SOUTH AFRICAN ASSOCIATION FOR
MARINE BIOLOGICAL RESEARCH

OCEANOGRAPHIC RESEARCH INSTITUTE

Investigational Report No. 50

Estimates of biomass, consumption and production of *Octopus vulgaris* Cuvier off the east coast of South Africa

by
P.R. Buchan and M.J. Smale

Published by
THE OCEANOGRAPHIC RESEARCH INSTITUTE
2 WEST STREET DURBAN
REPUBLIC OF SOUTH AFRICA
1981

ISBN 0 86989 025 5

Contents

ESTIMATES OF BIOMASS, CONSUMPTION AND PRODUCTION OF *OCTOPUS VULGARIS* CUVIER OFF THE EAST COAST OF SOUTH AFRICA

by

P.R. Buchan and M.J. Smale

Abstract

Estimates of consumption and production rates and biomass were made of *Octopus vulgaris* on a subtidal reef off the east coast of South Africa. Mean annual density was 0.007 m^{-2} or 10.9 on the whole 1 646 m^2 reef. Biomass, determined by two methods, was estimated at 2.3 or 1.9 g m^{-2} (dry mass) with respective production rates of 6.2 or 6.4 g $m^{-2}y^{-1}$. Mean P/B ratios were 2.8 or 3.3. Females and higher biomass, production rates and P/B ratios than males. On the basis of consumption rates of captive animals it was estimated that octopuses on the reef consume 489 kJ $m^{-2}y^{-1}$. Assimilation efficiencies of between 63.5% and 75.7% were recorded.

Introduction

This study forms part of a larger programme investigating the ecology of the communities of a subtidal rocky reef known as the ORI Reef. Situated near the Oceanographic Research Institute, Durban, on the east coast of South Africa, this reef is estimated to be 1 646 m^2 in area. It is entirely underwater at high tide although the surface is largely exposed at spring low tide.

An important aspect of production and consumption is their importance in the energetics equation $C = P+R+F+U$ where C represents the energy of the consumed food, P that devoted to somatic and gonad tissue production and F+U the energy lost in voided waste. A preliminary assessment of the biomass (thus production) and energy pathways of most of the organisms on the ORI Reef has already been reported (Berry *et al.* 1979) and more detailed studies have been made on production in the mussel *Perna perna* (Berry, 1978), on production and consumption rates of the spiny lobster *Panulirus homarus* (Berry and Smale, 1980) and of two blenny species, *Pictiblennius cornutus* and *Scartella cristata* (Joubert, 1980).

The present study deals with biomass, consumption and production of the common octupus, *Octopus vulgaris* Cuvier, on the ORI Reef and will ultimately contribute to a larger publication to be released on the energetics of the important organisms on the reef.

Methods

Density. Regular surveys of *O. vulgaris* on the ORI Reef between April 1977 and September 1978 yielded mass and density figures. All octopus sightings were recorded during systematic searches with Scuba gear at high tide.

Invest. Rep. oceanogr. Res. Inst. (50): 1-9, 1981.

Various attempts were made to estimate the size of octopuses in the wild without disturbing them. These included the use of underwater calipers to measure dimensions of the body which proved futile as the animals either retreated or grabbed the calipers. Finally, after observing tank-held octopuses, the mass of each animal seen under water on other reefs was estimated before capture. These estimates were then compared after capture with the actual masses (Fig. 1). A paired t test on the two sets of measurements was not significant at the 95% level with 37 degrees of freedom. On the strength of these results, the mass of octopuses on the ORI Reef were estimated on each dive and recorded on underwater slates. Mass was chosen as the parameter of measure since, according to Nixon (1966), this affords the clearest indication of difference in size.

No counts were made in four months of the study owing to bad diving conditions. In five months at least two counts were made and a mean figure was taken for these months.

Density was determined by monthly counts over a period of 18 months. It must be borne in mind that the numbers recorded will underestimate the population because newly settled animals are difficult to observe.

