. The smallest year class (0+) first appeared at 3 mm and longer because the dredge loses smaller individuals in the 3 mm size class. 0+ individuals were first evident in January and were abundant by February. Copulating pairs were seen from November to early February suggesting that peak hatching (Brown 1971) must occur in early January. Analysis of these histograms (Table 1) allows separation of the first four year classes and estimation of their numbers. Numbers and mean length of the 0+ class during January are estimated from back extrapolation of the survivorship curve (see Mortality below, and Fig. 4). Dry mass values in Table 1 were calculated from the following regression based on animals collected during April:

$$\log_{10} [\text{dry mass(mg)}] = 2{,}7 \log_{10} [\text{length(mm)}] - 1{,}77$$
$$(r = 0{,}98, p < 0{,}001, 31\text{d.f})$$

L_∞ (Fig. 2) was found to be 50 mm, which is smaller than the maximum size recorded, and altogether seven individuals of 51 – 55 mm were among the 2 339 collected. The growth curve (Fig. 3) is very similar to that calculated for the Kings Beach population, predicting a length of 42 mm at 10 years as opposed to 40 mm at 10 years on Kings Beach.

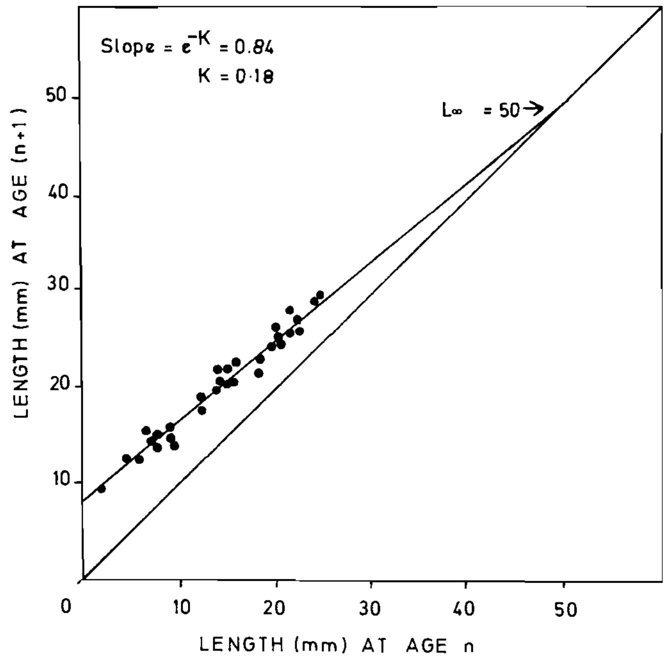

Fig. 2 Ford-Walford plot showing the constants L_∞ and K for *B. rhodostoma* on Maitland River beach.

Samples taken in 10 m strips from below LWS to above MTL indicated a vertical zonation of size classes (Table 2) with smallest individuals highest on the shore. This size decrease up the shore was found to be highly significant ($r_s = 1$, $p < 0{,}05$) using Spearman's Rank Correlation. A similar intertidal zonation of size classes was found by McLachlan, Wooldridge and Van der Horst (1979).

Table 1 Numbers per m² (N); mean lengths ($\bar{L}$) in mm; and mean dry mass values ($\bar{W}$) in mg of different year classes of *B. rhodostoma* at nine sampling dates on Maitland River beach

	0+ Year class			1+ Year class			2+ Year class		
Date	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$
8. 7.77	0	—	—	0,29	7,0	3,9	3,20	15,3	34,4
28. 8.77	0	—	—	1,86	7,5	4,7	10,03	14,4	28,9
15,10.77	0	—	—	1,21	7,6	4,9	23,67	15,0	32,4
24.11.77	0	—	—	6,05	9,5	9,1	11,07	15,8	37,6
11. 1.78	4,80[1]	2,0[1]	0,1	6,40	9,4	8,8	6,62	15,0	32,4
13. 2.78	9,80	4,8	1,3	10,38	12,5	19,5	4,62	18,5	58,2
5. 4.78	5,35	6,0	2,5	9,92	12,5	19,5	3,24	18,2	55,6
25. 5.78	19,81	7,8	5,2	3,99	14,0	26,7	1,86	19,9	71,5
13. 7.78	3,51	9,5	9,1	5,57	14,6	30,0	1,39	20,6	78,7

