CARBON AND NITROGEN FLUX THROUGH THE CAPE ROCK LOBSTER *JASUS LALANDII* (H. MILNE EDWARDS), WITH PARTICULAR REFERENCE TO THE NEARSHORE BENGUELA SYSTEM

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DEDICATION

To my Parents

for initial and continued encouragement,

to Hil

with thanks for the help and the many good times

and to our Children

who are the link to the Future.

DECLARATION

I declare that the initial concepts, the collection and analysis of data, and the final synthesis were of my doing, and I accept responsibility for them. Wherever comparisons have been made with published literature or published data used, the sources have been referenced in the text.

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"The 'Cape lobster', as it is sometimes called, although it does not possess the huge claw for which its European congener is so famous, is a most valuable asset of the Cape fishing industry; it is indispensable as bait in the west coast water, is much relished as food by the coloured population of the Cape Province, and is largely exploited for canning and export."

J. Wardlaw Thompson 1913

ABSTRACT

ZOUTENDYK, PETER 1989 - Carbon and nitrogen flux through the Cape rock lobster *Jasus lalandii* (H. Milne Edwards), with particular reference to the nearshore Benguela system.

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Observations and experiments on *Jasus lalandii* were undertaken over the period 1977 to 1986 to quantify the passage of carbon and nitrogen through populations at Oudekraal and Robben Island on the west coast of South Africa. The terms of the energy flow equation, $C=P+R+G+U_E+U_X+U_D+F$ (where C=consumption, P=production, R=respiration, G=reproduction, U_E=Exuvial loss, U_X=excretion of exogenous nitrogen, U_D=excretion of endogenous nitrogen and F=faeces), were quantified by combining field data and laboratory results. With this information the rôle played by *J. lalandii* in the kelp-bed ecosystem under the influence of the Benguela current was explored and quantified. In a natural unexploited population at a mean annual temperature of 13° C, feeding accounts for the mobilization of 59 $gC.m^{-2}.yr^{-1}$ of which 20 per cent is lost to the environment during ingestion, resulting in a consumption value of 47 $gC.m^{-2}$. Absorption efficiency is high (80 per cent) which results in only 8,7 $gC.m^{-2}$ (20 per cent) being returned to the system as faeces. Of the absorbed carbon, 77 per cent is returned to the environment as carbon dioxide as a result of respiration, with the associated conversion of chemical- to heat-energy. Thirteen per cent of the carbon goes into production (growth) and is returned to the system by natural mortality, while moulting and gonad output account for 7 and 3 per cent respectively. Of the carbon mobilized, 97 per cent remains within the system to be recycled but, of the energy only 47 per cent remains. With regard to nitrogen, 57 per cent is returned to the system as urea and ammonia. This fraction, together with remineralized nitrogen from the other terms of the equation, is readily available to primary producers and could provide as much as 14 per cent of the kelp and kelp-bed phytoplankton annual requirements. Therefore, *Jasus lalandii* is, on balance, an exporter of energy from the nearshore Benguela system, but of the nitrogen mobilized, 97,9 per cent remains, which may be a significant supplement to the primary producers during static conditions or weak downwelling when the availability of new nitrogen is limited.

SUMMARY OF RESULTS FOR THE TERMS OF THE ENERGY FLOW EQUATION

Absorption and faeces (A & F) - To estimate the absorption rate of carbon by the Cape rock lobster *Jasus lalandii*, the net amount of ingested carbon and gross carbon content of faeces must be known. The former was established by determining the carbon content of the prey (the mussel *Choromytilus meridionalis*) in relation to shell length and feeding mussels to *J. lalandii* under controlled aquarium conditions through five eating/defaecating cycles after a steady state had been reached. The losses of particulate and dissolved organic carbon due to messy feeding were measured and amounted to 20,1 per cent of the food mobilized. Of the net carbon ingested, 20,5 per cent was voided as faeces which gives a mean carbon absorption efficiency of 79,5 per cent. *J. lalandii*, a top carnivore in the inshore Benguela ecosystem, is thus highly efficient in the utilization of ingested carbon. In animals from the commercial size range (≥89mm carapace length), variations in absorption efficiencies were small and were dependent neither on body mass nor ingested mass. As a result of messy feeding and the voiding of faeces, 17,0 g carbon are returned to the environment m^{-2} annually and may be of significance to filter feeders during upwelling when phytoplankton biomass is at a minimum.

Consumption (C) - To determine long-term consumption rates, aquarium-held male rock lobsters in the size range 80-130 mm carapace length were fed mussels (*Choromytilus meridionalis*) over a period of 400 days. Annual patterns in consumption were closely linked to breeding and moulting cycles. Feeding activity was fastest in summer, declined in autumn during breeding and was at its lowest in winter prior to moulting. There was a pre-ecdysis period of mean duration of 44 d when consumption was zero, followed by a post-ecdysis period of a further 34 d without feeding. Consumption (C) ($gC.yr^{-1}$) was related to carapace length (CL) by the equation $C = 0,0001312CL^{2,877}$. The impact of *J. lalandii* in a sanctuary at Oudekraal is equivalent to removing 107 *C. meridionalis* (50 mm long).$m^{-2}.yr^{-1}$ (or 23.8 $gC.m^{-2}.yr^{-1}$). Using rock-lobster size-frequency data from Robben Island sanctuary, the impact of the *J. lalandii* population there would be to remove 35,3 $gC.m^{-2}.yr^{-1}$ from prey populations.

Respiration (R) - The metabolic rates of a wide size-range of lobsters (20-3000 g wet mass) over a temperature range covering normal annual fluctuations (8-19° C) were studied and this information used to estimate the energy demands at population level. Over the above temperature range and at standard oxygen consumption rates, *J. lalandii* had a Q_{10} value of 2,5. Plotted for the five temperatures the graph of oxygen consumption rates had a typical

sigmoidal appearance, with a flatter response (Q_{10}=1,7) between 10-13° C, which coincides with the modal habitat temperature. At 19° C *J. lalandii* appeared stressed and showed an easing in respiration rate with Q_{10}=1,4. Respiration is mass-dependent, metabolic rate being inversely proportional to body mass. Responses to a short-term drop in temperature of 5° C produces a rapid decrease in O_2 consumption rate, with no undershoot occurring and with no suggestion of acclimation taking place. An increase of 5° C also induced a rapid response which resulted in an overshoot, followed by a gradual return to the predicted rate over 2 to 5 d, which could not be interpreted as one of acclimation. For a population of lobsters off Robben Island NW of Cape Town at a mean annual temperature of 13° C, lobsters on average metabolize the equivalent of their body mass of carbon per annum. This represents an irreversible energy loss to the biotic community and is equivalent to the oxidation of 26 $gC.m^{-2}.y^{-1}$.

Excretion; exogenous and endogenous nitrogen (U_x & U_n) - The mean density and biomass of *Jasus lalandii* at Oudekraal is 0,48 $individuals.m^{-2}$ or 49,75g dry $mass.m^{-2}$. The main component of its diet is *Aulacomya ater*, the ribbed mussel, which has a mean biomass of 1,15 kg dry $mass.m^{-2}$. Daily consumption of carbon and nitrogen from this source reaches a maximum in summer and, when *J. lalandii* feeds on mussels, 14,1 per cent of the flesh nitrogen is lost to the environment as a result of "messy feeding". The absorption efficiency of ingested nitrogen is 86,2 per cent. Ammonia and urea excreted in the first 12 h after feeding (exogenous excretion) amount to 6,7 and 1,6 per cent respectively of the nitrogen ingested. Endogenous nitrogen excretion has a mean rate of 1,9 $\mu gN.g(dry\ mass)^{-1}.h^{-1}$. The range of estimates for combined figures of kelp and phytoplankton nitrogen requirements are 76,4 to 86,7 $gN.m^{-2}.yr^{-1}$. *J. lalandii* returns 6,3 $gN.m^{-2}.yr^{-1}$ to the ecosystem, accounting for 7,2 to 8,2 per cent of annual kelp and phytoplankton requirements. This could be of particular importance during static conditions or weak downwelling when the supply of new nitrogen is limited.