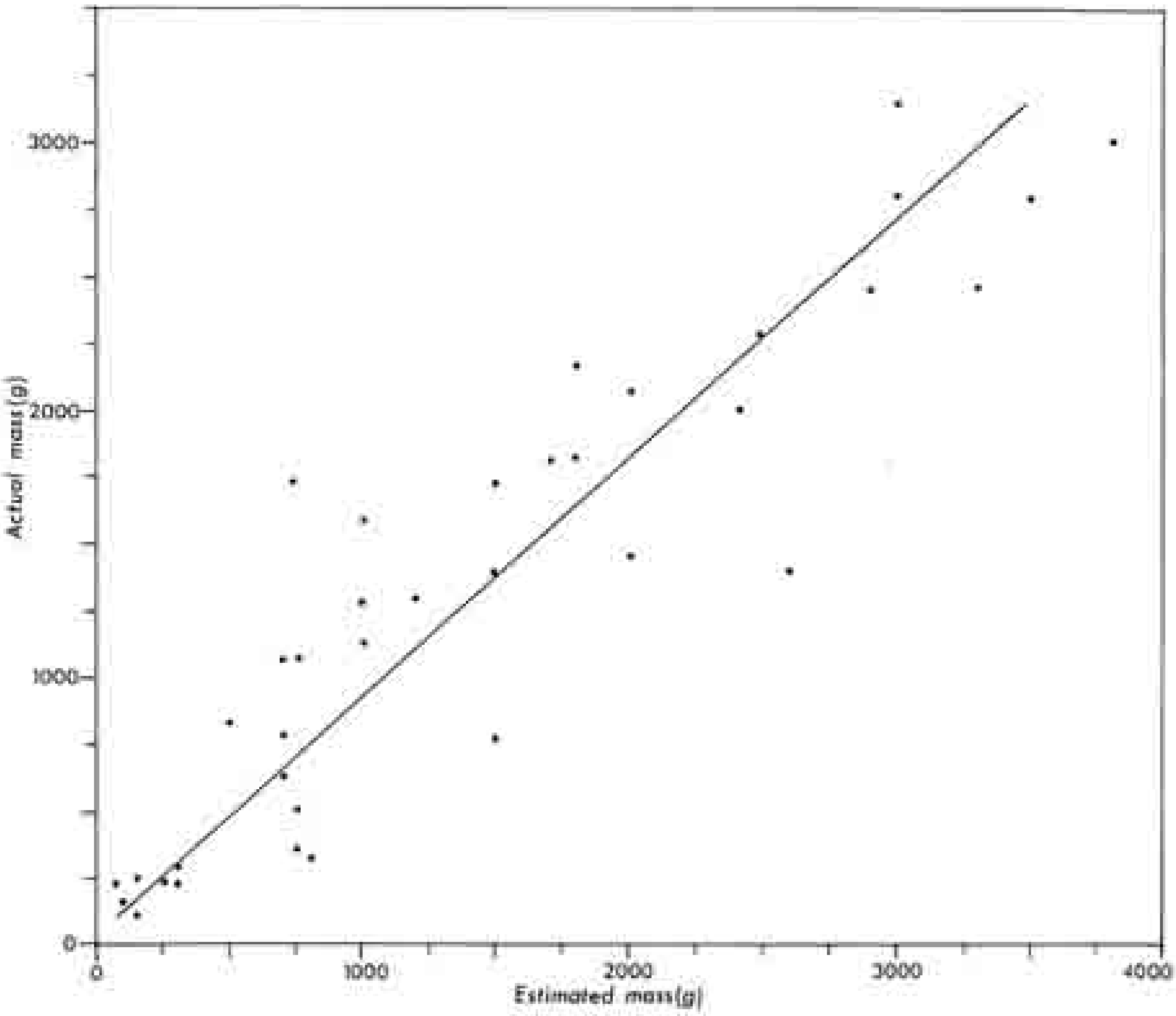

Fig. 1. The relationship between mass estimated in the field and actual mass, expressed by the equation: $Y = 1.12X - 39.28$; $r^2 = 0.83$; $n = 38$.

Production. The method used to estimate production was taken from Ricker (1971): $P = G\overline{B}$ where G is the instantaneous growth rate and $\overline{B}$ is the mean biomass. G was calculated from the formula $G = \log W_2 - \log W_1$ where W_2 is the mass at the end of the time interval chosen and W_1 the initial mass. Finally the product of the mean initial mass and the monthly mean density yielded the biomass.

The final mass (W_2) was read off the growth curve for *O. vulgaris* from Smale and Buchan (in press). Because the lifespan of *O. vulgaris* is between nine and twelve months for females and between twelve and fifteen months for males, production was calculated on a quarterly basis and these values summed to obtain annual production. The initial masses (W_1) were obtained in two different ways thus allowing two methods of calculating biomass.