	3+ Year class			4+ Year class			5+→ Year classes		
Date	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$
8. 7.77	0,80	20,5	77,7	2,02	25,3	139,0	1,36	34,1	321,4
28. 8.77	1,10	22,0	94,2	1,20	25,5	143,1	1,31	33,0	293,8
15.10.77	0,97	22,0	94,2	0,60	25,5	143,1	0,54	32,7	286,4
24.11.77	0,60	22,3	98,0	0,50	25,7	145,9	0,52	33,2	297,6
11. 1.78	5,18	20,5	77,7	0,83	26,0	150,7	0,97	34,1	321,4
13. 2.78	2,20	22,5	100,5	0,64	27,0	166,8	0,79	35,1	347,2
5. 4.78	2,16	21,6	90,2	0,39	28,0	184,9	0,74	34,2	323,6
25. 5.78	0,65	24,4	125,8	0,04	29,0	203,7	0,80	36,8	397,2
13. 7.78	0,50	24,7	130,6	0,30	29,3	210,4	0,25	35,8	367,7

[1] Estimated values, see text.

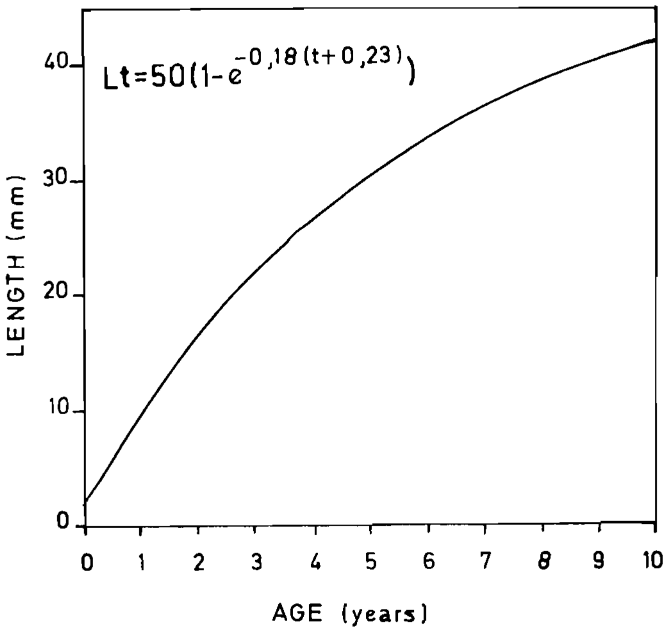

Fig. 3 The Von Bertalanffy growth curve for *B. rhodostoma* on Maitland River beach.

Table 2 Numbers (N); mean lengths ($\bar{L}$) in mm; and range of lengths of *B. rhodostoma* and *D. sordidus* recorded per 10 m² at six sampling levels from just below ELWS (Site 1) to just above MTL (Site 6) on Maitland River beach during November 1977

	B. rhodostoma			*D. sordidus*		
Site	N	$\bar{L}$	Range	N	$\bar{L}$	Range
1	0	—	—	78	9,2	4-22
2	4	36,8	30-52	76	15,1	2-26
3	49	20,5	9-50	197	16,3	3-27
4	372	17,2	7-52	66	15,6	5-25
5	662	14,0	5-35	8	9,8	4-24
6	35	12,9	7-26	0	—	—

Mortality

Survivorship is plotted in Fig. 4 assuming that peak hatching is on 1 January each year and that approximately the same numbers hatched during each of the previous years. The age specific mortality rate Z = 0,42 years^{-1}. The annual mortality rate $(1-e^{-z})$ is 0,34, which is considerably lower than on Kings Beach where annual mortality was 0,79. This is probably the main reason why few individuals reach a large size on Kings Beach.

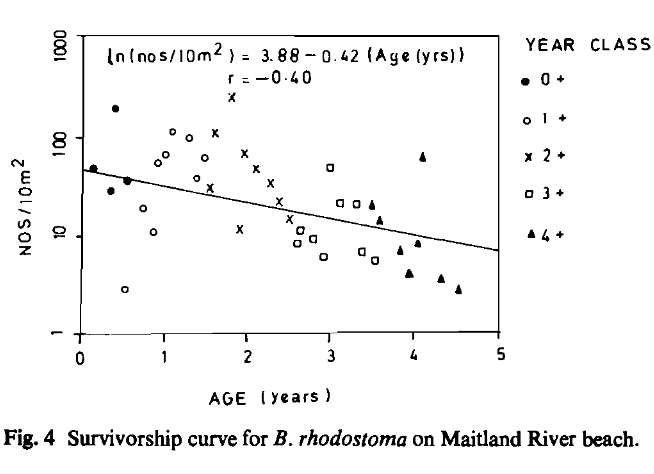

Fig. 4 Survivorship curve for *B. rhodostoma* on Maitland River beach.

