Growth and production of *Bullia rhodostoma* on an open sandy beach in Algoa Bay

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The plough shell, *Bullia rhodostoma* (Mollusca: Gastropoda), has been studied on an open sandy beach where it is a common scavenger. Samples taken over a year indicate hatching of young individuals from December to February. They reach a length of about 10 mm after 1 year and 40 mm after 10 years. The von Bertalanffy growth equation is $L_t = 47 (1 - e^{-0,19(t+0,23)})$ and the annual mortality rate is 0,79. Mean decalcified dry biomass is 209 mg m^{-2} and production by growth 189 mg m^{-2} y^{-1} giving a P/B of 0,9. Most production by adults (>15 mm shell length) goes into reproduction, particularly in the females which grow larger than the males. Production by reproduction is estimated to be about 135 mg m^{-2} y^{-1}. Average calorific values are 19,04 kJ g^{-1} dry tissue
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Die ploegskulp, *Bullia rhodostoma* (Mollusca: Gastropoda), is op 'n oop sandstrand bestudeer waar dit 'n algemeen teenwoordige aasvreter is. Monsters wat oor 'n jaar geneem is, dui aan dat die jong individue tussen Desember en Februarie uitbroei. Hulle bereik 'n lengte van ongeveer 10 mm na 1 jaar en 40 mm na 10 jaar. Die Von Bertalanffy groeivergelyking is $L_t = 47 (1 - e^{-0,19(t+0,23)})$ en die jaarlikse mortaliteitstempo is 0,79. Gemiddelde kalklose droë biomassa is 209 mg m^{-2} y^{-1} wat 'n P/B van 0,9 gee. Die meeste volwasse (>15 mm skulplengte) produksie is in die vorm van voortplanting, veral in die wyfies wat groter as die mannetjies word. Produksie deur voortplanting is omtrent 135 mg m^{-2} y^{-1}. Gemiddelde kaloriewaardes is 19,04 kJ g^{-1} droë weefsel.
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Plough shells of the genus *Bullia* are well represented on South African sandy shores with five intertidal and eight subtidal species (Brown 1971). They are carnivorous scavengers and feed on stranded organisms, particularly coelenterate medusae and siphonophores. Some aspects of the general biology and physiology of *Bullia* species in the Cape Peninsula have been studied by Brown (1961, 1971). However, despite the quantitative importance of this group on South African sandy beaches (McLachlan 1977 b,c) there are no published data on population parameters such as growth and production.

B. rhodostoma Reeve is the common intertidal species of the south and east coasts of South Africa (Day 1969, McLachlan in press) and is the dominant macrofaunal organism on many beaches in the eastern Cape Province (McLachlan 1977b). The aim of this study was to monitor a *B. rhodostoma* population on an open sandy beach for a year so that growth and production could be estimated, thereby supplying a P/B ratio which could be applied to other beaches in the area.

Materials and Methods

The study area, Kings Beach, is a 1,25 km open sandy beach in the city of Port Elizabeth. It experiences continuous moderate wave action. The beach slope is concave with an average gradient of 1/25 and a berm about 2 m above LWS, corresponding to the average spring high tide swash line. The substrate is clean, fine, quartz sand which is very well sorted and has median particle diameters of 200–220 µm. The annual temperature range is 13–25°C (McLachlan 1977a). Although this is a popular beach for bathing and is heavily patronized during summer it supports a relatively large population of *B. rhodostoma.*

Sampling was carried out approximately every six weeks from November 1975 to November 1976 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 whole shore from LWS to just above the mean tide level. This was necessary as the population occupies this whole zone and there tends to be a vertical zonation of size classes with small individuals highest on the shore. The total area sampled varied between 40 and 60 m^2 on different occasions. All animals collected were measured on the beach to 1 mm greatest shell length using sliding callipers.

On a number of occasions animals were collected for the determination of length-mass relationships and calorific contents. Shell lengths were measured to 0,1 mm and after decalcification of the shells with hydrochloric acid the organic matter, trapped on glass-fibre filter paper, was oven-dried at 95°C for 24 hours. For determination of calorific contents, tissue from a number of animals was pooled to make pills for combustion in an adiabatic bomb calorimeter.