The first calculation was based on mass estimates determined during the monthly density counts. The monthly sex ratio, calculated from specimens captured during simultaneous work on Vetch's Pier (Smale and Buchan, in press) was then applied to this to obtain mean male and mean female masses per size class per quarter.

Due to the small numbers of *O. vulgaris* resident on the ORI Reef it was not possible to get a good estimate of the population size frequency distribution. However, this was available from samples taken monthly on nearby Vetch's Pier. As the reefs are no more than 1.5 kilometres apart it was assumed tht the two populations were similar.

The second method of calculation was therefore devised whereby both sex ratio and size class frequency determined from the Vetch's Pier sample were applied to the density count on the ORI Reef, once again yielding mean male and female mass per size class per quarter.

Consumption. Data for consumption were taken from previous work monitoring food intake of eleven male and fourteen female *O. vulgaris* maintained in separate aquaria (Smale and Buchan, in press). The octopuses were fed mussels *(Perna perna)* daily throughout the experiment and rock lobsters *(Panulirus homarus)* when available. In all cases excess food was presented.

As mussels and rock lobsters have a different energy content, the daily intake in grams was converted to kilojoules using the energy values determined by bomb calorimeter. The mean intake was then calculated for each size class and for separate sexes. The monthly counts and the quarterly size class frequency obtained from previous work (Smale and Buchan, in press) were applied to these figures thus yielding the total consumption, in kilojoules, per size class per quarter of all octopuses on the ORI Reef.

The growth efficiency ratio of animal tissue to consumed food was obtained by dividing production (in kilojoules) by consumption (in kilojoules).

Finally, in an attempt to determine assimilation rates the faeces were collected from animals fed on either *P. perna* or on *P. homarus*. To prevent the loss in absorption of salts and organic matter the faeces were collected twice daily and frozen immediately. Samples taken over approximately a month were combined to provide workable quantities. These were then washed with ammonium formate, isotonic with sea water, dried to constant mass at 50° C and ashed in a furnace at 650° C, or burnt in a microbomb calorimeter.

The percentage utilization or assimilation of food by *O. vulgaris* was calculated according to the following formula derived by Conover (1966):

$$\text{Percentage utilization } U = \frac{F^1 - E^1}{(1-E^1)(F^1)} \times 100$$

where F^1 is the ash-free dry mass: dry mass ratio (fraction of organic matter) in the ingested food, and E^1 is the same ratio in a representative sample of faeces.

Results

Density. The density figures, together with a description of the extent of sanding up the reef, are summarised in Table 1. The mean monthly number was 10.93 ranging from 1-26 and the mean estimated wet mass was 15.69 kg ranging from 1.75 kg to 37.92 kg.

Biomass and Production. An example of the calculation of production of male *O. vulgaris* over the quarter of January to March is presented in Table 2. The quarterly biomass and production figures are summarised in Table 3 (based on estimated masses) and Table 4 (based on size class frequency) while the annual data are given in Table 5.

Using the two methods described above, the mean biomass was calculated to be 51.02 and 42.50 kJ m^{-2} yr^{-1} (or 2.26 and 1.89 g m^{-2} yr^{-1}) and production as 139.36 and 144.32 kJ m^{-2} yr^{-1} (or 6.18 and 6.40 g m^{-2} yr). Finally the PB ratios or turnover ratio (Ricker 1971) for males were 2.57 and 2.98 while for females they were 2.85 and 3.80 i.e. mean ratios of respectively 2.78 and 3.33.

Consumption. The mean daily consumption values per size class (of *O. vulgaris* held in aquaria) are summarised in Table 6. These figures are projected for the whole ORI Reef, with total quarterly consumption and consumption per square metre of the reef being summarised in Table 7.

The total consumption in kilojoules per year is 286 796 for males and 519 004 for females. Related to the ORI Reef and assuming that on a varied diet the animals would have a similar intake to that in tanks, males would consume 174.24 kJ m^{-2} yr^{-1} and females 315.31 kJ m^{-2} yr^{-1} i.e. 489.55 kJ m^{-2} yr^{-1} in all.

The growth efficiency was 28.5% when based on estimated masses and 29.5% based on size frequency data i.e. a mean of 29.0%.

The ash-free dry mass: dry mass ratio for mussel flesh was 0.8799 with standard error $\pm$ 0.0069 (n = 9) and for rock lobster flesh was 0.9357 $\pm$ 0.0099 (n = 14). The ratio for faeces of animals fed on mussel was 0.7742 $\pm$ 0.0793 (n = 22) and those fed on rock lobster was 0.7367 $\pm$ 0.0744 (n = 3).

