

# An Estimate of Production and Consumption Rates in the Spiny Lobster *Panulirus homarus* on a Shallow Littoral Reef off the Natal Coast, South Africa

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**ABSTRACT:** Production and consumption rates were studied in a population of the spiny lobster *Panulirus homarus* (Linnaeus) inhabiting an isolated reef. Estimated mean production rate ( $P$ ) (comprising somatic tissue, unliberated gonadal products and exoskeleton) was  $47.6 \text{ kJ m}^{-2}\text{y}^{-1}$  or, in terms of dry mass,  $2.1 \text{ g m}^{-2}\text{y}^{-1}$  ( $P/\bar{B} : 0.42$ ). Mean gonadal output ( $G$ ) was  $9.8 \text{ kJ m}^{-2}\text{y}^{-1}$  of which egg production comprised about 90%. Nevertheless, total production rate ( $P+G$ ) was approximately equal in the sexes suggesting that the slower growth rate and lower value for  $P$  in females is directly proportional to energy loss by egg production. The energy lost through moulted exuviae (conventionally assigned to excreta ( $U$ ) in the energy budget) was determined using the same basic method as for determination of  $P$  and amounted to  $28.1 \text{ kJ m}^{-2}\text{y}^{-1}$ . On the basis of the consumption rate of flesh of the mussel *Perna perna* in captive lobsters (the principal food organism of *P. homarus*) it was estimated that the reef population consumed  $1070 \text{ kJ m}^{-2}\text{y}^{-1}$ . The food in the form of mussels on the reef was substantially in excess of the requirements of the lobster population although an unknown proportion may be physically unavailable.

## INTRODUCTION

This study forms part of a programme in which the ecology of a shallow subtropical reef community on the Natal coast is being investigated in terms of energy flow. The area chosen for the project is a small isolated reef with a surface area of  $1646 \text{ m}^2$ , situated in front of the Oceanographic Research Institute (ORI), Durban, and known as the ORI Reef. A prolific and varied fauna is present on it which is regarded as being typical of shallow subtidal reefs in the nearshore zone of Natal.

The spiny lobster *Panulirus homarus* has the highest mean annual biomass of the invertebrate carnivores present on the ORI Reef and feeds largely on the brown mussel *Perna perna* which is the dominant filter feeder present (Berry, 1971, 1978). An attempt is made here to assess the consumption and production rates of the lobster population, production being defined as the total assimilated food or energy incorporated into tis-

total assimilated food or energy incorporated into tissue during any time interval  $\Delta t$  including that by individuals which do not survive to the end of  $\Delta t$  (Ivlev, 1966). Production ( $P$ ), comprising growth of somatic tissue, unliberated gonadal material and an element of the exoskeleton, was distinguished from production of liberated gonadal material ( $G$ ). Energy lost in the production of moulted exuviae was also determined being closely associated with the growth process although this is assigned to excreta ( $U$ ) following I.B.P. convention (Crisp, 1971).

## MATERIALS AND METHODS

Mean annual biomass of *Panulirus homarus* (Linnaeus) was determined on the basis of samples taken approximately quarterly over three consecutive years. Every lobster larger than 20 mm carapace length was collected from the reef by divers using SCUBA, measured to the nearest mm (carapace length) and returned. Wet mass ( $\gamma$ ) was obtained by conversion from carapace length ( $\chi$ ) using the regressions  $\gamma = 0.00253 \chi^{2.78}$  for males and  $\gamma = 0.00177 \chi^{2.86}$  females calculated by Berry (1971). An analysis of variance

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showed that the error introduced by this conversion did not exceed 6% which is unlikely to be greater than that of direct measurement of wet mass. Conversion to acid treated dry mass ( $\gamma$ ) from carapace length ( $\chi$ ) was obtained from the equations  $\gamma = 4.6517 \times 10^{-4} \chi^{2.78}$  for males and  $\gamma = 3.3646 \times 10^{-4} \chi^{2.86}$  for females. The ratio of whole animal wet mass to acid treated dry mass is 5.60 : 1 (Smale, 1978).