Production (P) - Carbon and nitrogen values from elemental analysis of whole *Jasus lalandii* have been used to quantify growth and production for a population of lobsters in the sanctuary off Robben Island, 10 km NW of Cape Town. A standing stock equivalent to 26,17 $gC.m^{-2}$ has an annual production of 4,35 g carbon, with the maximum output occurring between 90-110 mm carapace length. Females contribute 12,7 per cent of the total production. The P/B ratio of the lobster population is 0,166, while the mean gross growth efficiency (K_1) is 0,16. In a stable population carbon and nitrogen are returned to the ecosystem through natural mortality as a consequence of disease and age, or by predation.

Excretion; exuviae (U_E) - Data on moulting were collected from a size range of *J.lalandii* in an aquarium where field conditions of light intensity and temperature were simulated. Elemental analysis was carried out on intermoult exoskeletons, exuviae and whole lobsters. Lobsters lose a mean of 27 per cent of their dry mass per year at ecdysis. Exuviae contained a higher ash content and a 28,1 per cent lower organic carbon content (indicating reabsorption) and a similar inorganic carbon content when compared with intermoult exoskeletons. Estimates for a lobster population occupying 100 m^2 at Robben Island are that 228 g organic carbon and 57,3 g nitrogen are lost annually by moulting. The annual cost of moulting to *J. lalandii* in terms of exuvial mass, which includes carbon and nitrogen, is considerable when viewed in terms of lost production.

Reproduction (G) - Fluxes of carbon and nitrogen as a result of gonad output were estimated at both individual and population levels and their impacts on the nearshore Benguela system evaluated. Annual carbon and nitrogen output in ova for a large female lobster (107,5 mm CL) is 5,6 gC and 1,3 gN, while the C and N outputs of seminal fluid from a large male (150 mm CL) are only two per cent of the above amounts. Combined somatic and reproductive carbon in females is only 43 per cent of the carbon utilized in somatic growth by males. Thus the channelling of carbon by females into ova production cannot alone account for their slower somatic growth. The slower growth in females is probably accounted for by increased oxygen consumption during the three-month period of incubation. In a lobster population off Robben Island NW of Cape Town, combined male and female gonad output amounts to 1,25 gC and 0,29 $gN.m^{-2}.yr^{-1}$. As hatching takes place in spring when the south-east wind is dominant, it is expected that a large proportion of the larvae will be exported from the system. Reproductive output as carbon and nitrogen from *J. lalandii* can therefore play only a minimal rôle in the nearshore Benguela system as most of it is lost through export.

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CHAPTER 1

GENERAL INTRODUCTION

As a top predator in the nearshore Benguela system, Man goes back many thousands of years. The earliest records of his exploitation of lobster stocks are dated at 11 000 years BP, when *Jasus lalandii* constituted a component of the diet of the hunter-gatherers along the Cape west coast (Parkington 1981). Since then Man has firmly entrenched his position as the top predator on the Cape rock lobster, accounting for the removal of 3 860 tonnes of lobsters, worth R60 million, during the 1987/88 season.

Much of the research involving *J. lalandii* during the present century has focussed on those aspects of its biology which have a direct bearing on management problems. Included are extensive field surveys where large amounts of data covering biomass, feeding, growth rates, onset of sexual maturity and fecundity have been collected. On the other hand more basic research has covered such aspects as anatomy, behaviour, breeding and larval studies, and prey selection. A detailed literature review for *J. lalandii* is given by Branch and Griffiths (1988). However, much of the work on *J. lalandii* has little relevance to this thesis, but

Table 1.1. Select categorized references for *J. lalandii* off Southern Africa

CATEGORY	AUTHOR(S) AND DATE(S)
ANATOMY	Gilchrist & Von Bonde 1922 Paterson 1968, 1969b Silberbauer 1971b
BEHAVIOUR	Heydorn 1969 Paterson 1969a Silberbauer 1971b
GROWTH & PRODUCTION	Gilchrist 1918 Heydorn 1969 Newman & Pollock 1974a, 1974b Pollock 1973, 1976, 1978, 1979b Pollock & Beyers 1981
FECUNDITY	Beyers & Goosen 1987 Heydorn 1969 Matthews 1962
FEEDING	Barkai & Branch 1988a Heydorn 1969 Pollock 1978 Zoutendyk 1988a, 1988b
FISHERIES	Beyers 1979 Gilchrist 1913, 1914, 1918 Heydorn 1965, 1969 Heydorn *et al.* 1968 Lees 1969 Matthews 1962 Matthews & Smit 1979 Newman 1973 Newman & Pollock 1971, 1974a, 1974b, 1977 Pollock 1978, 1982, 1986 Pollock *et al.* 1982 Pollock & Beyers 1979 Thompson 1913 Von Bonde & Marchand 1935
LARVAL BIOLOGY	Gilchrist 1916, 1920 Lazarus 1967 Pollock 1986 Pollock & Goosen 1983

CATEGORY	AUTHOR(S) AND DATE(S)
	Silberbauer 1971a Von Bonde & Marchand 1935
MOULTING	Heydorn 1965, 1969 Paterson 1969a Zoutendyk 1988c
PHYSIOLOGY	Krijgsman & Krijgsman 1954 Rudd & Warren 1976 Zoutendyk 1987
PREDATOR-PREY	Barkai & McQuaid 1988 Griffiths & Seiderer 1980 Pollock 1979a Seiderer *et al.* 1982 Wickens 1985 Wickens & Field 1988
REPRODUCTION	Berry & Heydorn 1970 Gilchrist 1916 Heydorn 1965, 1969 Matthews 1962 Paterson 1969b Von Bonde 1936, 1937

for the sake of completeness has been summarized in Table 1.1. Those papers that are of significance are discussed in the appropriate chapters.

However, between the applied and the basic approaches lies an area which has links with both sides but, as yet, has received little attention. This is the energetics approach where the interactions of an organism with the environment are quantified and the resulting picture is greater than the sum of the constituent parts. These interactions with the environment fall into categories which

can be equated with the characteristics of Life. Crisp (1984) summarizes the concept in the form of an equation

$$C = P + R + G + U + F ,$$

where C = consumption, P = production or growth, R = respiration, G = gonadal output, U = excretion (including exuviae), F = faeces.

This equation may be referred to as the balanced growth equation (Peters 1983) or as the energy flow equation. Usually it is expressed in terms of heat (Cal or J), but can also be represented in terms of carbon which has an energy equivalent. In addition, with minor modifications, the equation can handle the flux of other elements not based on energy, for example nitrogen.

By quantifying the fluxes of energy, carbon or nitrogen through an organism it is possible to evaluate the role that the organism plays in flows within an ecosystem. As yet, and in spite of the considerable economic importance of *J. lalandii*, not a single component of the energy equation has been quantified.

In the following pages each chapter addresses an aspect of the energy equation and has been written as a complete unit in itself. Chapters 2, 3, 5 and 7 have already been

published. The final chapter (9) draws upon the results of the preceding chapters to answer the question: What rôle does *Jasus lalandii* play in terms of carbon and nitrogen flux through the nearshore Benguela system?