The assimilation rate was therefore 52.20% when octopus were fed on mussels and 80.77% on rock lobsters. However, the method of collecting and treating the faecal samples was not entirely satisfactory, firstly due to the time in which the faeces remained in the water and secondly due to possible bacterial build-up as the samples were thawed partially and refrozen with each daily addition.

Discussion

Abundance. A study of Table 1 shows no seasonal trend, either in average mass of the octopuses or in numbers present. Various factors may influence the abundance on the ORI Reef. One could be excessive sanding of the reef which drives the octopuses off to seek sheltering lairs elsewhere, although it can be seen that in January and February 1978, when the reef was very heavily sanded, nineteen and twelve octopuses were sighted i.e. 73% and 46% respectively of the maximum sighted monthly.

Other possibilities are breeding season and the size of the mussel settlement on the reef. There is some indication of a breeding season for *O. vulgaris* on the east coast of South Africa (Smale and Buchan, in press) in that the proportion of females to males is higher from October to February, possibly due to migration onto shallow reefs. This may have been the result of the increased density on the ORI Reef from August 1977 to February 1978.

Secondly *Perna perna* is known to form a major portion of the diet of *O. vulgaris* (Smale and Buchan, in press). Heavy sanding resulted in mussel mortality from January to May 1978 and the corresponding decrease in octopus numbers in these months may indicate that the octopus population size on the reef is influenced by the numbers of mussels available. Finally it may be that conditions on other reefs affect the density of octopuses on the ORI Reef, causing short-term immigration or emigration.

Biomass and Production. It is apparent from the results that the mean biomass, production and $P/\overline{B}$ ratio were all higher in *O. vulgaris* females than in the males. This would be expected when one considers the faster growth rate (Smale and Buchan, in press) and the relatively larger gonads of the females.

Table 1. Estimates of *Octopus vulgaris* biomass on the ORI Reef.

Month	No.	Mean No.	Mean Mass (kg)	Mean Total Mass (kg)	Conditions
APR. 1977		11.50	No estimate		
1st	16				very sanded.
18th	7				scouring beginning.
MAY 1977		10.50	No estimate		
6th	4				excessive sand movement.
16th	13				heavy sanding.
17th	13				ditto.
18th	12				
JUN. 1977		3.20	0.92	3.67	
8th	1				almost whole reef sanded.
9th	3				ditto.
13th	3				heavy sanding.
29th	6				beginning of scouring on south.
30th	3				ditto.
JUL. 1977		6.00	1.35	8.13	
14th	4				reef fairly scoured.
21st	8				sanding up slightly.
AUG. 1977		13.00	0.92	11.90	
29th	13				reef scoured on top.
OCT. 1977		20.00	1.80	36.05	
5th	20				scouring as late August.
18th	20				greater scouring.
NOV. 1977		14.00	0.70	9.74	
10th	14				little more sanded.
DEC. 1977		26.00	1.46	37.92	
20th	26				reef quite exposed.
JAN. 1978		19.00	1.04	20.90	
20th	19				reef excessibly sanded, high mussel mortality.
FEB. 1978		12.00	1.33	15.90	
22nd	12				heavy sanding.
MAY 1978		2.75	1.93	5.32	
5th	2				reef very scoured on top and sides; high mussel mortality evident.
9th	4				slightly more sanded.
12th	4				—
23rd	4				—
JUN. 1978		6.00	2.45	14.70	
6th					—
AUG. 1978		1.00	1.75	1.75	
1st	0				reef very sanded; many dead mussels.
29th	2				ditto.
SEP. 1978		8.00	2.79	22.30	
25th	8				reef well scoured on top and north.
MEAN		10.93		15.69	

Table 2. Production of *O. vulgaris* males: January – March (90 days)

Size Class (mm)	W_1	$\bar{N}$	W_2	G (log W_2 – log W_1)	$\bar{B}$ $W_1 x \bar{N}$)	P (Gx$\bar{B}$)
40- 59	57.11	0.06	740	2.56	3.42	8.78
60- 79	146.60	0.24	1035	1.95	35.18	68.60
80- 99	296.44	0.30	1340	1.51	99.93	134.28
100-119	520.13	0.59	1685	1.18	306.88	362.12
120-139	830.59	1.30	2130	0.94	1079.77	1014.98
140-159	1240.28	1.18	2575	0.73	1463.53	1068.38
160-179	1761.25	1.30	3820	0.77	2289.63	1763.02
180-199	2405.26	0.59	4440	0.61	1419.10	865.65
200-219	3183.81	0.35	4800	0.41	1114.33	456.88
Total wet mass (g)					7800.78	5742.69
Total dry mass (g)					1677.59	1234.99

Table 3. Summary of quarterly biomass and production of *O. vulgaris* on ORI reef based on estimated masses.

