Growth and production of *Donax sordidus* Hanley on an open sandy beach in Algoa Bay

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A population of *Donax sordidus* (Mollusca, Pelecypoda) has been studied for two years on an open sandy beach. There were summer and winter settlements each year with the former being larger. Growth was rapid, the animals reaching 20 mm length within one year. Few live longer than 17 months. Production averaged 168,7 mg dry matter $m^{-2}y^{-1}$ and the steady state $\bar{P}/\bar{B}$ was $1,30y^{-1}$. Energy values averaged 17,84 kJg^{-1} dry tissue and had a seasonal cycle with maximum values before spawning.

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'n *Donax sordidus* (Mollusca, Pelecypoda) bevolking is oor twee jaar op 'n oop sand strand bestudeer. Vestiging van larwes het in die somer en die winter plaasgevind met die somer vestiging die grootste. Groei was vinnig en die diere was 20 mm lank binne die eerste jaar. Min diere lewe langer as 17 maande. Produksie was gemiddeld 168,7 mg m^{-2} j^{-1} en die gemiddelde $\bar{P}/\bar{B}$ was $1,30y^{-1}$. Energiewaardes was gemiddeld 17,84 kJg^{-1} droë weefsel en het 'n seisoenale siklus met maksimum waardes net voor kuitskieting.

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Bivalves of the genus *Donax* inhabit intertidal sandy beaches in many parts of the world. They have attracted the attention of marine biologists because of the extensive populations that develop in such apparently impoverished environments (Coe 1955; Nayar 1954; Loesch 1957; Edgren 1959; Wade 1965; Smith 1971; Ansell *et al.* 1972*a, b;* McLusky *et al.* 1975; De Villiers 1974; Hanekom 1975; Mouëza & Chessel 1976) and because of their tidal migratory behavior (Mori 1938, 1950; Turner & Belding 1957; Wade 1967; Ansell & Trevallion 1969; Ansell & Trueman 1973; Trueman 1971).

On South African shores only the large species, *D. serra* Röding, has been studied (de Villiers 1974, 1975; Hanekom 1975) and nothing is known of the biology of the smaller *D. sordidus* Hanley, which is common on East Cape shores where it is the third most important macrofaunal species in terms of biomass (McLachlan 1977*a*). Unlike *D. serra* it is a tidal migrant (McLachlan *et al.* in press).

The aim of this study was to monitor a *D. sordidus* population over two years so that growth and production could be determined and a $\bar{P}/\bar{B}$ ratio obtained that may be applied to other beaches in the area.

Material and Methods

The study area, Kings Beach, is an open sandy beach the general features of which have already been described (McLachlan 1977*b*). Approximately every six weeks from November 1975 to November 1977 about 50 m^2 were sampled by dredge to 5 cm depth in the sand between the mid and spring low tide levels. All animals were measured to 1 mm greatest shell length with sliding callipers. During November 1975 a size range of animals was collected for determination of a length/mass relationship. Shell lengths were measured to 0,1 mm and after decalcification of the shell in hydrochloric acid soft parts were trapped on glass fibre filter paper and oven-dried at 95° C for 24 hours before weighing. On various occasions dried tissue from many animals was pooled for combustion in an adiabatic bomb calorimeter.

Age classes were separated from size-frequency histograms using probability paper (Cassie 1954). The age-specific mortality rate was calculated from the slope of the