From the population length measurements size-frequency histograms were constructed and year classes were separated using probability paper (Cassie 1954). A von Bertalanffy growth curve was computed using a Ford-Walford plot to estimate constants L_∞ and K as described by Crisp (1971). The age-specific mortality rate, Z, was calculated from the slope of the curve ln (numbers) against age (Crisp 1971).

Production was calculated for each year class over the whole year using both growth and mortality methods outlined by Crisp (1971).

$$P_M = \Sigma_t \Delta N_t . \bar{W}_t$$

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 $\bar{W}_t$ is its mean mass over time interval t.

$$P_G = \Sigma_t \Delta W_t . \bar{N}_t$$

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

Finally an attempt was made to estimate the production by reproduction (P_R) of adults by using length-weight regressions to estimate the differences in mass between ripe and non-ripe individuals.

Results and Discussion

Growth and mortality

The size/frequency histograms for *B. rhodostoma* on Kings Beach during 1975-76 are shown in Fig. 1. The largest specimen collected was 40 mm long and the smallest 3 mm, although it was found that the dredge tended to lose smaller individuals in the 3 mm size class. The 0+ year class first appeared in January 1976 when individuals were abundant in the 3 mm and 4 mm length classes and many smaller ones must have been missed. In February, 0+ individuals were still abundant and the smaller individuals of this year class again appear to have been missed.

Results of the analysis of these histograms appear in Table 1 which shows numbers per square metre and mean lengths of the year classes. Only 0+, 1+ and 2+ year classes could be clearly distinguished and above this the animals were lumped as 3+→. As it was obvious that a large proportion of the 0+ year class had been lost during January and February 1976 it was estimated that their actual numbers at these times were double their recorded numbers and that their mean lengths were 2,0 mm and 3,0 mm respectively. This estimate was based on back extrapolation of the survivorship curve (see below and Fig. 4) and the knowledge that spawning took place from November to February (unpublished data). Mean individual decalcified dry mass values for the year classes in Table 1 were derived from their mean lengths using the regression:

$$\log_{10}(\text{dry mass (mg)}) = 2{,}43 \log_{10}(\text{length (mm)}) - 1{,}22 \quad (1)$$
$$77 \text{ d.f.}; r = 0{,}74; P<0{,}01.$$

This was based on animals collected between January and June. The low correlation coefficient reflects the large variation in mass which was encountered and taken to arise mainly from differences between the sexes and short term changes in condition which are inevitable in an environment where food supply is very sporadic.

L_∞ was obtained from a Ford-Walford plot (Fig. 2) and found to be 47 mm which agrees well with observations (a 40 mm individual has been collected on this beach and animals longer than 50 mm have been collected on nearby beaches). The growth curve (Fig. 3) predicts a length of 40,3 mm at an age of 10 years and thus supports Brown's (1971) statement that this species may grow to 15-20 years of age (44-46 mm long). Unpublished histological work indicates that sexual maturity is reached at about 15 mm shell length and that most large adults (>25 mm) are females while most smaller ones (15-25 mm) are males. Brown (1971) has also suggested that females are broader than males, but this has not been found to be the case here.

From the numbers of different aged individuals in Table 1 an approximation can be made of survivorship in *B. rhodostoma* if it is assumed that 15 young hatch per square metre of beach each year and that the mean hatching date is

Table 1 Number per m², mean lengths and mean mass of different year classes of *Bullia rhodostoma* on Kings Beach.

Date	0+ year class			1+ year class			2+ year class			3+ year class		
	N[a]	$\bar{L}$ (mm)	$\bar{W}$[b] (mg)	N	$\bar{L}$ (mm)	$\bar{W}$ (mg)	N	$\bar{L}$ (mm)	$\bar{W}$ (mg)	N	$\bar{L}$ (mm)	$\bar{W}$ (mg)
24.11.75	0	—	—	5,68	7,2	7,3	1,08	16,0	50,8	0,92	27,5	189,2
5.1.76	15,36	2,0	0,3	2,44	8,7	11,6	1,45	16,5	54,8	0,62	25,5	157,7
15.2.76	11,44	3,0	0,9	1,68	9,9	15,8	0,34	16,0	50,8	0,68	26,0	165,4
1.4.76	3,90	4,0	1,8	2,10	11,0	20,3	0,13	17,0	58,8	0,45	26,0	165,4
7.5.76	3,68	4,7	2,6	2,56	12,7	29,0	0,22	18,0	67,6	1,06	29,0	215,6
22.6.76	2,80	3,6	1,4	1,35	13,8	35,5	0,50	18,4	71,3	0,35	29,0	215,6
2.8.76	6,48	5,7	4,1	0,68	14,2	38,0	0,15	20,2	89,5	0,30	31,0	253,5
21.9.76	1,64	7,9	9,1	0,69	14,8	42,0	0,09	20,5	92,8	0,82	30,5	243,7
11.11.76	0,74	8,5	10,9	0,75	15,0	43,5	0,25	20,5	92,8	0,64	30,5	243,7

[a] Number per m². [b] Dry mass values in mg, calculated from equation (1). [c] Estimated values (see text).