*Panulirus homarus* breeds throughout the year; consequently, cohorts or year classes are indistinguishable (Berry, 1971). Production rate ( $P$ ) was therefore estimated for individual size classes using the method described by Ricker (1968) and the formula derived by Ricker (1946) and Allen (1950),  $P = G\bar{B}$ . Taking growth to be exponential, its instantaneous coefficient  $G$  was estimated by:

$$G = \frac{\log_e \bar{W}_2 - \log_e \bar{W}_1}{t}$$

where  $\bar{W}_1$  and  $\bar{W}_2$  are the mean weights at times  $t_1$  and  $t_2$ , respectively. The growth rate of *P. homarus* determined by Berry (1971) was used to compute  $\bar{W}_1$  and  $\bar{W}_2$ .

Taking a straight line rather than an exponential curve as adequately representing change in mean biomass over the time intervals used,  $\bar{B}$  was estimated by

$$\bar{B} = \frac{B_1 + B_2 + B_3 + B_4}{4}$$

where  $B_1, B_2, B_3$  and  $B_4$  = the biomass at times  $t_1, t_2, t_3$  and  $t_4$ , respectively.

The same basic method was applied in estimation of whole-animal production, production of exoskeletons (exuviae), and gonadal output. In the latter, however, a complication arises in that *Panulirus homarus* breeds repetitively, the number of broods of eggs produced per year increasing progressively up to a maximum of 4 with increase in size of females (Berry, 1971). On the basis of the proportion of time during the year that the majority of females in each size class are carrying eggs and knowledge of their mean intermoult period it was possible to obtain a rough approximation of the proportions in each size class that produce 1, 2, 3 or 4 broods

Table 1. *Panulirus homarus*. Percentage of females producing 1, 2, 3 or 4 broods of eggs per year in each size class

Size class (mm)	Number of broods			
	1	2	3	4
50-59	50	45	5	0
60-69	25	60	15	0
70-79	15	20	60	5
80-89	5	15	70	10
90-99	5	10	75	10

per annum (Berry, 1971). Production was, therefore, corrected for repetitive breeding using the estimates of these proportions given in Table 1.

It was also necessary to take into account that in the 50-59 mm size class only approximately 75% of the population are sexually mature and breed at all.

Dry egg mass ( $\gamma$ ) was obtained by conversion from carapace length ( $\chi$ ) using the formula  $\gamma = 1.1069 \times 10^{-4} \chi^{2.93}$  ( $n = 153$ ;  $r^2 = 0.88$ ).

In the case of males, repetitive mating must also occur and in the absence of any data on its frequency the same correction was applied for each size class as was for egg production. *Panulirus homarus* males produce a large spermatophoric mass which is deposited on the females' sternum (Berry, 1970). Wet mass ( $\gamma$ ) was obtained from the following regression on carapace length ( $\chi$ ):  $\gamma = 5.7108 \times 10^{-9} \chi^{4.67}$  ( $n = 152$ ;  $r^2 = 0.71$ ). The ratio of wet spermatophoric mass to dry mass is 1.93 : 1.

Exuviae were acid treated (7% HNO<sub>3</sub>) to remove CaCO<sub>3</sub> and conversion from carapace length ( $\chi$ ) was effected using the regression  $\gamma = 2.4737 \times 10^{-5} \chi^{3.06}$  ( $n = 137$ ;  $r^2 = 0.92$ ), which was calculated for both sexes combined. In determination of the production rate of exuviae it was necessary for each size class to take into account the number of times the lobsters moulted annually and the mean growth increment. The exoskeletons grow from an initial mass ( $\bar{W}_1$ ) to successive masses ( $\bar{W}_2, \bar{W}_3, \bar{W}_4$ , etc.) at respective moults during a year. Thus instead of the instantaneous growth coefficient  $G$  being simply:  $\log \bar{W}_2 - \log \bar{W}_1$ , where  $\bar{W}_1$  is the initial mass and  $\bar{W}_2$  the mass at the end of the year,  $G$  was obtained by calculating instantaneous growth coefficients for each successive moult and summing them, i.e.

$$G = \sum_{\chi=n}^{\chi=1} \log \bar{W}_b - \log \bar{W}_a,$$

where  $a$  = initial mass,  $b$  = mass at  $n$  successive moults.