Production

Production estimates (Table 3) are similar to those found on Kings Beach. There was a nett drop in biomass over the year with P_M consequently exceeding P_G. $\bar{P}/\bar{B}$ (steady state) ratios were highest for the younger, faster-growing classes and dropped for the older classes with an overall $\bar{P}/\bar{B}$ of 0,94. This agrees well with the value of 0,90 for Kings Beach. On Kings Beach mortality is higher and younger classes more dominant. This should result in a higher $\bar{P}/\bar{B}$ than on Maitland River Beach. However, growth is slightly faster at the latter locality and this can raise production. The mean biomass during the study was 897,96 mgm^{-2} and mean numbers 20,28 m^{-2}. If these figures are multiplied by 45 m intertidal distance sampled, the result is 40,41 g biomass and 912,6 individuals per metre shoreline.

Reproductive output

Animals collected on 1 October and 1 November gave the following length/mass regressions:

1 October ... $\log_{10}$ [mass(mg)] = 2,85 $\log_{10}$ [length (mm)] − 1,82 (r=0,98; $p < 0,01$, 26 d.f.)

1 November ... $\log_{10}$ [mass (mg)] = 2,96 $\log_{10}$ [length (mm)] − 1,99 (r=0,96; $p < 0,01$, 18 d.f.)

Using these two equations and the April regression, mass values of standard animals may be compared as an indication of the reproductive season. For an animal of 15,4 mm length (2+ age class in October/November) mass values of 34,9 mg, 36,6 mg and 33,5 mg are obtained for April, October and November respectively. For a 33 mm animal (5 + → age classes) values are 293 mg, 322 mg and 320 mg, and for the largest animals of about 50 mm they are 934 mg, 1 052 mg and 1 094 mg. Mass values thus increase from April to 1 October. From then to 1 November there is a slight decrease in mass of small individuals (males), little change in medium-sized individuals (both sexes) and a slight increase in large individuals (females). (Recent work indicates a sex change with age (Van der Horst, *unpublished.*)) This suggests copulation and some spawning between 1 October and 1 November, this involving mainly males and smaller females. Although maximum ripeness may therefore occur in mid-October, the 1 October regression may be used to derive P_R by difference in mass of adults (2+, 3+, 4+ and 5+ → age classes) during October/November from their April values. This gives P_R = 58,15 mgm^{-2}y^{-1} and a $P_{R/B}$ of 0,06. This is undoubtedly an underestimate and McLachlan, Cooper and Van der Horst (1979) estimated $P_{R/B}$ of 0,5 for this species on Kings Beach based on decalcified dry mass, a less accurate method. As the latter value is probably too high and the value derived here an under estimate, it is suggested that a $P_{R/B}$ of 0,3 may be representative.

Energy values

Energy values were measured on only five occasions and showed a range of 17,92−20,74 kJg^{-1} with a mean of 19,34 kJg^{-1}. This is slightly higher than the Kings Beach mean of 19,04 kJg^{-1}.

Table 3 Production by growth by (P_G); production by mortality (P_M); annual change in biomass (ΔB); mean biomass ($\bar{B}$); mean or steady state $\bar{P}/\bar{B}$ ($\bar{P}/\bar{B}$); mean production ($\bar{P}$); and mean numbers ($\bar{N}$) of different year classes of *B. rhodostoma* on Maitland River beach during 1977/8