	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	
MALES					
Mean Biomass					Mean
g quarter^{-1} (wet)	7605.00	3720.00	8262.50	10202.50	7447.50
g quarter^{-1} (dry)	1635.48	800.00	1776.88	2194.09	1601.61
g m^{-2} quarter^{-1} (dry)	0.99	0.49	1.08	1.33	0.97
kJ m^{-2} quarter^{-1}	22.32	11.05	24.35	29.99	21.93
Production					Total
g quarter^{-1} (wet)	6092.50	2445.98	4780.48	5812.44	19131.40
g quarter^{-1} (dry)	1310.22	526.02	1028.06	1249.99	4114.29
g m^{-2} quarter^{-1} (dry)	0.80	0.32	0.62	0.76	2.50
kJ m^{-2} quarter^{-1}	18.04	7.22	13.98	17.14	56.58
FEMALES					
Mean Biomass					Mean
g quarter^{-1} (wet)	12712.50	25470.50	4375.00	19905.00	9885.00
g quarter^{-1} (dry)	2733.87	547.85	940.86	4280.65	2125.81
g m^{-2} quarter^{-1} (dry)	1.66	0.33	0.57	2.60	1.29
kJ m^{-2} quarter^{-1}	37.43	7.44	12.85	58.63	29.09
Production					Total
g quarter^{-1} (wet)	11627.11	1875.10	2554.45	12147.10	28203.76
g quarter^{-1} (dry)	2500.45	403.25	549.34	2612.28	6065.32
g m^{-2} quarter^{-1} (dry)	1.52	0.24	0.33	1.59	3.68
kJ m^{-2} quarter^{-1}	34.28	5.41	7.44	35.85	82.98

Table 4. Summary of quarterly production and biomass of *O. vulgaris* on ORI reef based on size class frequency data.

	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	
MALES					
Mean Biomass					Mean
g quarter^{-1} (wet)	7800.78	5913.81	6049.15	8669.42	7108.29
g quarter^{-1} (dry)	1677.59	1271.79	1300.89	1864.39	1528.67
g m^{-2} quarter^{-1} (dry)	1.02	0.77	0.79	1.13	0.93
kJ m^{-2} quarter^{-1}	23.00	17.36	17.81	25.48	20.91
Production					Total
g quarter^{-1} (wet)	5742.69	4392.90	4553.13	6520.36	21209.08
g quarter^{-1} (dry)	1234.99	944.71	979.17	1402.23	4561.10
g m^{-2} quarter^{-1} (dry)	0.75	0.57	0.59	0.85	2.76
kJ m^{-2} quarter^{-1}	16.91	12.85	13.30	19.17	62.23
FEMALES					
Mean Biomass					Mean
g quarter^{-1} (wet)	9835.97	3192.66	2477.73	13761.61	7316.99
g quarter^{-1} (dry)	2115.26	686.59	532.85	2959.49	1573.55
g m^{-2} quarter^{-1} (dry)	1.29	0.42	0.32	1.80	0.96
kJ m^{-2} quarter^{-1}	29.09	9.47	7.22	40.59	21.59
Production					
g quarter^{-1} (wet)	9297.03	3034.38	2371.12	13171.84	26874.37
g quarter^{-1} (dry)	1999.36	652.55	509.92	2832.65	5994.48
g m^{-2} quarter^{-1} (dry)	1.21	0.40	0.31	1.72	3.64
kJ m^{-2} quarter^{-1}	27.29	9.02	6.99	38.79	82.09

Table 5. Summary of mean biomass and annual production of *O. vulgaris*

Calculated from masses estimated during biomass density counts.