Consumption rate ( $C$ ) for *Panulirus homarus* fed on excess quantities of mussel *Perna perna* (its chief food organism) and held at various temperature regimes in tanks was determined by Smale (1978). The rate he obtained for lobsters held at ambient temperature with sea water was applied to each quarterly sample of the population, enabling the annual consumption rate to be computed for the ORI Reef population over the three years of study.

Calorific values were determined using an adiabatic bomb calorimeter on tissue that had been dried to constant mass at 60°C. The following ash-inclusive calorific values were applied: whole animal (acid treated), 22.266 kJ g<sup>-1</sup>; acid treated exoskeleton, 18.350 kJ g<sup>-1</sup>; spermatophoric mass, 27.906 kJ g<sup>-1</sup>; eggs, 33.270 kJ g<sup>-1</sup>.

**RESULTS**

Numbers of *Panulirus homarus* captured from the ORI Reef in quarterly samples are presented in Table 2. A considerably higher mean number was recorded in the first year than in the subsequent two years. The numbers for the three years sampled ranged from 353.5 (0.21 m<sup>-2</sup>) to 129.5 (0.08 m<sup>-2</sup>) with a mean of 206.5 (0.13 m<sup>-2</sup>). The size frequency distributions of the samples conformed closely to those of much larger samples taken by Berry (1971) and are considered to reflect the typical population composition of *P. homarus* on near-shore reefs in Natal.

Mean biomass on an annual basis is summarized in Table 5. A substantially higher biomass was recorded in 1974/75 than in the following two years. The fact that the biomass in 1976/77 was slightly lower than for 1975/76, despite higher numbers, reflects the somewhat smaller size composition of the lobster population that year. The mean dry biomass over the three years was 5.03 g m<sup>-2</sup> (112.02 kJ m<sup>-2</sup>).

Estimates of whole animal production ( $P_1$ ), production of exoskeleton (exuviae) ( $P_2$ ) and gonadal output corrected for repetitive breeding ( $P_3$ ) by both sexes each year are presented in Tables 3 and 4 with data used for computation of ( $P_1$ ) given in full in Table 3. In Table 5 annual production rates (kJ m<sup>-2</sup>y<sup>-1</sup>) and  $P/\bar{B}$  ratios for  $P_1$ ,  $P_2$ , and  $P_3$  are summarised with  $P_2$  and  $P_3$  expressed as percentages of  $P_1$ .

Over the three years the mean whole animal production rate ( $P_1$ ) for both sexes was 47.63 kJ m<sup>-2</sup>y<sup>-1</sup> (2.14 g m<sup>-2</sup>y<sup>-1</sup> dry mass) with a range of

Table 2. *Panulirus homarus*. Numbers captured from ORI Reef in quarterly samples over three consecutive years

Month	Number of males	Number of females	Total
Jul. 1974	316	264	580
Oct. 1974	113	89	202
Jan. 1975	186	131	322
May 1975	144	166	310
<b>Total</b>	<b>759</b>	<b>655</b>	<b>1414</b>
Aug. 1975	44	47	91
Oct. 1975	80	56	136
Mar. 1976	67	58	125
May 1976	92	74	166
<b>Total</b>	<b>283</b>	<b>235</b>	<b>518</b>
Jul. 1976	97	77	174
Oct. 1976	38	28	66
Apr. 1977	105	105	210
June 1977	56	40	96
<b>Total</b>	<b>296</b>	<b>250</b>	<b>546</b>

84.95–27.85 kJ m<sup>-2</sup>y<sup>-1</sup>. The mean  $P/\bar{B}$  ratio for the sexes combined was 0.42, the slightly higher ratio in 1976/77 probably being attributable to the smaller size composition of the population in that year. The mean  $P/\bar{B}$  ratio for males was 0.43 and for females 0.42.