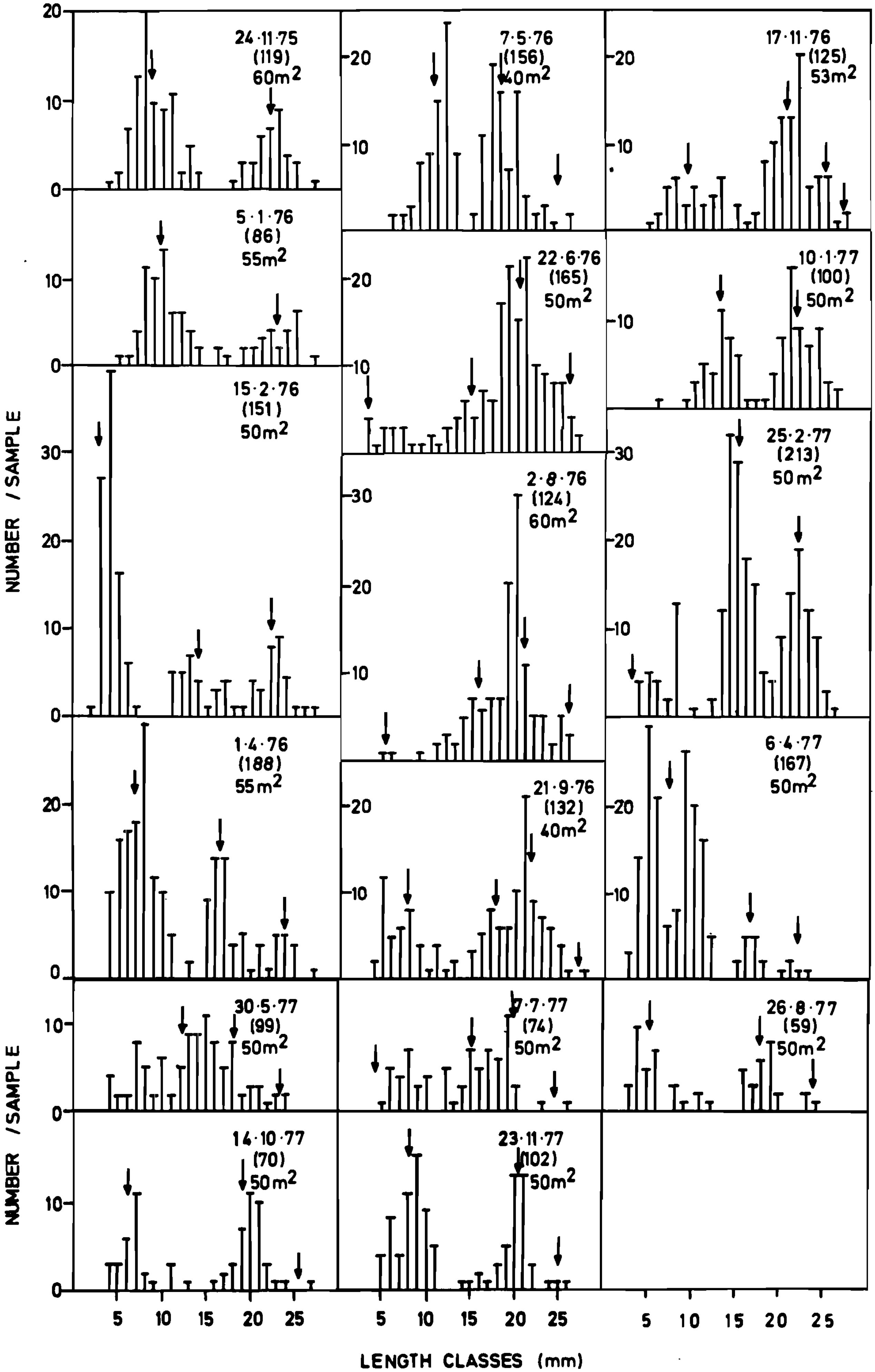

Fig. 1 Size/frequency histograms for *D. sordidus* on Kings Beach during 1975 - 77. Included in each histogram is the sampling date, the area sampled and the total number of animals collected. Arrows indicate mean lengths of age classes.

regression for *ln* (numbers) against age (Crisp 1971). Production was calculated for each year class during each year as both growth (production) and mortality (elimination) (Crisp 1971):

$$P_M = \sum_t \Delta N_t \,.\, \overline{W}_t$$

where P_M is the production by mortality of a year class, ΔN_t is the decrease in its numbers over time interval t, and $\overline{W}_t$ is its mean mass over time interval t, and

$$\sum_t \Delta W_t \,.\, \overline{N}_t$$

where P_G is the production by growth of a year class, ΔW_t is the increase in its mean mass over time interval t, and $\overline{N}_t$ is the mean number of individuals in the year class over time interval t.