CHAPTER 2

FEEDING, DEFAECATION AND ABSORPTION EFFICIENCY IN THE CAPE ROCK LOBSTER *JASUS LALANDII*

(Published in: *S. Afr. J. mar Sci.* 6: 59-65. 1988)

2.1. INTRODUCTION

There appear to be few available data on organic carbon loss to the environment sustained during feeding by spiny lobsters or allied taxa. Valiela (1984) states, in general terms, that the quantity of organic matter lost by consumers during feeding may be considerable. Similarly, quantitative information on faecal production in spiny lobsters and the loss through solution of organic carbon is equally scant.

Apart from build up of dissolved organic carbon (DOC) during feeding, it has been assumed that the only other contribution to DOC is through loss from faeces. This implies that there is no loss through urine or by diffusion through the exoskeleton. Evidence that this is a valid assumption comes from Burger (1957), who showed that the urine of *Homarus* is both protein- and glucose-free. Although both gills (Dall 1974) and the general integument

(Gross 1957) are permeable to ions, there appears to be no evidence to suggest that larger organic molecules pass to the exterior via this route.

The diet of the Cape rock lobster *J. lalandii* includes species from several invertebrate phyla. However, mussels are the major constituent of the normal diet and were found in the stomachs of 97 per cent of a wild population (Pollock 1979a). In the present investigation, the quality of the food has been kept constant by feeding the experimental animals a diet of mussels only, in quantities approximating an average daily ration (Chapter 3).

This paper is one of a series dealing with the energetics of *J. lalandii*. It aims at solving two problems associated with the estimation of absorption. They are, first, the measurement of food loss during ingestion as a result of messy feeding, and second, the quantitative estimation of faeces production. From these two results, a measure of absorption efficiency, which can be used in drawing up a carbon budget for the species, can be derived.

2.2. MATERIALS AND METHODS

Assimilation or absorption may be measured using radionuclides as tracers (Lasker 1966). It is also possible to measure it directly, provided that the net consumption is

known, together with the gross loss of organic matter from the alimentary canal in the form of faeces.

The terms assimilation and absorption are often used loosely and without adequate definition. Crisp (1984, pp. 289-290) defines assimilation as "...that part of consumption that is retained for physiological processes, namely, production (including gonoproducts) and respiration", and absorption as "...that part of the consumed energy that is not rejected as faeces". Absorption efficiency may be expressed as

100 x (Consumption - Faeces) / Consumption .

In this investigation all samples were assessed for carbon content, thereby giving a common basis for the interpretation of results.

2.2.1. Capture and holding of specimens

Male *J. lalandii* in the size range of 90-140 mm carapace length and aged between 10 and 15 years (Pollock 1978) were caught by SCUBA divers at Oudekraal on the west coast of the Cape Peninsula (south of Cape Town) in early summer 1985. All the animals were in the intermoult phase, having moulted during early spring. Each animal was held at 12°C in a 100-*l* tank of aerated seawater in a flow-through system. They were fed *Choromytilus meridionalis* (black

mussels) of known carbon content each day. Only those animals which showed a consistent feeding pattern over at least one week were used for the experiment. Prior to the actual experiment, they were starved for 72 h to clear the alimentary canal and washed thoroughly under a stream of fast-flowing filtered seawater to remove particles adhering to the exoskeleton.

2.2.2. Experimental procedure

Sterilized glass tanks each capable of holding a single *J. lalandii* plus 8 *l* of 5-µm-filtered, UV-sterilized seawater were set up in a constant temperature room at 12°C. Four rock lobsters were placed in separate tanks. A further 2 tanks acted as controls; one contained seawater plus two *C. meridionalis* and the other seawater only. The water was aerated and the tanks covered by sheets of glass to reduce evaporation. The formation of particulate organic carbon (POC) from dissolved organic carbon (DOC) may take place due to aeration (Riley 1963, 1970, Wangersky 1977, Velimirov 1980) but, because the tanks and the animals were carefully rinsed to avoid loss, it was assumed that this would not affect the total organic carbon (TOC).

At the start of the experiment, five 3-m*l* water samples were collected from each tank for DOC measurements. At the same time, 10 *l* of 5-µm-filtered seawater were refiltered to determine the particulate load of the 1,2 - 5 µm size

fraction. Whatmans 47 mm GF/C (glass fibre) filters with a mean mesh size of 1,2 µm, pre-ashed at 450°C for 4 h, were used throughout the investigation. Three of the four rock lobsters (Specimens A, B and C) were presented with two black mussels each, the mussels having been collected 15 km north of Cape Town from a discrete site. Due to the relatively short duration of the experiment, seasonal variations in flesh mass will be small and therefore should have had little effect. The mussel shell lengths were in the range 60-80 mm. Flesh dry mass (DM) was deduced from shell by means of the regression:

$$\text{Dry mass} = 0{,}00014\ \text{Shell length}^{2{,}18} \qquad (2.1)$$

($r^2 = 0{,}97$; $n = 26$).

The dry flesh from 20 *C. meridionalis* (range 24 - 69 mm) was blended and analyzed with the aid of a Carlo Erba 1106 elemental analyzer, standardized to acetanilide. From the results of 4 replicates, it was established that the conversion factor for flesh DM to carbon was 0,3873 ($n = 4$; SD = 0,00867). Thus the carbon content of the mussel was predicted from shell length.

Rock lobsters were induced to feed by controlling the light level in the presence of mussels. When the lights were switched off after a continuous period of illumination, feeding commenced immediately. Generally within three hours

both *C. meridionalis* had been consumed, after which any unopened shells plus shell fragments were removed. Due to the relatively short duration of the feeding phase, the output of faeces was minimal. Particles of faeces found at the beginning of the experiment were removed and discarded. From the second and subsequent feeding periods during the experiment, all faecal particles produced were removed and processed with the faeces samples collected immediately prior to feeding.

Subsequent to each feeding period, faecal production was monitored every 24-h for three days. In all, five continuous feeding/defaecating cycles were carried out for each of the three experimental animals, giving a total of 15 data sets.

After feeding, and then at 24-h intervals, the water was drained from each tank. Each 8 *l* from the lobster tanks was filtered through 44-µm mesh plankton netting to remove large particles. To remove all remaining food particles, 0,5 - 2 *l* of the filtrate was then filtered through GF/C filters. To this sample were added any fragments of flesh left adhering to the shell. Five 3-m*l* samples of the filtrate from each tank were taken and stored at -20°C for later DOC determination. The tanks were then refilled with 8 *l* of newly filtered seawater.

2.2.3. Leaching of DOC from faeces

The faeces of *J. lalandii* consists of a granule-size shell fraction and an organic fraction. The organic fraction when in suspension is fine textured and ribbon-like. It was assumed that leaching of DOC would occur during the 24-h period between water changes. On analysis of the DOC samples, difficulty was experienced in separating the experimental DOC values from background values of the control. Therefore to determine the extent of the losses, a separate experiment was set up as described below.

A total of twenty freshly caught *J. lalandii* were held in the aquarium for one week and fed a diet of *C. meridionalis*. They were then killed, the recta dissected out and faeces from the distal region removed. Faeces of 1 g wet mass were added to 500 m*l* filtered seawater and held at 12°C. Five 3-m*l* samples for DOC were collected initially, followed by similar sets at 4-h intervals for a total of 24 h. At the end of the period, the remaining 410 m*l* water plus solids was filtered through a GF/C filter. In calculating the extent of the leaching, allowance was made for the reduction in the water volume due to the withdrawal of samples. The shell fragments in the faeces were assessed for dry mass and then returned to the sample for analysis *in toto*. The percentage of shell in the faeces is given in Table 2.1.