	Age class						
	0+	1+	2+	3+	4+	5+→	Total
P_G mgm^{-2}y^{-1}	97,77	170,17	253,95	74,45	37,67	25,81	659,82
P_M mgm^{-2}y^{-1}	65,83	4,20	254,64	71,31	255,33	370,99	1 022,30
ΔB mgm^{-2}y^{-1}	31,94	165,97	−0,69	3,14	−217,66	−345,18	−362,48
$\bar{B}$ mgm^{-2}	17,95	88,52	276,55	142,38	109,61	262,95	897,96
$\bar{P}/\bar{B}$	4,56	0,98	0,92	0,51	1,34	0,75	0,94
$\bar{P}$ mgm^{-2}y^{-1}	81,80	87,19	254,30	72,88	146,50	198,40	841,07
$\bar{N}$ m^{-2}	4,81	5,07	7,30	1,57	0,72	0,81	20,28

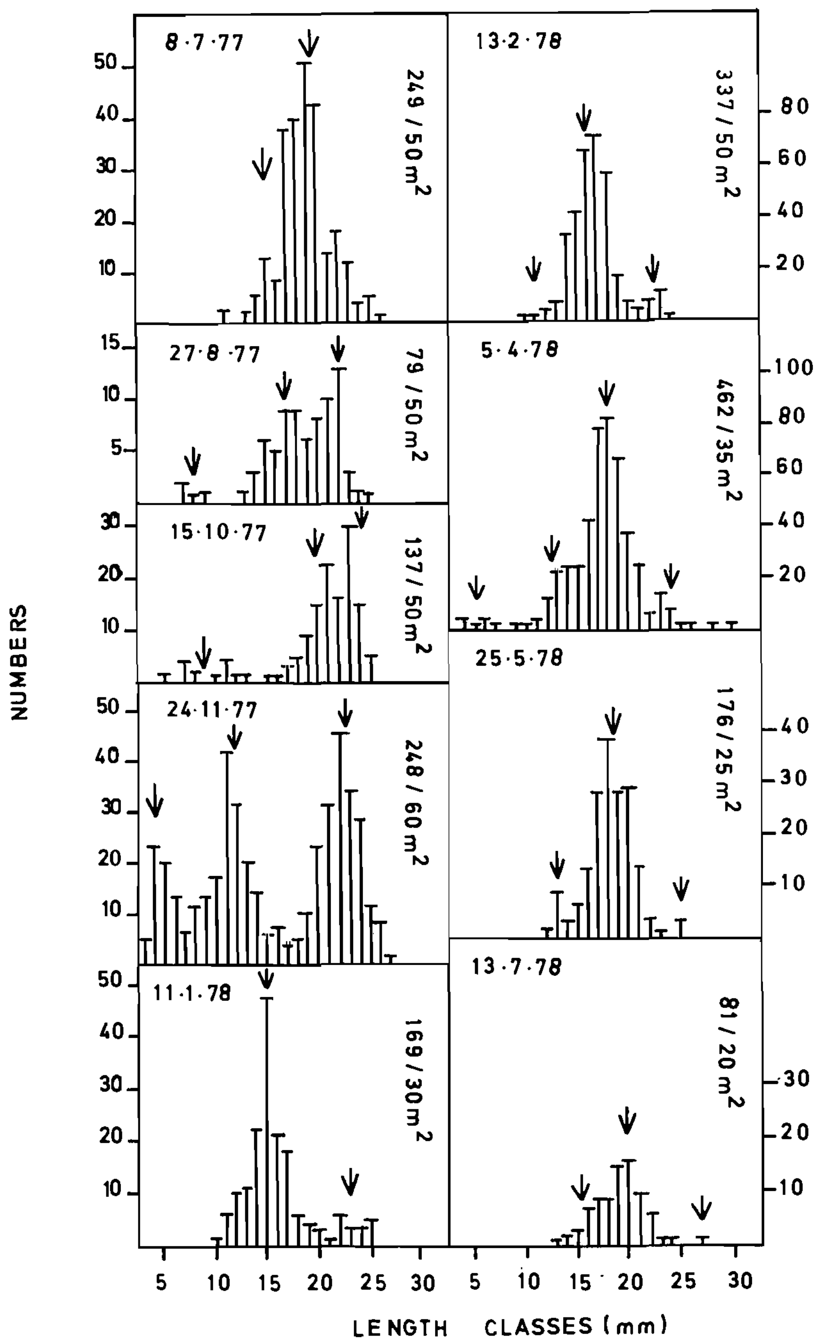

Fig. 5 Size frequency histograms for *D. sordidus* on Maitland River beach during 1977/8. Included in each histogram is the sampling date, the area sampled and the total number of animals collected. Arrows indicate the mean lengths of age classes.