Results

Growth

The size-frequency histograms for *D. sordidus* on Kings Beach during 1975-1977 are shown in Fig. 1. Two age classes were evident in November 1975 and January 1976, both originating from spawning periods during 1975, and they were named the 1 + *a* and 1+ *b* classes (mean lengths 22,0 mm and 8,6 mm respectively). In February 1976 a new age class had appeared, the 0 + *a* class and in June 1976 a less distinct new class, the 0 + *b* class, also appeared. Individuals of these small classes first appear at a length of 3-4 mm as the dredge loses individuals smaller than about 3 mm. By November 1976 the 1 + *a* age class had almost disapeared and only a few individuals remained at 26-27 mm; the 1 + *b* class had reached nearly 25 mm; the 0 + *a* class about 20 mm and the 0 + *b* class about 10 mm. Approximately the same pattern was repeated in 1977 with the old 0 + *a* and 0 + *b* classes now becoming the new 1 + *a* and 1 + b classes. Again the winter settling (0 + *b*) was much smaller than the summer settling. Both new classes tended to exhibit a bimodal size distribution, this being very clear in the 0 + *a* class during April 1977. This is probably due to each spawning season being extended and possibly with a lag in the middle or otherwise a temporary unfavourable change in the environment. (Histological data (van der Horst *pers. comm.* indicates two.) extended spawning seasons, one in summer from October to February and one in winter from May to July). As this bimodal distribution becomes indistinct later, the size distribution of these classes was treated as being unimodal.

Table 1 shows mean lengths, mean numbers and mean mass values of each class from each sample. As the dredge missed individuals less than 3 mm the initial numbers of the youngest age classes were estimated by back-extrapolation of the survivorship curve (Fig 3; *Mortality* on p. 65) and their mean lengths estimated from the resulting numbers greater and less than 3 mm. Early appearance of some individuals of the 0 + *b* class in May 1977 has been ignored. Mean decalcified dry mass values were computed from the mean lengths using the regression:

log (mass(mg)) = 2,52 log (length (mm)) -
1,45 (28 d.f.; r = 0,95; p <0,001)

Condition and mass of the animals varies during the year as in most species (Ansell 1972; Hanekom 1975) but was not investigated in this study.

Assuming peak settling on 20 January and 20 June each year a plot was made of mean age against mean length for the 0 + *a* and 0 + *b* classes of 1976 which became the 1 + *a* and 1 + *b* classes in 1977 (Fig. 2). This shows more rapid initial growth of the summer (*a*) class, probably as a result of higher temperatures. In both classes, however, the final length at 20 months is close to 25 mm. The *a* class reaches 21 mm at 12 months when the *b* class reaches 19,3 mm and in both cases growth levels off after about 12 months. These data do not fit von Bertalanffy or Gompertz growth curves satisfactorily.