	$\bar{B}$		P		P/$\bar{B}$
	(g m^{-2}yr^{-2})	(kJ m^{-2}yr^{-1})	(g m^{-2}yr^{-1})	(kJ m^{-2}yr^{-1})	
Males	0.97	21.93	2.50	56.38	2.57
Females	1.29	29.09	3.68	82.98	2.85
Total	2.26	51.02	6.18	139.36	

Derived from previous size-frequency analyses (Smale & Buchan, in press)

	$\bar{B}$		P		P/$\bar{B}$
	(g m^{-2}yr^{-1})	(kJ m^{-2}yr^{-1})	(g m^{-2}yr^{-1})	(kJ m^{-2}yr^{-1})	
Males	0.93	20.91	2.76	62.23	2.98
Females	0.96	21.59	3.64	82.09	3.80
Total	1.89	42.50	6.40	144.32	

Table 6. Consumption of captive *O. vulgaris* according to sex and size classes.

SIZE CLASS		CONSUMPTION	
Mass (g)	Mantle length (mm)	Males ($kJ\ d^{-1}$)	Females ($kJ\ d^{-1}$)
0 - 4	(0 - 19)	–	–
4 - 28	(20 - 39)	13.38	–
30 - 91	(40 - 59)	28.66	40.55
95 - 206	(60 - 79)	67.83	57.89
213 - 387	(80 - 99)	60.22	120.88
398 - 648	(100 - 119)	105.11	158.25
664 - 1002	(120 - 139)	142.83	220.22
1022 - 1460	(140 - 159)	144.66	256.61
1486 - 2035	(160 - 179)	137.75	248.48
2067 - 2738	(180 - 199)	193.38	347.07
2777 - 3581	(200 - 219)	328.96	247.77

Table 7. *O. vulgaris.* Quarterly consumption for males and females on the ORI reef.

QUARTER	CONSUMPTION (kJ)		$kJ\ m^{-2}$	
	Males	Females	Males	Females
Jan - Mar	77649.30	171839.70	47.17	104.40
Apr - Jun	59465.77	56444.57	36.13	34.29
Jul - Sep	61514.88	44307.20	37.37	26.92
Oct - Dec	88168.20	246412.80	53.57	149.70
TOTAL	286798.15	519004.27	174.24	315.31

Comparison with other species on the ORI Reef reveals that the mean annual biomass of *O. vulgaris* is relatively high despite the low density (a maximum of 26 animals sighted in one survey). The lobster *Panulirus homarus* has the largest biomass of all the invertebrate carnivores on the reef. viz. 112.0 $kJ\ m^{-2}\ yr^{-1}$ with a maximum number of 580 individuals (Berry and Smale. 1980) while that of *O. vulgaris* is 6.68 $kJ\ m^{-2}\ yr^{-1}$ (mean value). A study of the production figures, on the other hand, reveals that the mean production rate of *O. vulgaris* of 141.8 $kJ\ m^{-2}\ yr^{-1}$ was 1.66 times that of *Panulurus homarus* (85.6 $kJ\ m^{-2}\ yr^{-1}$) Berry and Smale, 1980).

The mean $P/\bar{B}$ ratios (or turnover ratios) of 2.78 for male and 3.33 for female *O. vulgaris* were also considerably higher than that of 0.42 for *Panulirus homarus* (Berry and Smale, 1980). However, the blennies on the Ori Reef, *Pictiblennius cornutus* and *Scartella cristata*, have comparable values of 2.53 and 2.84 respectively (Joubert 1980) while the mussel *Perna perna* had flesh $P/\bar{B}$ of 3.9 in 1975/1976 and 4.87 in 1976/1977 (Berry 1978). These species, with the exception of the slow-growing *Panulirus homarus*, are comparable with fresh water invertebrates, which according to Waters (1969) as quoted by Ricker (1971) attain turnover ratios between 2.5 and 5.0.

Consumption and growth efficiency. Relating consumption to biomass of food on the reef there would appear to be an excess of mussel available to *O. vulgaris*. The annual production of *Perna perna* on the reef is 25 458 kJ m^{-2} yr^{-1} (flesh only) (Berry *et al*, 1979), while the total consumption of *O. vulgaris* is 490 kJ m^{-2} yr^{-1} which includes other prey species. However, it must be borne in mind that the standing crop of mussels varies and that small size mussels, which are necessary for smaller octopuses, are not always readily available. Besides this, one of the major blenny species on the reef, *Pictiblennius cornutus*, consumes large amounts of *Perna perna* (almost 19% of the total consumption of 37 398 kJ m^{-2} yr^{-1} (Joubert 1980). The *Panulirus homarus* population consumes 1 070 kJ m^{-2} yr^{-1} (Berry and Smale 1980) 76% by volume of which is *Perna perna* (Berry 1971). It would be necessary therefore to estimate the exact energy value of the various prey species consumed by *O. vulgaris* and by the other carnivores and also to evaluate the quantity and quality of the standing crops of prey species to obtain a more accurate picture of the availability of food to the OR1 Reef carnivores.