1 January. Plotting ln (numbers) per 10 m^2 against age in years (each point based on the mean numbers of 2-4 consecutive months around one particular age) yields a straight line (Fig. 4) the slope of which is the age-specific mortality rate, $Z = 1{,}54\ y^{-1}$. The annual mortality rate $(1 - e^{-z})$ is 0,79. Annual survivorship is thus 0,21 over the first three years of life. After this age mortality appears to be lower, because the line intercepts the axis at less than four years of age and significant numbers of older individuals are found.

Production

Production estimates (Table 2) show that there was a net fall in biomass (negative ΔB) over the study year and P_M exceeds P_G by almost exactly ΔB. The slight discrepancy ($P_M + \Delta B = P_G + 3{,}99$ mg $m^{-2}\ y^{-1}$) is due to the initial production of the 0+ year class which was not picked up during recruitment, i.e. between hatching and 5 January. The ratio of production to biomass is high for the 0+ year class (about 5) and drops considerably for the older adults (3+→ year class P/B is about 0,25).

Neither P_M or P_G derived here can give an accurate average P/B ratio as the population declined over the study year but remains relatively constant, with natural fluctuations, over many years (unpublished data). Therefore, correcting P_G for the additional initial production of

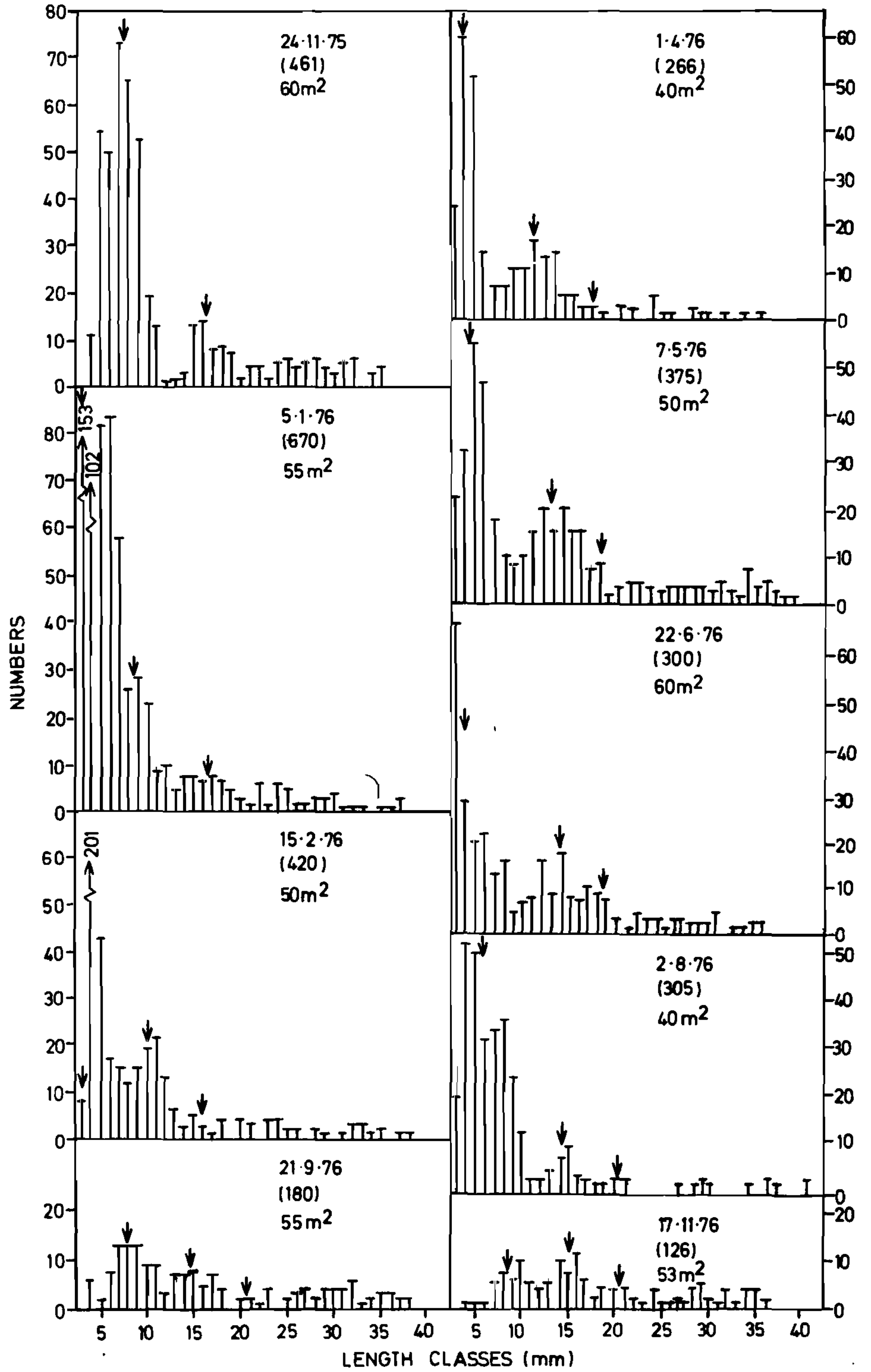

Fig. 1 Size/frequency histograms for *B. rhodostoma* on Kings Beach at nine sampling times during 1975-76. Included in each histogram is date of sampling, total numbers collected and total area sampled. Arrows indicate mean lengths for year classes.

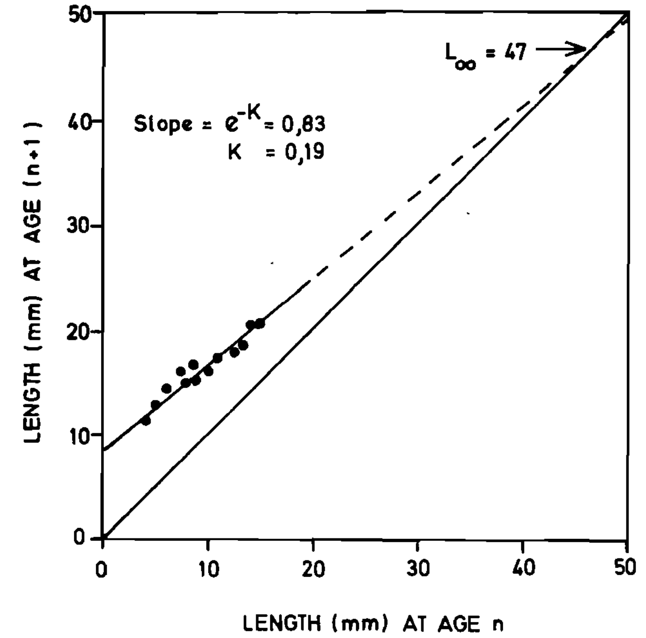

Fig. 2 Ford-Walford plot showing the constants L_{∞} and K for *B. rhodostoma* on Kings Beach during 1975-76.

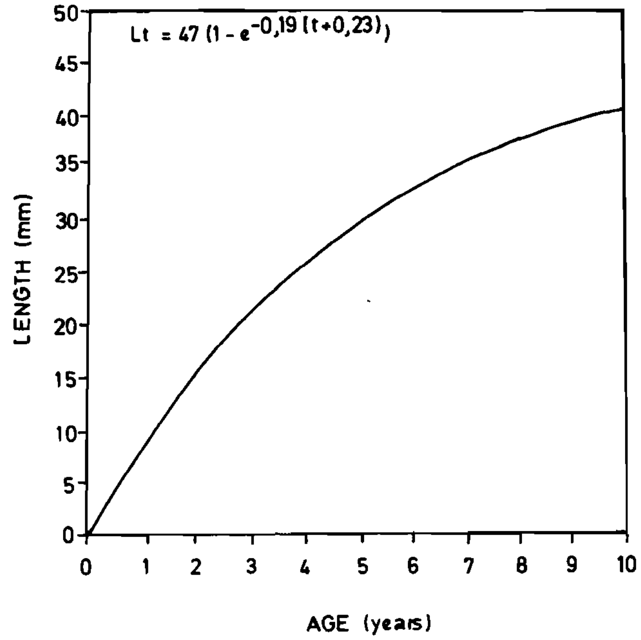

Fig. 3 The von Bertalanffy growth curve for *B. rhodostoma* on Kings beach.