Table 2.1. Analysis of *J. lalandii* food and faeces

MATERIAL	MEASUREMENT	CONC.
C. meridionalis Flesh (dry)	Organic Carbon	38,7%
	Nitrogen	10,2%
	Hydrogen	5,98%
	kiloJoules	18,9kJ.g^{-1}
J. lalandii Rectal faeces(wet)	Organic material	52,7%
	Ash (mainly shell)	47,3%
Rectal faeces(dry)	Organic Carbon	8,14%
	Inorganic Carbon	11,0%
	Nitrogen	2,45%
	Hydrogen	1,65%
	Ash (mainly shell)	77,7%
	kiloJoules	4,0kJ.g^{-1}
Tank faeces (dry) Particles >44µm	Carbon	49,0%
	Nitrogen	8,5%
Particles <44µm	Carbon	42,1%
	Nitrogen	7,0%

Faeces derived from rectal dissection were also analyzed in the CHN elemental analyzer to act as a control before leaching took place. Further samples were oxidized in a muffle furnace at 450°C, following the method of Bligh *et al.* (1984). Conversion factors for wet mass to dry mass and for dry mass to ash-free dry mass were calculated. The mean of three faecal replicates processed in a Coalcor CP500 macrobomb calorimeter to determine the energy content (kJ) is also given in Table 2.1.

2.2.4. Processing water samples for DOC

Samples collected for DOC were processed through a Technicon autoanalyzer which used the UV photo-oxidation process. (Schreurs 1978, as modified by Mostert 1983).

2.2.5. Processing filters for POC

Filters were first rinsed with three successive irrigations of a 3,033 per cent iso-osmotic solution of ammonium formate (M. Delafonteine, University of Cape Town, pers. comm.). This was followed by oven drying at 60°C for 24 h (Lovegrove 1966) and weighing to 0,1 mg, after which the resultant dry mass of the retained material could be ascertained. Filters plus particulate material collected during the fourth day of the run were finely ground in an agate mortar and the resulting powder divided into two fractions.

One of the fractions was analyzed in the CHN elemental analyzer. Samples were kept desiccated and processed individually to eliminate the influence of water-derived hydrogen. Results could then be used to yield additional information regarding proportions of protein, carbohydrate and lipid. (After Gnaiger and Bitterlich 1984). The second fraction was heated to 450°C for 4 h to eliminate the organic component. Inorganic carbon residing in the ash was subjected to elemental analysis and the resulting carbon

value subtracted from the total carbon to give an estimate of organic carbon. The remaining POC samples from Runs 1, 2, 3, and 5 were oxidized as above to yield values of ash-free dry mass (AFDM).

In Figure 2.1, POC loss resulting from messy feeding has been regressed against the AFDM of particles during feeding. From this formula, the remaining feeding losses can be derived from the values of AFDM. Similarly in Figure 2.2, faecal POC has been regressed against AFDM. The formula was used to derive POC values from the remaining faecal AFDM data. In both cases the origins of the lines were forced through zero to yield a more realistic fit to the data.

2.3. RESULTS AND DISCUSSION

2.3.1. Composition of food and POC resulting from messy feeding

CHN analysis of *C. meridionalis* flesh gave a mean value of 38,7 per cent of carbon (Table 2.1). POC as a result of messy feeding was separated into two size fractions (>44 µm and 1,2-44 µm), the mean carbon value for the larger particles was 44,54 per cent and that for the fine fraction 41,49 per cent. As this difference is not significant (p = 0,60), the data for fine and coarse fractions were combined yielding a mean value of 42,1 per cent.

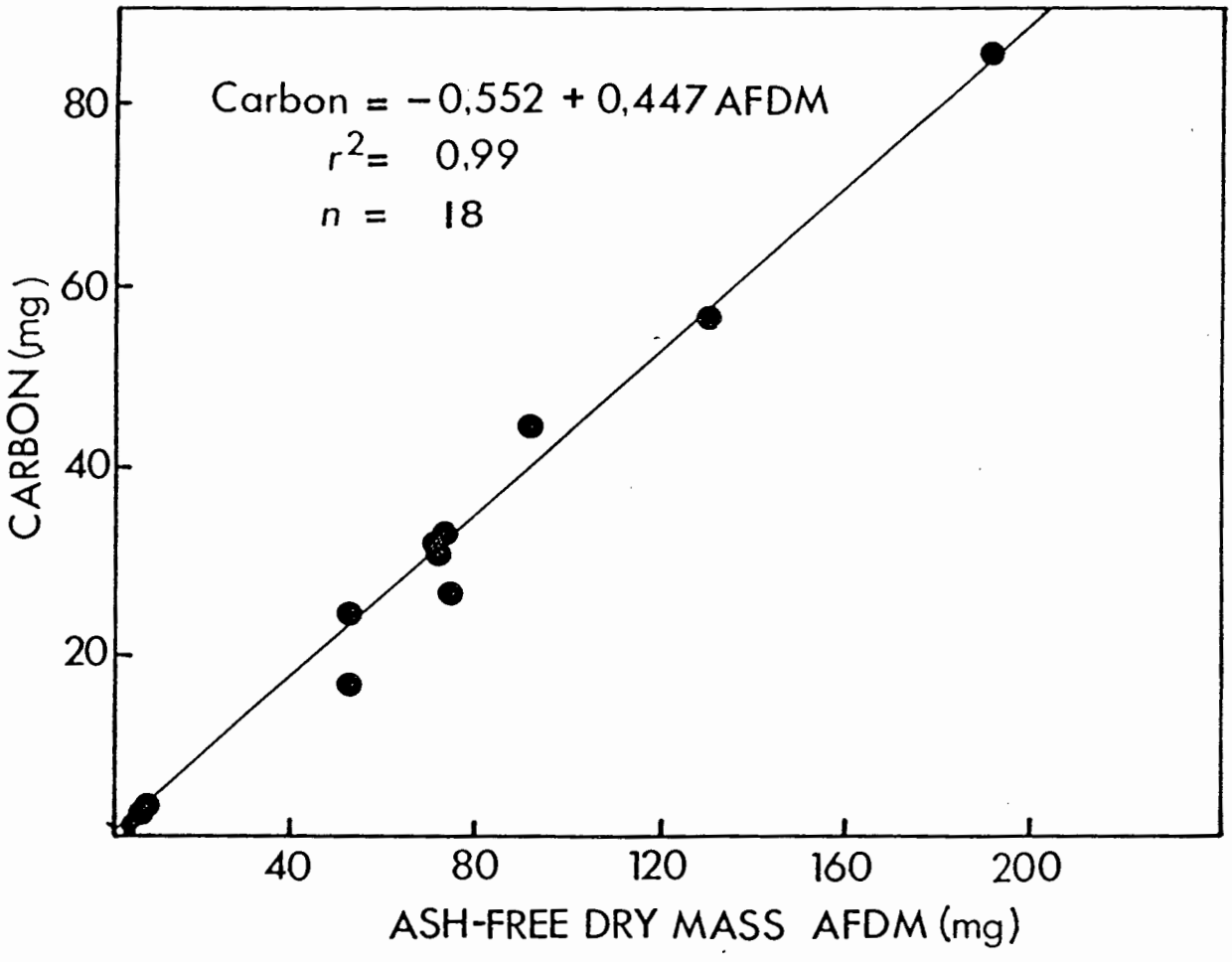

Figure 2.1. Linear regression of organic carbon against AFDM of particles resulting from messy feeding