The mean annual production of exuviae ( $P_2$ ) was 28.14 kJ m<sup>-2</sup>y<sup>-1</sup> (59.07 % of  $P_1$ ).

The mean annual gonadal output ( $P_3$ ) was 9.83 kJ m<sup>-2</sup>y<sup>-1</sup> (20.64 % of  $P_1$ ). Mean egg production rate comprised 90.8 % of total gonadal output. In 1976/77, egg production rate was only 8.65 % of  $P_1$  as opposed to about 25 % in the previous two years. This again can probably be attributed to the smaller size composition of the population in 1976/77. Mean total production ( $P_1 + P_3$ ) was 57.46 kJ m<sup>-2</sup>y<sup>-1</sup>. For the three years total production (kJ m<sup>-2</sup>y<sup>-1</sup>) for males and females respectively was: 50.8 and 53.3 (1974/75), 18.2 and 19.5 (1975/76), and 16.1 and 14.13 (1976/77).

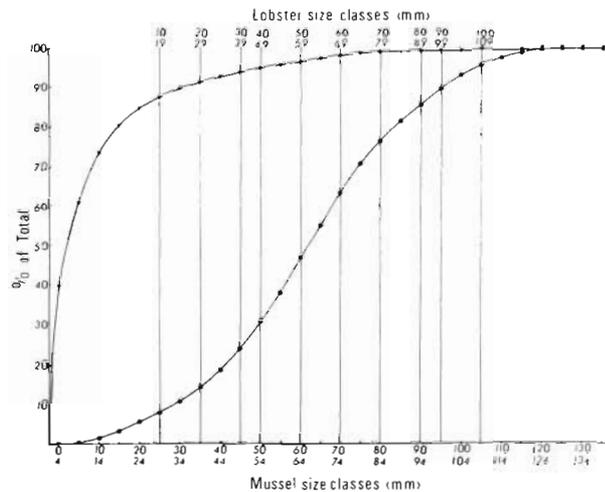


Fig. 1. Calculated proportion of mean standing crop of *Perna perna* potentially available as food for *Panulirus homarus* on the ORI Reef. Proportion plotted as cumulative percentage of total with increase in size in terms of biomass (circles) and numbers (triangles). Vertical lines indicate availability or non-availability of mussels to different-sized lobsters in terms of the maximum mussel size they are capable of opening

*Panulirus homarus* in Natal feeds principally on the mussel *Perna perna* (Berry, 1971). This was confirmed on the ORI Reef where it was found to constitute 85.3 % of the dry mass of food in lobster foreguts. Estimates of consumption rates ( $C$ ) of the *Panulirus homarus* population over the three consecutive years sampled, based on the consumption rate of *P. perna* flesh obtained by Smale (1978) in captive animals were 1808.3 kJ m<sup>-2</sup>y<sup>-1</sup>, 770.9 kJ m<sup>-2</sup>y<sup>-1</sup> and 631.8 kJ m<sup>-2</sup>y<sup>-1</sup>, respectively. The mean was 1070.3 kJ m<sup>-2</sup>y<sup>-1</sup>; Smale's consumption-rate data were, however, supplemented with additional

data to cover the size range of lobsters encountered on the ORI Reef. Total production rate, therefore, represents a mean of 5.4 % of total consumption rate, a value which appears to be low but which cannot be evalu-

ated until the other components of the energy equation are available.