Donax sordidus

Growth

The size frequency histograms (Fig. 5) show an individual length range of 2–30 mm while the largest recorded on Kings Beach was 28 mm. Two age classes were evident in July 1977 although a third became evident at 8 mm in

Table 4 Number per m² (N); mean lengths in mm ($\bar{L}$); and mean mass value in mg ($\bar{W}$) of different age classes of *D. sordidus* at nine sampling dates on Maitland River beach

	0 + *b*			0 + *a*			1 + *b*		
Date	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$
8. 7.77	0	—	—	0	—	—	0	–	–
27. 8.77	0	0	0	0	—	—	0,08	7,8	4,7
15.10.77	0	—	—	0	—	—	0,28	9,5	8,0
24.11.77	0	—	—	4,00[1]	4,0[1]	0,8	2,75	11,7	13,8
11. 1.78	0	—	—	0	—	—	4,93	15,0	26,6
13. 2.78	0	—	—	0,08	11,0	11,6	6,26	16,6	34,8
5. 4.78	4,47[1]	5,0[1]	1,5	1,23	12,5	16,4	10,88	18,0	43,0
25. 5.78	0	—	—	0,56	13,0	18,2	6,36	18,5	46,2
13. 7.78	0	—	—	0,70	15,5	29,0	3,30	19,8	55,5

	1 + *a*			2 + *b*		
Date	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$
8. 7.77	1,03	15,4	28,6	3,95	19,5	53,2
27. 8.77	0,72	17,0	36,9	0,78	22,0	73,0
15.10.77	1,38	20,4	60,0	1,08	23,6	88,1
24.11.77	3,30	22,2	74,7	0	—	—
11. 1.78	0,70	23,0	82,4	0	—	—
13. 2.78	0,48	22,7	79,4	0	—	—
5. 4.78	0,63	23,8	90,2	0	—	—
25. 5.78	0,12	25,0	102,5	0	—	—
13. 8.78	0,05	27,0	125,2	0	—	—

[1] Estimated values, see text.

August. This latter class must have been present during July although not collected. In November an 0+ class appeared at 4 mm and in April another appeared at about 5 mm, these coming from winter and summer spawning and being called the 0 + *a* and 0 + *b* classes respectively. Analysis of these histograms in Table 4 includes conversion of mean lengths of age classes to mean mass values using the following regression based on animals collected during April:

$\log_{10}$ [mass(mg)] $= 2,64 \log_{10}$ [length(mm)] $- 1,68$ ($r = 0,96; p < 0,001$; 24 d.f.)

Numbers of 0 + *a* individuals during November and 0 + *b* individuals during April have been estimated by back extrapolation of the survivorship curve (see Mortality below, and Fig. 7). Small specimens were generally scarce and during May and July 1978 no 0 + *b* individuals could be found. This is because they occur subtidally while small. McLachlan, Wooldridge and Van der Horst (1979) found an intertidal zonation of size classes with the smallest lowest on the shore. However, such a pattern was not evident during this study (Table 2).

Growth is plotted in Fig. 6 for *a* and *b* classes assuming peak settlement on 1 August and 1 February respectively. Lines drawn by eye through these points produce two undulating curves roughly six months out of phase. This may be explained by the fact that both classes experience faster growth in summer and slower growth in winter. The size reached at one year, about 16 mm for both classes, is smaller than the 20 mm found for the Kings Beach population. This may be due partly to settlement being slightly later than estimated and consequently the animals being