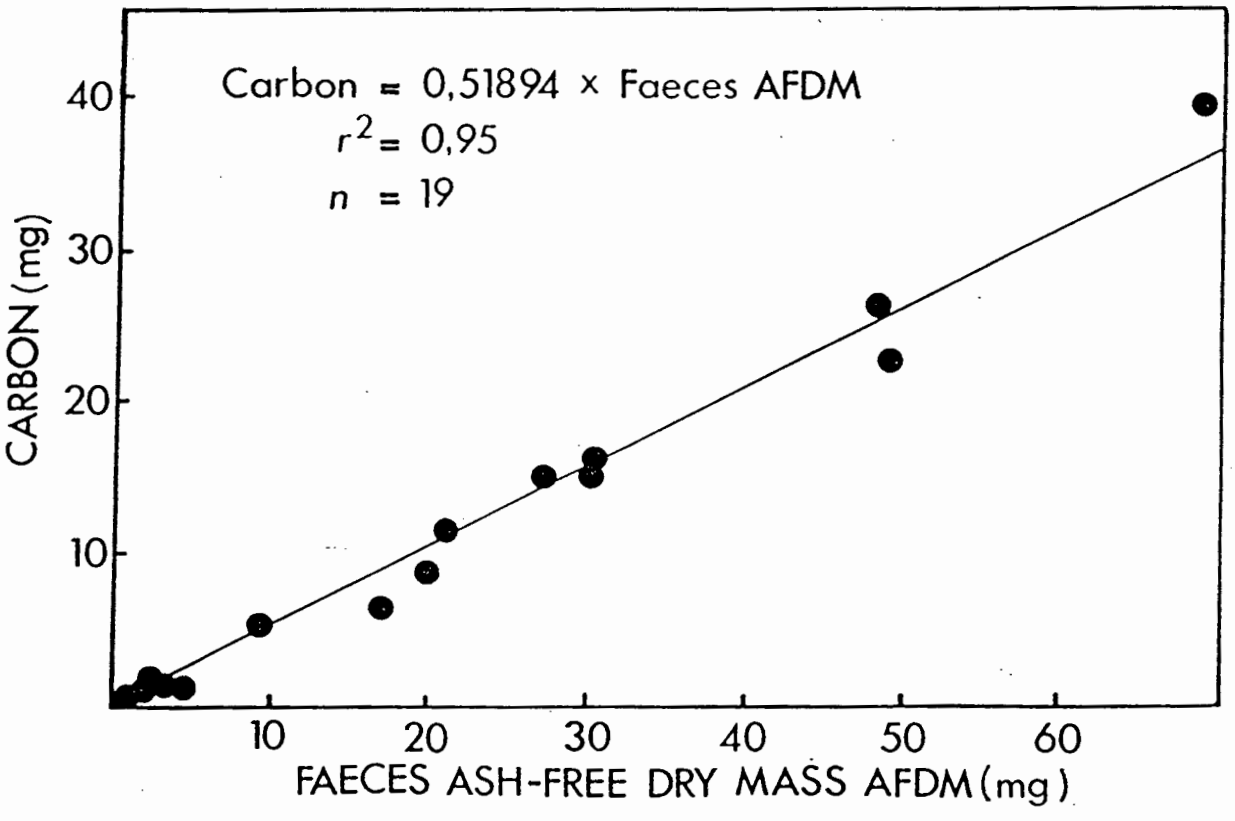

Figure 2.2. Linear regression of organic carbon against AFDM of faecal particles collected from the experimental tanks. The regression origin has been forced through zero

2.3.2. Background DOC

In spite of the use of filters and a protein skimmer in the processing of the experimental seawater, a detectable level of DOC still remained. Samples from the blank control were taken at regular intervals throughout the running of the experiment. In the 8 *l* of seawater supplied to each experimental tank, the mean level of DOC was 1,74 mg.l^{-1} (n = 27, SD = 0,45). However, in calculating the net DOC resulting from messy feeding or faecal production, specific values for DOC for the control, relating to the time of the experimental samples, were subtracted.

2.3.3. Release of DOC by *C. meridionalis*

Because the black mussels were present in the tank before the rock lobsters commenced feeding, the possibility existed that the mussels may have contributed significantly to the DOC level. From data collected from the control tank containing *C. meridionalis*, and the blank control, a Student's t-test revealed no significant difference (p = 0,30) between DOC concentration in the tanks containing *C. meridionalis* and the controls containing seawater only. It was therefore not necessary to make corrections for the presence of mussels in the tanks containing *J. lalandii*.

2.3.4. Loss of POC and DOC through messy feeding

Organic carbon loss during feeding is caused by the maceration of the mussel flesh during the opening of the

shell and its subsequent ingestion. The losses of carbon resulting from messy feeding are summarized in Table 2.2. The loss varies considerably between animals. The mean loss is 20,1 per cent (SD = 8,4 per cent, range = 11,3 - 44,9 per cent, *n* = 15). The lower limit shows how efficiently feeding can take place in an aqueous medium. The upper limit may be the result of time constraints placed on the animal by the experiment. Under field conditions the lower values may well be more realistic.

Table 2.2. *J. lalandii* carbon budget for feeding, defaecation and absorption (*n* = 15)

PARAMETER	MEAN	SD
FEEDING		
Food available (mg C)	837	177
POC loss (mg C)	64	49
DOC loss (mg C)	103	45
TOC loss (mg C)	167	73
Loss (C %)	20,1	8,4
FAECES		
POC (mg C)	85	20
DOC (mg C)	49	12
TOC (MG C)	135	33
Loss (C %)	20,5	4,6
Absorption (mg C)	535	104
Absorption (%)	79,5	4,6

2.3.5. Correlation of rectal faeces mass with *J. lalandii* body mass

In order to ascertain whether a correlation existed between *J. lalandii* rectal faeces content and wet body mass from the data gathered during the faeces leaching

experiment, wet faecal mass was plotted against wet body mass. The relationship was not significant. (r = 0,37, n = 19). This may be the result of sporadic feeding followed by the filling and voiding of the rectum at irregular intervals.

2.3.6. Faeces production and DOC losses

The build-up of DOC through leaching is rapid in the first 4 h when 67 per cent of the total production took place (Figure 2.3). The leaching rate dropped during the next 4 h and thereafter reached a steady state. Using the results of leaching in Figure 2.3 and reducing the DOC concentration to 86,9 per cent of the observed value to allow for incomplete leaching due to intermittent voiding of faeces during 24 h, the relationship between DOC concentration and faecal POC can be expressed as

$$\text{DOC (mg)} = \text{Faecal POC (mg)} \times 0{,}580 \; . \qquad (2.2)$$

The results of autoanalyzed DOC samples were compared with concentrations predicted from Equation (2.2). There was no significant difference (p = 0,60, n = 8) between the two sets of data. Therefore, all further values of DOC arising from faeces are derived from Equation (2.2).

The mean observed value for POC originating from faeces remaining in the tank after 24 h was 85,3 mg, i.e. some 12,9 per cent of the carbon ingested (see Table 2.2). A further