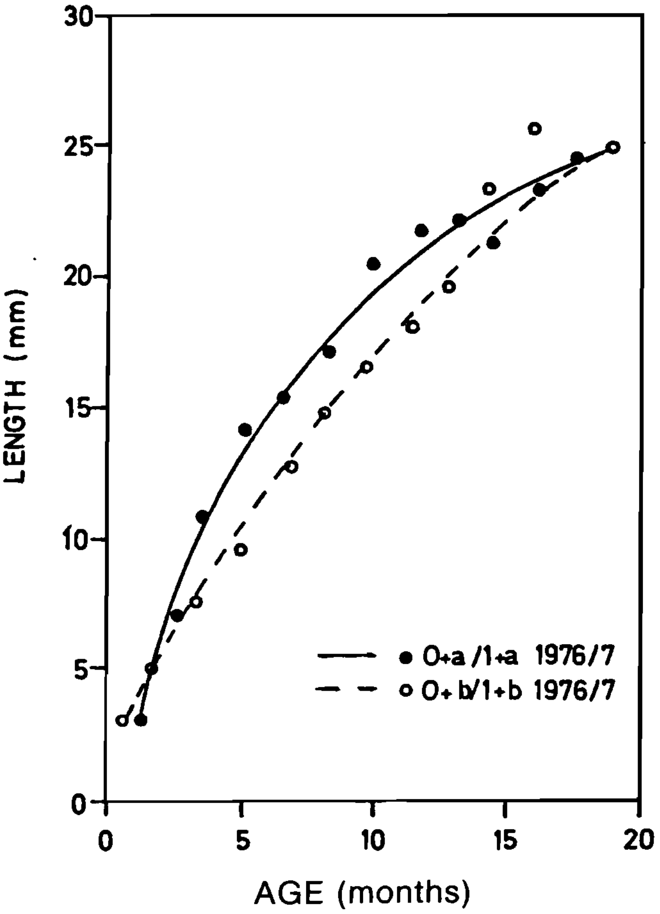

Fig. 2 Growth curves for *a* and *b* classes of *D. sordidus* on Kings Beach during 1976/77.

Mortality

Using only the data from 0 + *a* and 1 + *a* classes in Table 1 a plot of *ln* (numbers) against age yields a straight line (Fig. 3). As the slope is not significantly different for the 1975/6 and for the 1976/7 data all points were pooled to obtain a single regression. The slope is the age-specific mortality rate, $Z = 1{,}98y^{-1}$. The annual mortality rate $(1 - e^{-Z})$ is 0,86. This appears to be fairly constant over the first 1,5 years, which is virtually the whole life span. The 0 + *b* and 1 + *b* data were not used as these settlements were relatively small and consequently the low numbers sampled resulted in large errors.

Production

Production estimates (Table 2) indicate P greater than P during 1975/6 due to a nett increase in biomass (positive Δ B). The $P_G/\bar{B}$ ratio is high for the 0 + *b* class (4,17) and drops for older classes to 0,58 for the 1 + *a* class. From this the steady state $\overline{P}/\overline{B}$ ratio ($P_M = P_G$; $\Delta B = 0$) would be $181{,}53/116{,}39 = 1{,}56y^{-1}$. During 1976/7 there was a nett drop in biomass and P_M exceeded P_G. The younger

Table 1 Results of analysis of size/frequency histograms of *D. sordidus* on Kings Beach during 1975-77. $\bar{L}$ = mean length; $\bar{W}$ = mean mass; N = numbers m^{-2}; * = values corrected from the survivorship curve (Fig. 3). 17 November 1976 is repeated to indicate the start of the second study year.