In previous research on *O. vulgaris*, Smale and Buchan (in press) estimated growth efficiency at 33.8%. This figure is lower than the mean rate of 43.6% demonstrated by Choe (1966) for *Sepia esculenta* and 46% for *O. vulgaris* from the Bay of Naples (Nixon 1966). However, it is higher than the 29% quoted in Results above. As the rate determined in this investigation was based on masses of animals estimated in the wild while using tank-feeding data for consumption it probably would be more realistic to accept the higher figure (33%), obtained when growth and feeding were both determined in tanks. A point to note is that food intake of *O. vulgaris* was high, ranging from 1% to 21% of the body mass per day with a mean of 5%, probably resulting in the low conversion efficiency.

Ideally one should be able to balance the energetics equation $C = P+R+U+F$. P and R together equal the assimilated food therefore in the altered equation F should be calculable in $F = C - (P+R)$ (energy lost in urine is negligible). However, as mentioned previously, the assimilation results are not satisfactory so that the energetic cost of respiration is needed to complete the equation.

If possible a programme involving tag-recapture should be initiated to quantify feeding and production in the wild. Until such time as this is possible the above estimates must suffice.

Acknowledgements

We are grateful to Dr P. Berry who supervised this project and made a number of density counts; to Dr A. de Freitas, Prof. J. Field and Dr G. Branch who gave helpful criticism of the manuscript and to Mr L. Arumugan who cared for the octopuses in the aquaria; to Mr C. Joubert for undertaking density counts and Mrs L. Cameron who typed the manuscript. Finally, grateful acknowledgement is made of the funding of this programme by the Natal Parks Board.

References

BERRY, P.F., 1971. The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of southern Africa. *Invest. Rep. oceanogr. Res. Inst.*, **28:** 1-75

—, P.F., 1978. Reproduction, growth and production in the mussel, *Perna perna* (Linnaeus), on the east coast of South Africa. *Invest. Rep. oceanogr. Res. Inst.*, **48:** 1-28

—, P.F., HANEKOM, P.B., JOUBERT, C.S.W., JOUBERT, I., SCHLEYER, M., SMALE, M.J. and VAN DER ELST, R.P., 1979. A preliminary account of the biomass and major energy pathways through a Natal nearshore reef community. Fourth National Oceanographic Symposium, *Cape Town, 10-13 July 1979*: 1-11. Unpublished paper.

—, P.F. and SMALE, M.J., 1980. An estimate of production and consumption rates in the spiny lobster *Panulirus homarus* (Linnaeus) on a shallow littoral reef off the Natal coast, South Africa. *Mar. Ecol. (Prog. Ser.)*, **2:** 337-343

CHOE, S., 1966. On the growth, feeding rates and the efficiency of food conversion for cuttlefishes and squids. *Korean J. Zool.*, **9**(2): 12-20

CONOVER, R.J., 1966. Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.*, **11:** 338-345

JOUBERT, I., 1980. The biology of *Blennius cristatus* L. and *Blennius cornutus* L. (Teleostei — Blennicidea) on a Natal reef. Unpublished M.Sc. thesis, University of Natal, Durban: 1-90

NIXON, M., 1966. Changes in body weight and intake of food by *Octopus vulgaris*. *J. Zool.*, **150:** 1-9

RICKER, W.E. *ed.*, 1971. Methods for assessment of fish production in fresh waters. Oxford, Blackwell Scientific Publications: 1-348

SMALE, M.J. and BUCHAN, P.R. (in press). The biology of *Octopus vulgaris* Cuvier off the east coast of South Africa. *Mar. Biol.*

WELLS, M.J. and WELLS, J., 1972. Sexual displays and mating of *O. vulgaris* Cuvier and *O. cyanea* Gray and attempts to alter performance by manipulating the glandular conditions of the animals. *Anim. Behav.*, **20:** 293-308

WINBERG, G.G. *ed.*, 1971. Methods for the estimation of production of aquatic animals. London, Academic Press: 1-175