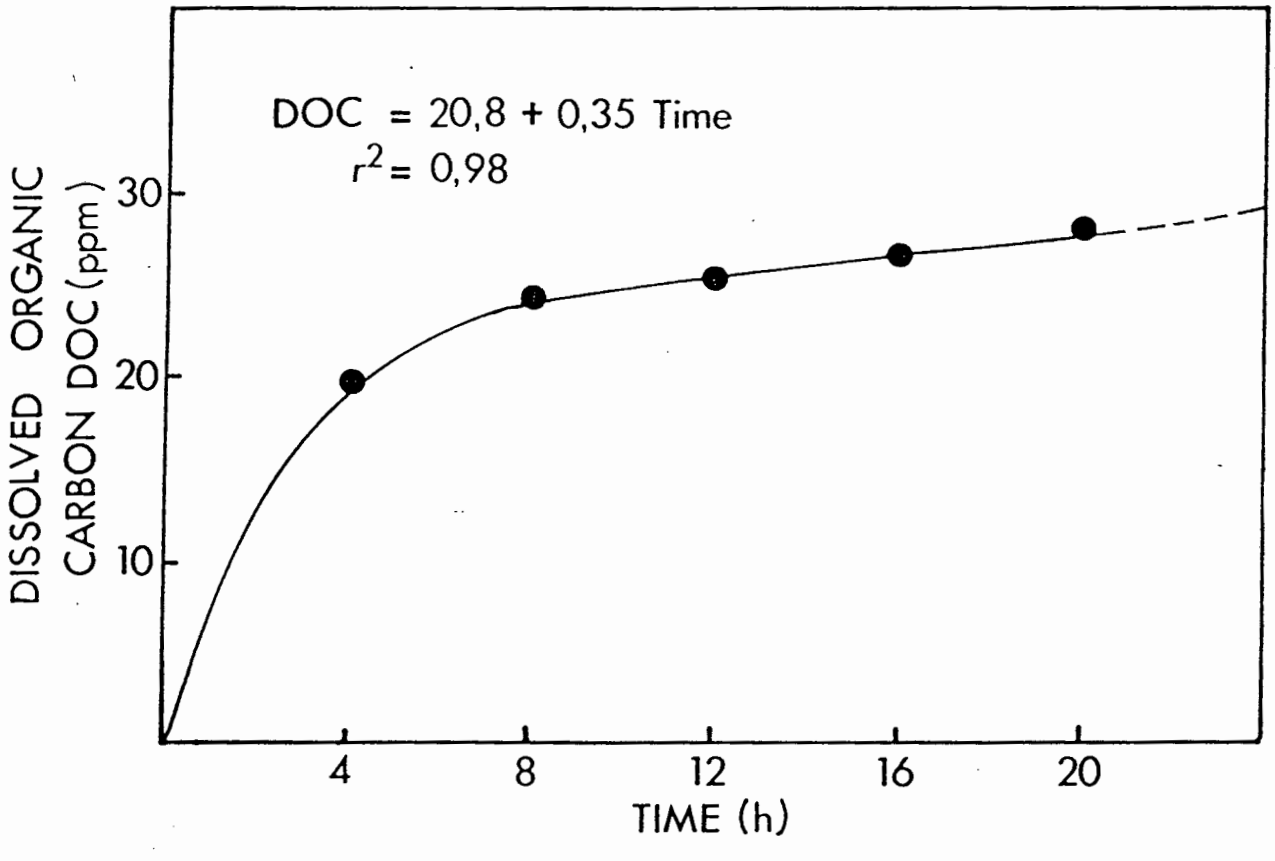

Figure 2.3. Cumulative loss of DOC from faeces as a result of leaching

7,6 per cent ended up in solution in the form of DOC. Therefore, a total of 20,5 per cent of the TOC is lost as faeces and, by subtraction the percentage of absorbed carbon can be calculated.

2.3.7. Fate of DOC and POC from feeding and faeces

The inshore reefs of the southern African west coast are populated by a range of filter-feeding organisms (Velimirov *et al.* 1977, Pollock 1979a, Field *et al.* 1980a, Pollock and Beyers 1981). DOC and POC as a result of both messy feeding and faeces may be utilized directly by bacteria and may be incorporated into a faecal loop (Newell 1981, Newell and Field 1983a,b), or DOC may be formed into aggregates as in foam (Riley 1970, Velimirov 1980), again both becoming available to filter-feeders. In Figure 2.4, DOC and POC from feeding and faeces are presented as the annual mass produced by each size-class of a lobster population at Robben Island 12 km NW of Cape Town (raw data from Pollock 1978, method of treatment in Chapter 3). The greatest contribution comes from lobsters with carapace lengths of 70-80 mm.

The total carbon produced by rock lobsters in one year amounts to 17,0 $g.m^{-2}$. By comparison, Carter (1982) records phytoplankton production for the same region as 1,131 $kg.m^{-2}.yr^{-1}$. Therefore, although the contribution of DOC and

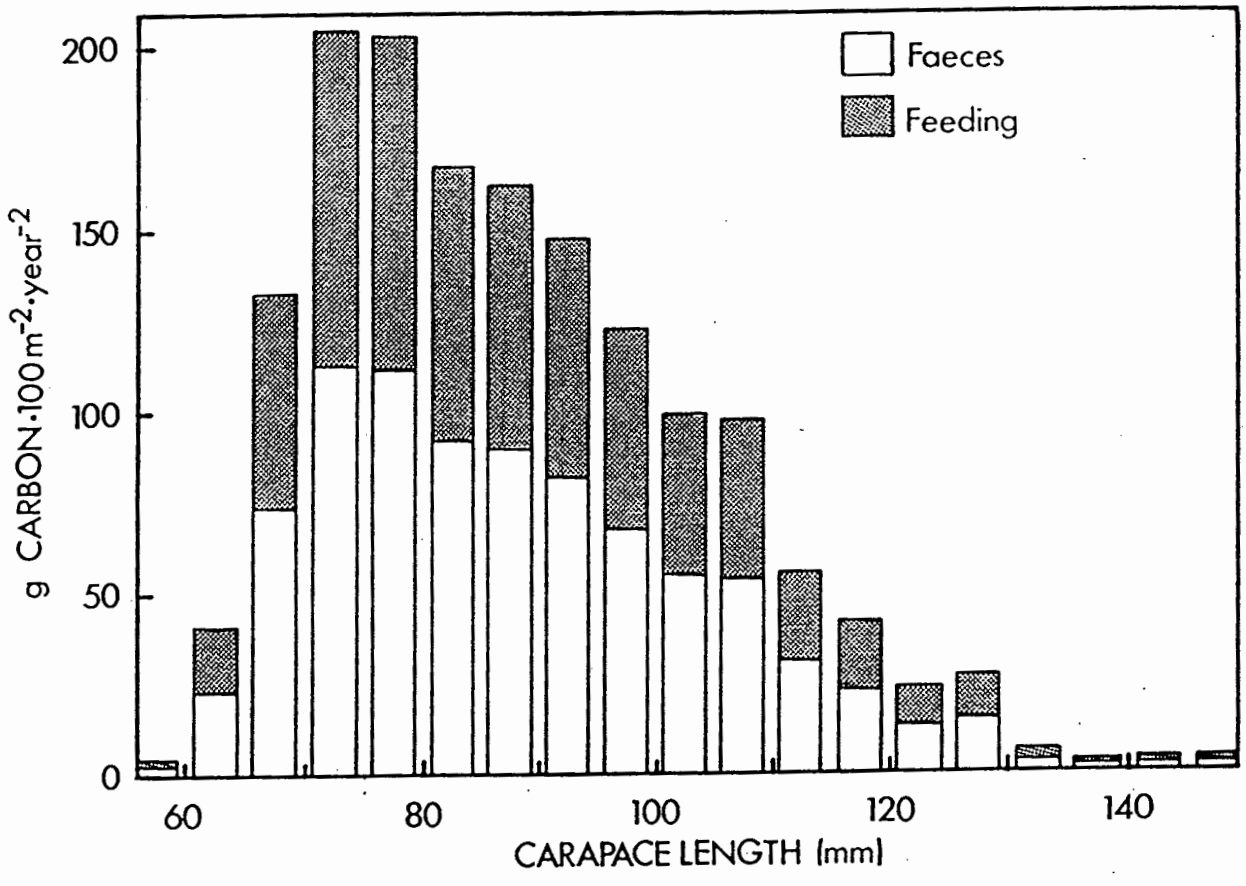

Figure 2.4. Total organic carbon from messy feeding and faeces released in one year to the environment by the different size classes of *a Jasus lalandii* population occupying 100 m² off Robben Island

POC by *J. lalandii* at Robben Island amounts to only 1,4 per cent of phytoplankton production, it may be of significance during upwelling when phytoplankton biomass is at a minimum.