Date	Age Class 0 + *b*			0 + *a*			1 + *b*			1 + *a*		
	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N	$\bar{L}$	$\bar{W}$	N
24.11.75	0	0	0	0	0	0	8,6	8,1	1,37	22,0	85,3	0,61
5.1.76	0	0	0	0	0	0	9,8	11,1	1,11	22,9	94,8	0,45
15.2.76	0	0	0	*3,0	0,7	3,62*	13,9	26,9	0,60	23,0	95,9	0,60
1.4.76	0	0	0	7,1	4,9	2,96	16,7	42,1	1,25	24,0	106,5	0,49
7.5.76	0	0	0	10,9	14,6	1,44	18,9	58,6	1,48	25,0	118,2	0,20
22.6.76	*3,0	0,7	0,95*	14,4	29,9	0,89	20,5	71,8	1,58	25,4	123,0	0,18
2.8.76	5,0	2,1	0,10	15,5	35,4	1,50	21,0	75,9	1,37	25,5	124,3	0,13
21.9.76	7,4	5,5	0,78	17,2	45,8	0,76	21,5	80,7	0,82	27,0	143,5	0,04
17.11.76	9,6	10,5	0,66	20,3	70,2	1,07	24,7	114,9	0,58	26,7	139,6	0,05
17.11.76	0	0	0	0	0	0	9,6	10,5	0,66	20,3	70,2	1,07
10.1.77	0	0	0	0	0	0	13,0	22,8	0,78	21,6	81,8	1,22
25.2.77	0	0	0	*3,0	0,7	3,00*	14,8	31,5	2,32	22,0	85,7	1,36
6.4.77	0	0	0	7,5	5,7	2,96	16,5	41,7	0,28	21,3	78,8	0,10
30.5.77	-	-	-	12,6	21,0	1,10	18,0	51,6	0,66	23,3	98,8	0,10
7.7.77	*4,0	1,2	1,24*	15,2	33,4	0,52	19,5	63,1	0,30	24,5	112,3	0,04
26.8.77	5,3	2,4	0,62	18,1	52,5	0,50	23,3	98,8	0,06	0	0	0
14.10.77	6,5	4,0	0,60	19,9	66,6	0,76	25,5	124,3	0,04	0	0	0
23.11.77	8,7	8,3	1,16	20,2	69,0	0,82	25,0	118,2	0,06	0	0	0

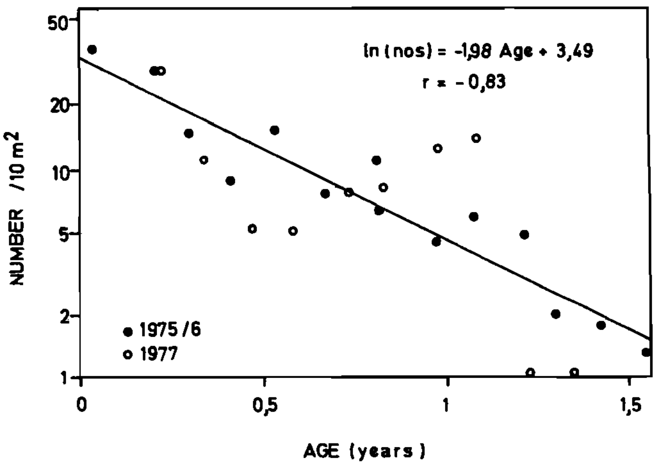

Fig. 3 Survivorship curve for *a* age classes of *D. sordidus* on Kings Beach.

classes again had higher $P_G/\bar{B}$ ratios than the older classes. Overall $\bar{P}/\bar{B}$ for steady state conditions was 1,03y^{-1}. The average $\bar{P}/\bar{B}$ for the two study years is thus 1,30y^{-1} for somatic production.

The 0 + *b* and 1 + *b* classes had an overall total $(P_M + P_G)$ for the two years production of 278,40 mgm^{-2} as opposed to 396,43 mgm^{-2} for the 0 + *a* and 1 + *a* classes. This emphasises the larger settlement and greater contribution of the summer (*a*) age classes. On average the 0 + *b* classes made up 12,3% of numbers; 1,1% of biomass and 1,3% of production; the 0 + *a* classes made up 43,8% of numbers; 17,5% of biomass and 31,4% of production; the 1 + *b* classes 30,6% of numbers; 56,8% of biomass and 39,9% of production; and the 1 + *a* classes made up 13,3% of numbers; 24,6% of biomass and 27,3% of production.

Energy values

Figure 4 shows energy values recorded during 1975/6 and numbers recorded during both study years. This reveals a clear trend: energy values are highest and numbers low before the summer spawning (October); after spawning and settlement, in February, energy values are at their lowest and numbers, boosted by the new settlement of 0 + *a* individuals, at their highest. The same pattern occurs, but to a much smaller degree, before and after the winter spawning. The winter spawning is thus of less magnitude and probably involves fewer individuals than the summer spawning.