$3{,}99 \text{ mg m}^{-2} \text{ y}^{-1}$, $P = (P_M + P_G)/2 = 190{,}51 \text{ mg m}^{-2} \text{ y}^{-1}$ and thus the average $\bar{P}/\bar{B} = 0{,}90$. During years of nett biomass decrease $P_M/\bar{B}$ will exceed this and $P_G/\bar{B}$ will be smaller, while the opposite will hold during years of nett biomass increase.

Table 2 shows that although the 0+ and 1+ year classes dominated the population in terms of numbers (62% and 24% respectively) they made up a minor proportion of the biomass (5% and 19% respectively). For a species that can grow to at least 10 years age and in which 63% of the biomass is made up of individuals older than 3 years, P/B would be expected to be below unity (Waters 1969, Zaika 1972).

Reproductive output

From late winter to the start of spawning in November there is an increase in mass of the adults due mainly to ripening of the gonads but probably also partly due to a general increase in condition. A length/mass regression for adults collected from September to November expresses this increased mass as:

Table 2 Population and biomass changes with age in *Bullia rhodostoma* on Kings Beach.

	Year class				
	0+	1+	2+	3+→	Total
Mean numbers $\bar{N}$ m^{-2}	5,11	1,99	0,47	0,65	8,22
Mean biomass $\bar{B}$ mg m^{-2}	9,44	38,73	28,30	132,76	209,23
P_M mg $m^{-2}y^{-1}$	45,22	82,75	44,20	43,59	215,76
P_G mg $m^{-2}y^{-1}$	49,06	73,98	12,55	25,67	161,26
Biomass mg $m^{+2}y^{-1}$	+8,07	−8,83	−31,66	−18,09	−50,51

$$\log_{10} \text{mass (mg)} = 2{,}58 \log_{10} \text{length (mm)} - 1{,}2 \quad (2)$$

37 d.f.; r = 0,85; P< 0,01.

When the mean numbers and lengths of adults (2+ and 3+→ classes) over the spawning season November to January are known, an estimate of production by reproduction can be obtained from the differences between biomass calculated from equations (1) and (2). This indicates that P_R was $40{,}00 \text{ mg m}^{-2} \text{ y}^{-1}$ for the 2+ year class and $94{,}87 \text{ mg m}^{-2} \text{ y}^{-1}$ for the 3+→ year classes. Total P_R is $134{,}87 \text{ mg m}^{-2} \text{ y}^{-1}$, which gives a P_R/B of 0,64. As, however, some of this may be due to an increase in condition a P_R/B of 0,5 is suggested. It can therefore be concluded that for *B. rhodostoma* on Kings Beach production is related to biomass as follows: $P_G/B = 0{,}9$; $P_R/B = 0{,}5$; and $P_{G+R}/B = 1{,}4$. As the total macrofauna biomass over this part of Kings Beach averages

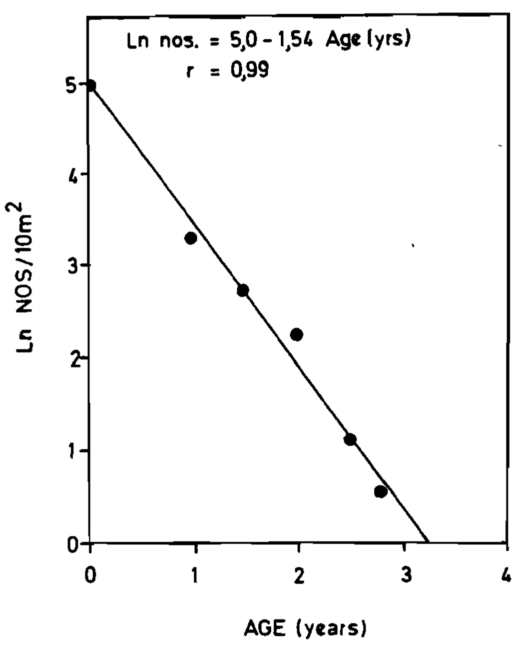

Fig. 4 Survivorship curve for *B. rhodostoma* on Kings Beach.