Smale (1978) showed in tank studies that the maximum size mussel that a rock lobster is physically

Table 3. *Panulirus homarus*. Female annual production rates ( $P_1$ ) (with data used to calculate them); production rates of dry exoskeleton (exuviae) organics ( $P_2$ ); and gonadal output corrected for repetitive breeding ( $P_3$ ) for each carapace length size class for 1974/75. Totals only of each are presented for 1975/76 and 1976/77

Size class (mm)	$\bar{W}_1$	$\bar{N}$	$\bar{W}_2$	G ( $\log \bar{W}_2 - \log \bar{W}_1$ )	$\bar{B}$	$P_1$	$P_2$	$P_3$
25-29	23.07	5.25	178.02	2.04	121.12	247.08	34.12	0
30-34	37.19	5.25	187.23	1.62	195.25	316.31	48.63	0
35-39	55.99	8.25	194.81	1.25	461.92	577.40	100.76	0
40-44	80.08	12.75	202.59	0.93	1021.02	949.55	143.80	0
45-49	110.06	14.25	225.03	0.72	1568.36	1129.22	136.95	0
50-54	146.52	24.50	255.83	0.56	3589.74	2010.25	283.48	52.64
55-59	190.05	22.75	316.11	0.51	4323.64	2205.06	231.42	60.89
60-64	241.21	20.25	352.94	0.38	4884.50	1856.11	264.00	136.44
65-69	300.57	15.25	425.09	0.35	4583.69	1604.29	222.30	114.03
70-74	368.71	18.25	524.28	0.35	6728.96	2355.14	324.40	276.54
75-79	446.16	9.00	581.01	0.26	4015.44	1044.01	127.72	118.51
80-84	533.48	4.50	631.21	0.17	2400.66	408.11	65.34	64.18
85-89	631.21	1.75	688.51	0.09	1104.62	99.42	26.70	27.87
90-94	739.90	1.50	770.02	0.04	1109.85	44.39	25.62	11.10
95-99	860.08	0.25	872.75	0.01	215.02	2.15	4.00	2.14
<b>Totals (1974/75):</b>		g y <sup>-1</sup> (wet mass)			36323.79	14848.49	-	-
		g y <sup>-1</sup> (dry mass)			6486.39	2651.52	2039.24	864.34
		g m <sup>-2</sup> y <sup>-1</sup> (dry mass)			3.94	1.61	1.24	0.53
		kJ m <sup>-2</sup> y <sup>-1</sup>			87.74	35.87	22.73	17.47
<b>Totals (1975/76):</b>		g y <sup>-1</sup> (wet mass)			14613.19	5183.81	-	-
		g y <sup>-1</sup> (dry mass)			2609.50	925.68	472.47	343.58
		g m <sup>-2</sup> y <sup>-1</sup> (dry mass)			1.58	0.56	0.29	0.21
		kJ m <sup>-2</sup> y <sup>-1</sup>			35.30	12.52	7.75	6.94
<b>Totals (1976/77):</b>		g y <sup>-1</sup> (wet mass)			8382.71	4971.37	-	-
		g y <sup>-1</sup> (dry mass)			1496.91	887.74	694.07	105.00
		g m <sup>-2</sup> y <sup>-1</sup> (dry mass)			0.91	0.54	0.42	0.06
		kJ m <sup>-2</sup> y <sup>-1</sup>			20.25	12.01	7.74	2.12

Table 4. *Panulirus homarus*. Male annual production rate ( $P_1$ ) and production rates for dry exoskeleton (exuviae) organics ( $P_2$ ); spermatophoric mass corrected for repetitive breeding ( $P_3$ ) for each size class