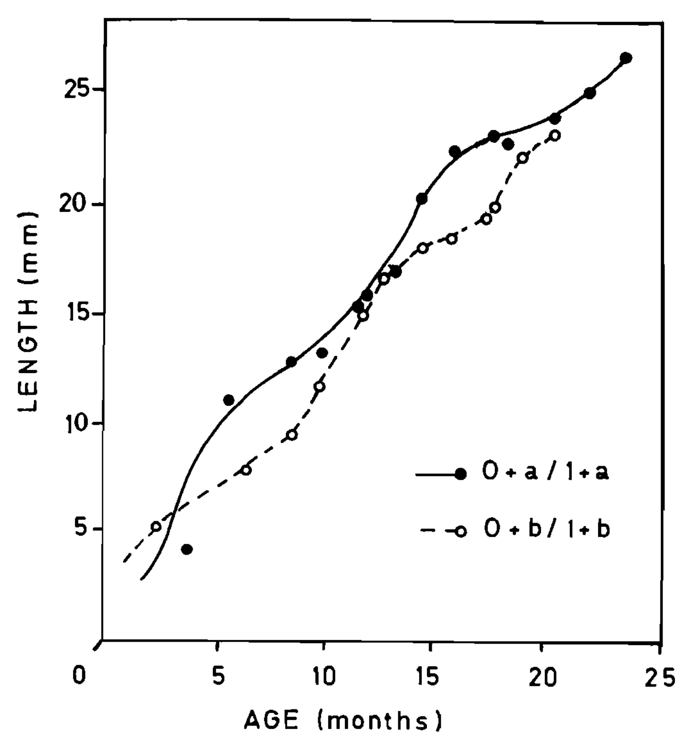

Fig. 6 Growth curves for *a* and *b* classes of *D. sordidus* on Maitland River beach during 1977/8.

younger. The colder water during occasional upwellings may also be important. Where a length of 25 mm was reached at 20 months on Kings Beach this was attained at 22 months on Maitland River beach. Thus if spawning and settlement at Maitland River beach were about two months later than estimated (which is 2,5 months later than on

Kings Beach), growth rates would be the same as at Kings Beach.

Mortality

Figure 7 shows a plot of *ln* (numbers) against age, assuming peak settling of the *a* and *b* classes as being 1 August and 1 February respectively. The age specific mortality rate $Z = 1{,}27\ y^{-1}$ which gives an annual mortality rate $(1 - e^{-z})$ of 0,72. Mortality appears to increase towards two years of age as very few specimens exceed 25 mm and they probably die after their second spawning. Mortality on Kings Beach was higher: 0,86. Absence of small individuals, which have the greatest mortality, is probably the cause of the low mortality rate on Maitland River beach. Sampling of small individuals may have been quantitatively incomplete in which case the above mortality estimate would be too low.

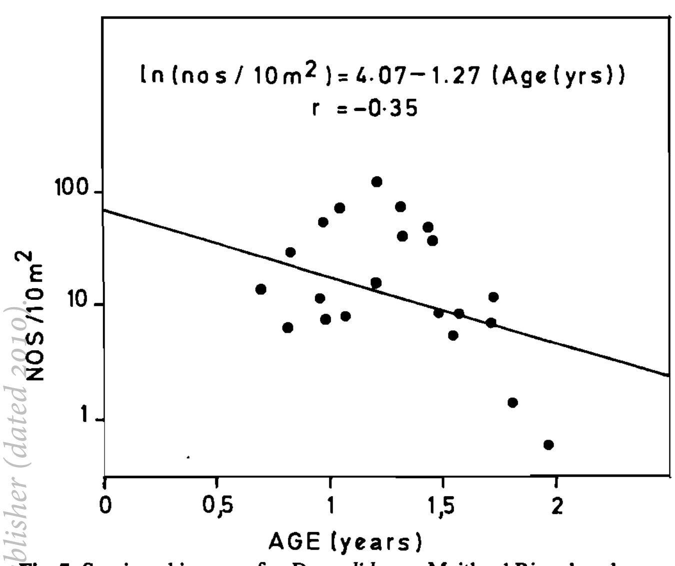

Fig. 7 Survivorship curve for *D. sordidus* on Maitland River beach.

Production

Production estimates (Table 5) show a nett drop in biomass over the study year and thus P_M greater than P_G. Steady state $\bar{P}/\bar{B}$ ratios were highest for the younger classes and the overall $\bar{P}/\bar{B}$ was 1,78. On Kings Beach $\bar{P}/\bar{B}$ values of 1,55 and 1,03 were recorded over two years. For a species with rapid growth a $\bar{P}/\bar{B}$ above 2 would be expected (Zaika 1972; Chambers & Milne 1975). Considering the scarcity of small individuals intertidally the Maitland River $\bar{P}/\bar{B}$ of 1,78 for somatic production appears reasonable.

Total $\bar{P}$ for the winter (*a*) classes was 129,71 $mgm^{-2}y^{-1}$ while that for the summer (*b*) classes was 328,45 $mgm^{-1}y^{-1}$. This confirms the findings on Kings Beach that the summer spawning and settlements is of greater importance than that during winter. The mean biomass was 257,18 mgm^{-2} and mean numbers 6,68 m^{-2} which convert to 11,57 g and 300,6 individuals per metre shoreline.