550 mg m^{-2} ash-free dry weight (McLachlan 1977b) *B. rhodostoma* is responsible for about 38% of the standing crop (210 mg m^{-2}).

P_R increases markedly with age and greatly exceeds P_G in older animals which are mainly females. It is possible to estimate the relative contributions of P_G and P_R over an individual's life using the von Bertalanffy growth curve and equations (1) and (2). P_R can simply be calculated as the difference in mass before and after spawning (from equations (1) and (2)) of an animal at a series of ages corresponding to lengths above 15 mm. P_G can be calculated from the growth curve and equation (1) as the increase in mass of an animal over each year of its life; e.g. P_G for an animal of 1 year is its mass at an age of 1,5 years less its mass at an age of 0,5 years. This is illustrated for the first five years of age in Fig. 5. It can be seen that while an animal's somatic production (P_G) levels off and even decreases with age after 4 years, total production increases in a linear fashion because of an exponential increase in P_R. Of the total production the amount going into reproduction increases from 0% at an age of 1 year to 73% at an age of 5 years. As the females lay large egg-cases (Brown 1971) it is not surprising that reproduction is responsible for such a high proportion of adult production.

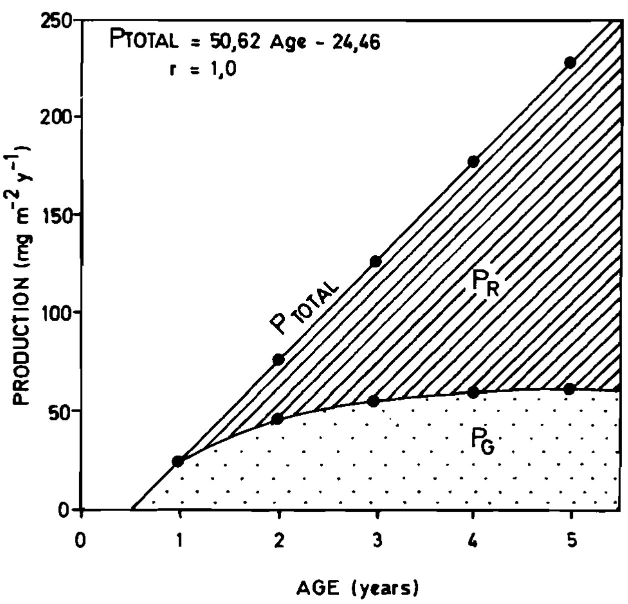

Fig. 5 Estimated production by growth (P_G) and reproduction (P_R) for an individual *B. rhodostoma* during its first five years of life. P_G is derived from the von Bertalanffy growth curve and the length/mass regression (equation (1)) and P_R from the difference in mass between ripe and non-ripe individuals (equations (1) and (2)).

Calorific values

There is wide fluctuation in calorific values without any obvious seasonal trend except for higher values just before spawning in November. The overall mean (± S.D.) was 19,04 ± 1,55kJ g^{-1} and that for November was 20,75 kJ g^{-1}. Ansell *et al.* (1973) recorded values in the range 16,3–18,9 kJ g^{-1} for *B. (Dorsanum) melanoides*, their values being lower than those recorded here. Lombard (1977), however, found a mean calorific value of 19,5 kJ g^{-1} for *Turbo sarmaticus* in Algoa Bay. If these energy values are substituted in the production and biomass estimates P_G/B remains at 0,9 but P_R/B increases to 2,80/3,98 = 0,70 because of the higher calorific values in November.

Conclusions

Bullia rhodostoma is a successful scavenger on exposed sandy beaches in the eastern Cape Province where it appears well adapted to a physically controlled environment and an erratic food supply. It is a long-lived species that has a slow growth rate and produces relatively few eggs that are well cared for by the females (Brown 1971). Until sexual maturity at just less than two years (15 mm length) production is made up entirely by growth and the P_{TOTAL}/B ratio for a one-year-old individual is 1,77. Reproduction contributes significantly to total production after sexual maturity, making up about 73% of P_{TOTAL} at an age of five years, but the P_{TOTAL}/B ratio drops to 1,02 for an individual of this age. After five years reproduction makes up most of the production and individual P_{TOTAL}/B ratios level off around 1. However, though individuals may grow to 20 years of age, animals over five years (30 mm) make up only 3% of the population.

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