The mean energy value was 17,84 kJg^{-1}. The average production by *D. sordidus* on Kings Beach is thus B.17,84 kJm^{-2}y^{-1} or 3,01 kJm^{-2}y^{-1} for the two years studied.

Discussion

Many intertidal animals exhibit a zonation of size classes and this has also been recorded for species of *Donax* (Coe 1955; de Villiers 1974; Hanekom 1975) although it is not distinct in *D. sordidus*. Further, population densities recorded here are very low compared to some previously recorded values such as 20 000 m^{-2} for *D. gouldi* (Coe 1955). Larger populations of *D. sordidus* do, however, develop on other East Cape beaches. Population abundance is probably largely determined by the quantity of organic material in the surf water (Wade 1965) suggesting poor conditions off Kings Beach. Ansell *et al.* (1972*b*) have pointed out that most beaches harbour two species of *Donax* which differ in ecology, behaviour and often also in size. This applies to Kings Beach, which also supports a sparse population of the large *D. serra* around the mean tide level.

Table 2 Production estimates for *D. sordidus* on Kings Beach during 1975/76 and 1976/77. P_G = production by growth; P_M = production by mortality; ΔB= final biomass - initial biomass; $\bar{B}$ = mean biomass; $\bar{N}$ = mean numbers.

		Age class			
	0+ *b*	0+ *a*	1+ *b*	1+ *a*	Total
1975/6					
P_G mg $m^{-2}y^{-1}$	5,83	93,86	109,49	18,10	227,28
P_M mg $m^{-2}y^{-1}$	-0,43	19,44	53,71	63,05	135,77
ΔB mg m^{-2}	6,93	75,11	55,55	-45,05	92,54
$\bar{B}$ mg m^{-2}	1,29	25,30	58,79	31,01	116,39
P_G $\bar{B}$/	4,17	3,71	1,86	0,58	1,95
$\bar{N}$ m^{-2}	0,28	1,36	1,13	0,31	3,08
1976/7					
P_G mg $m^{-2}y^{-1}$	5,88	76,52	53,17	16,22	151,79
P_M mg $m^{-2}y^{-1}$	-2,26	22,40	53,01	86,84	159,99
ΔB mg m^{-2}	9,63	56,58	0,16	-75,11	-8,74
$\bar{B}$ mg m^{-2}	1,67	21,43	93,13	34,86	151,09
P_G / $\bar{B}$	3,52	3,57	0,57	0,47	1,00
$\bar{N}$ m^{-2}	0,40	1,07	0,57	0,43	2,47

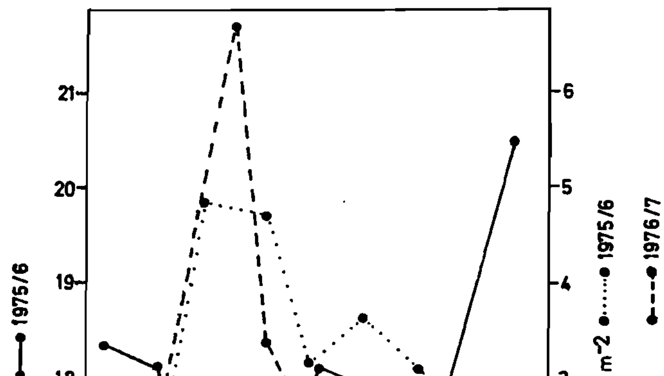

Fig. 4 Calorific values during 1975/76 and numbers during 1975/76 and 1976/77 for *D. sordidus* on Kings Beach.