Totals			$\bar{B}$	$P_1$	$P_2$	$P_3$
<b>Totals (1974/75):</b>	g y <sup>-1</sup> (wet mass)		49385.20	20317.32	-	198.14
	g y <sup>-1</sup> (dry mass)		8818.79	3628.09	2408.54	102.66
	g m <sup>-2</sup> y <sup>-1</sup> (dry mass)		5.36	2.20	1.46	0.06
	kJ m <sup>-2</sup> y <sup>-1</sup>		119.29	49.08	26.85	1.74
<b>Totals (1975/76):</b>	g y <sup>-1</sup> (wet mass)		17880.72	7278.15	-	75.84
	g y <sup>-1</sup> (dry mass)		3192.99	1299.67	904.42	38.86
	g m <sup>-2</sup> y <sup>-1</sup> (dry mass)		1.94	0.79	0.55	0.02
	kJ m <sup>-2</sup> y <sup>-1</sup>		43.19	17.58	10.01	0.66
<b>Totals (1976/77):</b>	g y <sup>-1</sup> (wet mass)		12542.18	6559.35	-	32.72
	g y <sup>-1</sup> (dry mass)		2239.67	1171.31	836.53	16.95
	g m <sup>-2</sup> y <sup>-1</sup> (dry mass)		1.36	0.71	0.51	0.01
	kJ m <sup>-2</sup> y <sup>-1</sup>		30.30	15.84	9.33	0.29

capable of opening increases in direct proportion to the size of the lobster. In view of this it was necessary to calculate what proportion of the mean standing crop of mussels was potentially available as food for each size of rock lobster. This is summarised in Figure 1. Mussel numbers and biomass available are those to the left of each vertical line and those unavailable are to the right for each size class of rock lobster, e.g. for a 50–59 mm carapace length lobster 47% of the total mussel biomass is available (all those up to 60–64 mm size

class) which represent 95% of the total numbers of mussels on the reef.

For the rock lobster population as a whole the mean annual consumption rate was only 3.6% of the total available mussel flesh and this rate was not exceeded by any individual size class, indicating that on the basis of the maximum size of mussel that can be opened there was a surplus of flesh available to the rock lobster population. Moreover, this is on the basis of the 'standing' crop of mussel flesh. If it is considered

Table 5. *Panulirus homarus*. Summary of mean biomass ( $\text{kJ m}^{-2}$ ), production rates ( $\text{kJ m}^{-2} \text{y}^{-1}$ ) and  $P/\bar{B}$  ratios for whole-animals, plus production rates,  $P/\bar{B}$  ratios and production rates of exuviae and gonadal output expressed as percentages of whole-animal production

	Whole animal			$P_2$	Exuviae		$P_3$	Gonadal output	
	$\bar{B}_1$	$P_1$	$\frac{P_1}{\bar{B}_1}$		$\frac{P_2}{\bar{B}_2}$	$P_2$ as % of $P_1$		$\frac{P_3}{\bar{B}_3}$	$P_3$ as % of $P_1$
1974/75									
males	119.29	49.08	0.41	26.85	1.43	54.71	1.74	0.50	3.54
females	87.74	35.87	0.41	22.73	1.79	63.37	17.47	0.31	48.70
<b>Total</b>	<b>207.03</b>	<b>84.95</b>		<b>49.58</b>		<b>58.36</b>	<b>19.48</b>		<b>22.92</b>
1975/76									
males	43.19	17.58	0.41	10.01	1.46	56.94	0.66	0.50	3.75
females	35.30	12.52	0.35	7.75	1.48	61.90	6.94	0.31	55.43
<b>Total</b>	<b>78.49</b>	<b>30.10</b>		<b>17.76</b>		<b>59.00</b>	<b>7.60</b>		<b>25.25</b>
1976/77									
males	30.30	15.84	0.51	9.33	2.09	58.90	0.29	0.44	1.83
females	20.25	12.01	0.59	7.74	2.65	64.45	2.12	0.23	17.65
<b>Total</b>	<b>50.55</b>	<b>27.85</b>		<b>17.07</b>		<b>61.29</b>	<b>2.41</b>		<b>8.65</b>
<b>Mean of 3 years</b>	<b>112.02</b>	<b>47.63</b>	<b>0.42</b>	<b>28.14</b>		<b>59.07</b>	<b>9.83</b>		<b>20.64</b>

Table 6. Comparison of density and biomass between several palinurid lobster species of the genera *Panulirus* and *Jasus*