Energy values

Energy values measured on five occasions varied between 17,49 and 20,38 kJg^{-1} with a mean of 18,84 kJg^{-1}, this being substantially above the Kings Beach mean of 17,84 kJg^{-1} but close to values recorded for other species of *Donax* (Ansell 1972; Ansell *et al.* 1973).

Discussion

The pattern emerging for *B. rhodostoma* on Maitland River beach is very similar to that found on Kings Beach by McLachlan, Cooper and Van der Horst (1979). The average values for East Cape beaches may thus be suggested as follows: copulation mainly October/November and hatching of juveniles December/January each year; growth fairly slow to 40 − 42 mm at 10 years and mortality low, between 0,3 − 0,8; steady state $\bar{P}/\bar{B}$ for somatic production 0,92 and for reproduction (P_R) 0,3; the latter due to a significant contribution by old individuals; average energy value of dry tissues 19,19 kJg^{-2}.

The presence of larger individuals on Maitland River beach seems a result of lower mortality rates and slightly faster growth and confirms Brown's (1971) contention that *Bullia* may attain an age of 20 years. Almost no predators on *Bullia* are known and despite inspection of stomachs of numerous birds and fishes the only definite predators to date are the crab *Ovalipes punctatus* (De Haan) and the sanderling, *Calidris alba.* Low predation is therefore the main cause of the low mortality rate.

The findings for *D. sordidus* on Maitland River beach are also very similar to those on Kings Beach (McLachlan 1979) and the following generalizations can be made for the East Cape: spawning occurs twice annually, in early summer and early winter; spat settle in mid summer and late winter, the summer sattlement being greatest; growth is very rapid to 16 − 20 mm within one year and the animals

Table 5 Production by growth (P_G); production by mortality (P_M); annual change in biomass (ΔB); mean biomass (B); steady state $\bar{P}/\bar{B}$ ($\bar{P}/\bar{B}$); mean production ($\bar{P}$); and mean numbers ($\bar{N}$) of age classes of *D. sordidus* on Maitland River beach during 1977/8

	Age class					
	0 + *b*	0 + *a*	1 + *b*	1 + *a*	2 + *b*	Total
P_G $mgm^{-2}y^{-1}$	6,71	35,22	247,45	92,35	60,97	442,70
P_M $mgm^{-2}y^{-1}$	6,71	16,49	64,23	115,35	271,01	473,79
ΔB $mgm^{-2}y^{-1}$	0,00	20,30	183,15	−23,20	−210,14	−29,89
$\bar{B}$ mgm^{-2}	0,75	6,09	148,26	61,83	40,25	257,18
$\bar{P}/\bar{B}$	8,95	4,25	1,05	1,68	4,12	1,78
$\bar{P}$ $mgm^{-2}y^{-1}$	6,71	25,86	155,84	103,85	165,90	458,25
$\bar{N}$ m^{-2}	0,50	0,73	3,87	0,93	0,65	6,68

die after about two spawning seasons, generally before they reach two years; mortality during the first 1,5 years, is probably around 0,7 – 0,9; steady state $\bar{P}/\bar{B}$ is probably about 1,7 for somatic production only and the average energy value is 18,34 kJg^{-1} dry tissue.

On Maitland River beach energy values for *Donax* and *Bullia* tissues are generally higher than those on Kings Beach and this is almost certainly the result of more available food. In growth, however, there is a discrepancy as *B. rhodostoma* grew faster on Maitland River beach while *D. sordidus* grew faster on Kings Beach. Slower growth of *D. sordidus* on Maitland River beach may possibly be due to the presence of vast populations of the large sand mussel, *D. serra*, which is virtually absent on Kings Beach.

It has been stated (Brown 1964) that particulate food is in constant supply on the sandy beach while the presence of carrion is erratic. However, the great success of scavenging *Bullia* species on East Cape beaches suggests that input of carrion from the sea and land is perhaps not as erratic as might be thought. The vast populations of *D. serra* (McLachlan 1977; McLachlan & Hanekom 1979) leave no doubt, however, that in total quantity particulate food dominates on most beaches.

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