2.3.8. Absorption

The results of the 5 feeding/defaecating cycles for Animals A, B and C are represented in the form of a histogram in Figure 2.5. Variations exist between runs and between animals, both in the mass of food ingested and the mass of faeces voided. To identify common trends or exclusive differences, the data was subjected to several tests.

Similarity of runs - The mean of Run 1 differs at the 95-per-cent level from the mean of the remaining four runs. This lower mean absorption in that run appears to be the result of a carry-over of faeces from the pre-experimental starvation phase. In the subsequent runs there are no significant differences, indicating that an equilibrium between ingested carbon and voided carbon had been reached.

Differences due to variations in animal mass - The masses of the three experimental animals lay in the range of 813 - 1065 g wet mass. The means of five runs for Animals A, B and C were tested for differences between pairs (A *v.* B, A *v.* C and B *v.* C). There was no significant difference at the 95-per-cent level between the paired comparisons. It may therefore be concluded that, in the

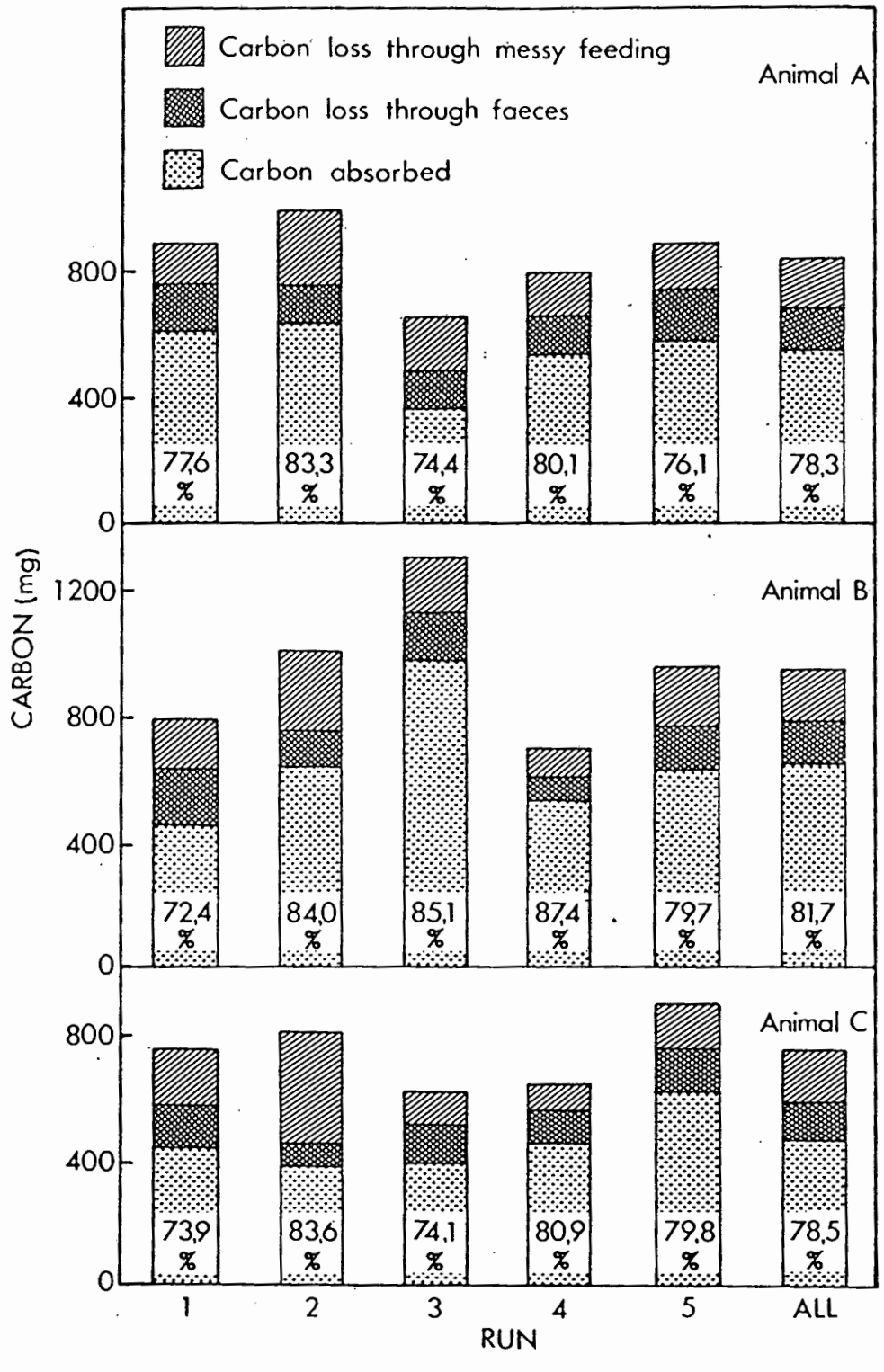

Figure 2.5. Comparison of carbon budgets for Animals A, B and C

above size range tested, absorption efficiency is not mass dependent.

Differences due to mass variations of ingested ration - Differences in absorption efficiency may be related to variations in mass of ingested ration. Plotting absorption efficiency against the mass of ingested carbon by least squares, $r = 0,38$ ($n = 15$). There is thus no significant correlation between the mass of ingested carbon and the efficiency with which it is absorbed.

Absorption efficiency - Absorption efficiency may vary within one species due to factors such as quality and quantity of food, and the age of the consumer (Valiela 1984). Lasker (1966), measured levels of efficiency of 66-95 per cent in the euphausiid *E. pacifica*, and Fowler *et al.* (1971), working on another euphausiid, *M. norvegica*, recorded a similar range (73,9-91,9 per cent).

In *J. lalandii* the mean absorption efficiency is 79,5 per cent (SD = 4,6 per cent, $n = 15$). This high level of efficiency suggests a close adaptation of predator to prey where an appropriate suite of enzymes is employed to optimize carbon absorption.

In contrast to Valiela's (1984) general statement, the difference in absorption efficiency exhibited by *J. lalandii* in the normal commercial size range is neither dependent on

body mass (c.f. age) nor ingested mass. Rather, absorption efficiency exhibits a relatively narrow range of values in the form of typical variability which is inherent in all biological systems.

CHAPTER 3

CONSUMPTION RATES OF CAPTIVE CAPE ROCK LOBSTER *JASUS LALANDII*

(Published in: *S. Afr. J. mar. Sci.* 6: 267-271. 1988)

3.1. INTRODUCTION

The South African rock lobster *Jasus lalandii* (H. Milne-Edwards) has engendered a considerable volume of literature related to stock management. Heydorn (1965, 1969) studied its biology within the context of an exploitable resource. Newman and Pollock (1974a) related rock-lobster growth rates to availability of benthic food supplies (mainly mussels). Their work on growth and feeding was carried further by Pollock (1978, 1979a) and Pollock and Beyers (1981). Mathematical models incorporating feeding and growth have been constructed by Seiderer *et al.* (1982), among others. Energetics-related research has been carried out by Zoutendyk (1987, 1988) (Chapters 5 and 2), who investigated the relationships between consumption and both absorption efficiency and nitrogen excretion.

There is, however, an absence of long-term measurements of consumption rate for use as an input to management models or energy budgets. This paper reports the daily consumption rates of a group of male rock lobster with carapace lengths 80-130 mm, held in captivity over a 400 d period and fed *ad libitum* with black mussels, *Choromytilus meridionalis*. The size range covers the bulk of commercial catches. The results provide the basis for some estimates of the possible impact of *J. lalandii* on the West Coast infratidal environment, although they depend on the inherent assumption that consumption rates of aquarium-held specimens are similar to those of lobsters in the wild and that male and female consumption rates are similar, a question that was not tested due to the scarcity of female lobsters at the Oudekraal study site.