Species	Density (No. $\text{m}^{-2}$ )	Wet biomass ( $\text{gm}^{-2}$ )	Locality	Method	Source
<i>P. homarus</i>	0.13 (0.35–0.04)	28.17	ORI Reef, S. Africa (sanctuary)	Diving	Present study
<i>J. lalandii</i>	0.81	230	Robben Island, S. Africa (sanctuary)	Diving	Pollock (1979)
<i>P. cygnus</i>	0.10 (0.04–0.21)	–	Abrolhos Island, W. Australia (closed area in fishing ground)	Tag/ recapture	Morgan (1974)
<i>P. cygnus</i> (juv.)	0.12–0.54	–	Garden Island, W. Australia (sanctuary)	Tag/ recapture	Chittleborough (1970)
<i>P. argus</i>	0.0065	5.8	Dry Tortugas, USA (sanctuary)	Diving/ tagging	Davis (1977)
<i>P. argus</i>	0.001	–	St. John, USA (sanctuary)	Diving/ tagging	Olsen et al. (1975)

that the mean  $P/\bar{B}$  ratio for the whole mussel population of the ORI Reef exceeds 3 and for the first year of growth may be as high as 6 (Berry, 1978) the available food is even greater, particularly for small lobsters. This situation was the case throughout the year as with spring and winter settlements the biomass and size composition of *Perna perna* on the ORI Reef remained fairly constant (Berry, 1978).

Smale (1978) also showed that there is a linear relationship between size of rock lobsters and the size of mussels selected as a first choice from a range. Using this relationship, the proportion of the mussel population available as first choice food was again determined. On this basis a mean of 14.3% of the total available population was consumed per annum and the maximum proportion was 32% for the 30–39 mm carapace length size class.

## DISCUSSION

There are few published records of density and biomass in palinurid lobsters. Most of these are summarized in Table 6. Fluctuations in the density of *Panulirus homarus* on the ORI Reef in the twelve consecutive samples and between the three years sampled were substantial with coefficients of variation for the latter of 59.8%, 23.9% and 49.0%, respectively. This is attributed mainly to large-scale sand movements which affect the availability of shelter for lobsters on the reef (Smale, 1978). Considerable variation in standing crop, due largely to seasonal recruitment, has been recorded by other authors, e.g. Chittleborough (1970) and Morgan (1974). However, in *P. homarus* this was not evident and no substantial changes attributable to recruitment occurred in the size composition of samples.

While the density and biomass of *Panulirus homarus* on the ORI Reef are somewhat higher than have been recorded in other members of the genus *Panulirus* they are substantially lower than those recorded for *Jasus lalandii* by Pollock (1979). *J. lalandii* is, however, a comparatively slow growing, long-lived cold water species which could be expected to accumulate a high biomass in conditions of low mortality rate provided that adequate food and shelter are available which, according to Pollock (1979) is the situation at Robben Island. A high production rate of 30.3 g m<sup>-2</sup>y<sup>-1</sup> for males and 2.8 g m<sup>-2</sup>y<sup>-1</sup> for females (wet mass) has been recorded for *J. lalandii* by Pollock (1978) compared with equivalent values of 6.9 g m<sup>-2</sup>y<sup>-1</sup> and 5.1 g m<sup>-2</sup>y<sup>-1</sup>, respectively for *P. homarus*. The high production rate of *J. lalandii* is apparently a function of its higher biomass as  $P/\bar{B}$  ratios for males and females are 0.22

and 0.04, respectively, as opposed to 0.43 and 0.42, respectively, in *P. homarus*.

The results obtained for the production rate of *Panulirus homarus* are obviously determined by prevailing conditions on the ORI Reef which influence growth rate and biomass. However, as an excess of food appeared to be available it seems unlikely that growth rate would have been significantly different over the three years of investigation. The  $P/\bar{B}$  ratios obtained for whole animal production rate show a reasonable degree of consistency, variations being attributable to differences in the population composition. The fact that there is not a great discrepancy in  $P/\bar{B}$  ratios between the sexes in *P. homarus* as has been recorded in *Jasus lalandii* is probably because the difference in growth rates between the sexes is substantially less than that recorded by Pollock (1978) in *J. lalandii*.