Most species of *Donax* occur in warm regions and have a short life span (1-2 years), often with two spawning seasons each year. *D. cuneatus* grows to adult size, 16-18 mm in nine months to one year, is mature at 12 mm and spawns once before dying (Nayar 1954). *D. gouldi* grows to 12 mm at one year, 18 m at two years and 20 mm at three years although most individuals die after spawning at 1-1,5 years (Coe 1955). *D. variabilis* grows to about 20 mm at one year, is mature at 3 mm and spawns twice a year, while *D. tumida,* which also has two spawning seasons, is mature at 4 mm and grows to 12-15 mm in one year (Loesch 1957). *D. denticulatus* has a life span of about one year, growing to 14-18 mm depending on food availability (Wade 1965, 1968). *D. rugosus* studied by Smith (1971) was thought to grow to 24 mm after seven years but this is probably incorrect. *D. incarnatus* has two annual settlements, one usually unsuccessful, and grows rapidly to about 20 mm although individuals of 30 mm have been recorded (Ansell *et al.* 1972*b*; McLusky *et al.* 1975). *D. spiculum* grows to 15 mm and is mature at 6-8 months (Ansell *et al.* 1972*b*). The cold-temperate species, *D. vittatus,* differs from all the above warm-water forms in having relatively slow growth and a life span of 5-6 years (Ansell 1972). On the other hand the large warm-temperate form, *D. serra,* has relatively slow growth and reaches more than 60 mm length (de Villiers 1974; Hanekom 1975).

It seems that three general patterns in biology are found in the species of *Donax* studied. This may be summarized as follows: (1) most species, including *D. sordidus,* are small (<30 mm) warm-water forms confined to exposed sand beaches where they exhibit tidal migratory behaviour; they have rapid growth rates and 1-2 year life spans; (2) the cold-water form, *D. vittatus,* does not show tidal migration and has a slow growth rate and (3) *D. serra,* a very large (>60 mm) warm-temperate form has relatively slow growth; it does not exhibit normal tidal migratory behaviour but does have a semilunar pattern of movement up and down the shore with spring and neap tides (McLachlan *et al.* in press).

Mass mortalities in *Donax* have been documented by Coe (1955) for *D. gouldi* and de Villiers (1974) for *D. serra*. Normal mortality rates are high in tropical forms (Ansell *et al.* 1972*b*). Wade (1965, 1968) mentions extremely high mortality during the planktonic larval phase, high mortality during the first four months after settling and thereafter very low mortality in *D. denticulatus*. Various authors, quoted above, mention death after spawning. In *D. sordidus* mortality seems to be very low after settlement and the annual mortality rate recorded is very conservative for a short-lived benthic population. The sparseness of the population may be partly responsible for this by making predation uneconomical. There does appear to be death after spawning as very few animals grow larger than 25 mm.

The only production figures available for species of *Donax* are those of Ansell *et al.* (1972*b*) who got an average $\overline{P}/\overline{B}$ value of 6,5 for *D. incarnatus*. This was total production and included reproductive output. Chambers & Milne (1975) give average $\overline{P}/\overline{B}$ ratios for northern temperate marine and estuarine bivalves as 1,5 - 2,5. For a species with 1-2 year life span $\overline{P}/\overline{B}$ around 3 would be expected according to Zaika (1972). The value recorded for *D. sordidus* is thus very low. This may be partly a result of an abnormally low $\overline{P}/\overline{B}$ in 1976/7 but is probably largely due to the low mortality rate. Waters (1969) has shown that low mortality lowers turnover ratios.

Reproductive output has not been assessed in this study but it must be substantial, and mass changes during the year must be associated with gonad condition. Ansell *et al.* (1972*b*) found that this contributes a substantial part of total production in *D. incarnatus* and with the addition of reproductive output a $\overline{P}/\overline{B}$ above 2 may be expected for *D. sordidus*.

Calorific determinations for other *Donax* species have given higher values than recorded here. Ansell *et al.* (1973) recorded means of 18,64 and 19,44 kJg^{-1} for *D. incarnatus* from two localities and 19,65 kJg^{-1} for *D. spiculum*. The cold-water species, *D. vittatus*, had values of 18-23 kJg^{-1} (Ansell 1972), and Hanekom (1975) recorded a mean of 19,3 kJg^{-1} for *D. serra*. The reason for the lower values in *D. sordidus* is not clear.

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