Production rate estimates of gonadal products are necessarily very rough because of the lack of accurate determinations of the proportion of females in each size class that spawn 1, 2, 3 or 4 times per year. In the case of males, application of the same correction for repetitive breeding as for females may result in a considerable difference from the true situation, as *Panulirus homarus* is polygamous (Berry, 1970) and a higher proportion of mating is probably done by large males than small ones. Nevertheless, the fact that values obtained for total production in males and females were similar suggests that the error introduced in the correction for repetitive breeding was not substantial.

The proportion of energy involved in egg production is relatively high – about 50% of the whole animal production rate in the first two years of the study and 18% in the third year, when a higher proportion of small females was present. A progressive increase in the proportion of production being channelled into egg production is evident with increase in size (Table 3). This is probably due to increasing brood size and number of broods produced per annum and would account for the progressive divergence in growth rates of the sexes recorded by Berry (1971).

The morphology and structure of the spermatophoric mass of *Panulirus homarus* has been described by Berry (1970). Its colour and consistency suggested that it was probably largely composed of CaCO<sub>3</sub>. However, in determination of its calorific value this was found not to be the case; it is almost entirely composed of organic material of surprisingly high energy content (27.9 kJ g<sup>-1</sup>).

The results demonstrate that moulting with successive complete loss of exoskeletons and the necessity to replace what has been lost in addition to the new growth added at each successive moult, is an inefficient means of growth. In fact on the basis of the

present results, it utilizes, for the population as a whole, approximately four times more energy than is the case if exoskeleton production is calculated without taking into account the number of moults involved, i.e. as if it were a continuous growth process.

Although an attempt has been made to take into account the availability of the mean standing crop of mussel flesh as food for the rock lobster population, this may not reflect the actual situation as it is not known to what degree mussels are protected from predation by existing in dense aggregations. Another unknown factor is the extent to which excessive surge conditions caused by rough seas limit feeding activity. If this is substantial it is probable that Smale's (1978) consumption rates in which individually separated mussels were fed under calm tank conditions are over-estimated. Nevertheless, it is considered unlikely that food availability limits the standing crop or growth rate of lobsters on the ORI Reef, particularly in view of the substantially higher mean biomass of *Jasus lalandii* supported by a lower biomass of mussels (Pollock, 1979).

Both *Jasus lalandii* and *Panulirus homarus* feed predominantly on the filter feeding mussels *Aulacomya ater* and *Perna perna*, respectively. The availability of food to these mussels and hence their productivity is dependent in both cases on physical energy subsidies. In *A. ater* this is largely the southeasterly wind which upwells nutrient rich water resulting in plankton blooms (Pollock, 1979), while in the case of *P. perna* it is the wind-driven surf action in the littoral zone which ensures the availability of detritus as food (Berry, 1978). It is suggested that a reason that the stocks of *P. homarus* are smaller than those of *J. lalandii* may lie in the fact that the energy subsidy on which *P. perna* and consequently *P. homarus* are dependent is present over the restricted area of the nearshore zone. The size of the lobster population is, therefore, limited by the amount of reef in this zone where its food organism occurs. The energy subsidy on which *A. ater* and *J. lalandii* are dependent gives rise to a much larger scale phenomenon and affects primary productivity over a considerably greater area. *A. ater* and *J. lalandii* have a greater vertical distribution than their east-coast counterparts and the total area inhabited by *J. lalandii* and its total biomass is consequently substantially larger. Thus *J. lalandii* with a comparatively lower turnover rate supports a large-scale fishery whereas *P. homarus* with a much higher turnover rate but lower total biomass does not.

*Acknowledgements.* This study was financially supported by the South African Association for Marine Biological Research, the South African National Committee for Oceanographic Research and the Natal Provincial Administration through the Natal Parks Board. We wish to thank C. Griffiths and D. Pollock for their critical comments.

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