3.2. MATERIALS AND METHODS

3.2.1. Collection and holding of specimens

Specimens of *J. lalandii* in the intermoult stage were caught by SCUBA divers in the rock-lobster sanctuary at Oudekraal on the west coast of the Cape Peninsula during early summer 1983. Animals were kept singly in 100-*l* tanks in a recirculating seawater system. The water was aerated and the temperature held at 12°C (range 11,5-12,5°C). The salinity was maintained at 35×10^{-3} by the addition of deionized water at regular intervals to compensate for

evaporation. Illumination was indirect daylight at a level of 35 lux, which is close to the level experienced at 15 m water depth at Oudekraal. The animals were thus subjected to both diurnal and seasonal photoperiodicity under conditions of light intensity as close to natural as possible.

3.2.2. Feeding of specimens

Mussels form a major constituent of the normal diet of *J. lalandii*. Pollock (1979a) found that 97 per cent of stomachs sampled from a population at Robben Island contained mussel remains. Two species of mussel are preyed upon by the Cape rock lobster. They are the ribbed mussel *Aulacomya ater* and the black mussel *Choromytilus meridionalis*. Most large mussels consumed by *J. lalandii* in the wild are *A. ater* (Pollock 1979a, Pollock and Beyers 1981). However, Griffiths and Seiderer (1980) demonstrated that, in food-choice experiments on captive *J. lalandii*, *C. meridionalis* were selected in preference to *A. ater*. For this reason, plus the relative ease with which they could crack black mussel shells and the similarity of carbon and nitrogen values of flesh (Chapter 5), together with the accessibility of the species which provided an assured supply, it was decided to use *C. meridionalis* in determining consumption rates of rock lobster. All mussels used for the purpose came from a single population at a site approximately 15 km north of Cape Town. Shell lengths were

in the range 40-80 mm, which is below the critical lengths for the sizes of the experimental lobsters (Griffiths and Seiderer *op. cit.*). These shell lengths were converted to carbon values by means of Equation 2.1 and the factor of 0,3873 (Zoutendyk 1987) (Chapter 5).

A total of 19 *J. lalandii* was monitored for a period of 400 d for daily food intake. During this time respiration studies were carried out. Feeding data were only used for those months in which there had been no interruption. Each animal was presented with mussels of known size. At regular intervals, usually on a daily basis, it was noted which mussels had been eaten. Once a rock lobster has cracked a shell, it will generally ingest the entire flesh mass. On the rare occasions when this did not occur, the quantity of uneaten flesh was estimated and the consumption figure adjusted accordingly. Zoutendyk (1988) (Chapter 2) has shown that 20,1 per cent of the carbon content of the mussel flesh may be lost before ingestion takes place. Daily consumption figures have been modified to allow for this loss. Dry mass for each experimental rock lobster was derived from wet mass by application of the relationship given by Field *et al.* (1980a), i.e. 1 g dry mass = 3.43 g wet mass. Daily rates of consumption are expressed as mg carbon per g lobster dry mass.

3.3. RESULTS AND DISCUSSION

3.3.1. Mass-specific consumption

The mass of food ingested varies between individuals, a large animal consuming more than a small one. Small individuals of a species may have a higher mass-specific consumption than large individuals (Ikeda 1970, Peters 1983). Mass-specific daily consumption for 10 lobsters over the period December to February, when the feeding rate was fastest, was regressed against dry body mass. However, within the size range of the experimental animals (85-315 g dry mass), the negative slope of the regression was not significant at the 5-per-cent level.

3.3.2. Patterns of seasonal consumption

The changes in daily mass-specific consumption, expressed as monthly means, are illustrated in Figure 3.1. Testing 71 cases with the Kruskal-Wallis one-way analysis of variance (Zar 1984), the means were found to differ significantly (p = 0,01). The fast rate of consumption in summer (December - February) provides for the replacement of fluid which was taken in during spring ecdysis (Aiken 1980), with tissue resulting from the absorbed organic matter from food. It also allows energy to be stored as reserves prior to the breeding activities which take place mainly in late autumn and early winter (Heydorn 1969). During autumn (March - May) consumption declines. In winter, consumption

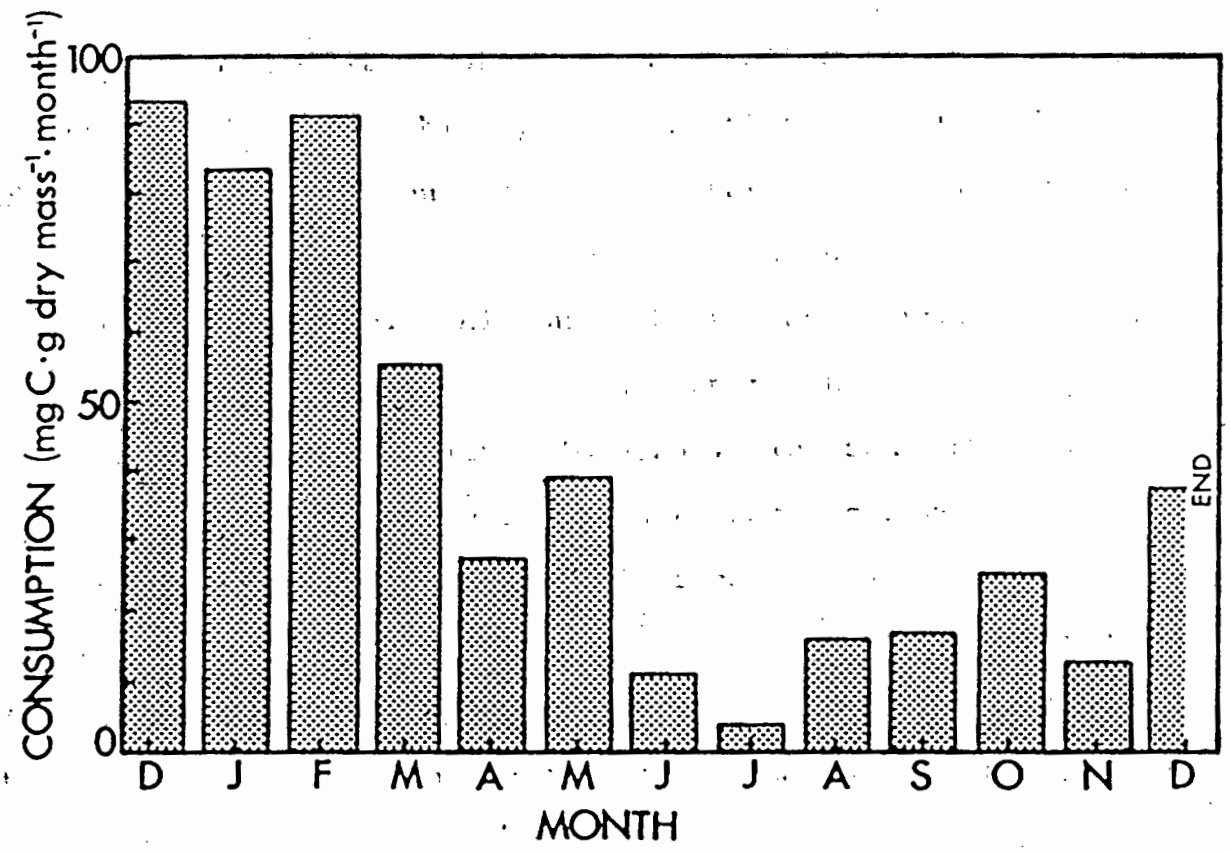

Figure 3.1. Variations in monthly mean mass-specific consumption of *Jasus lalandii*

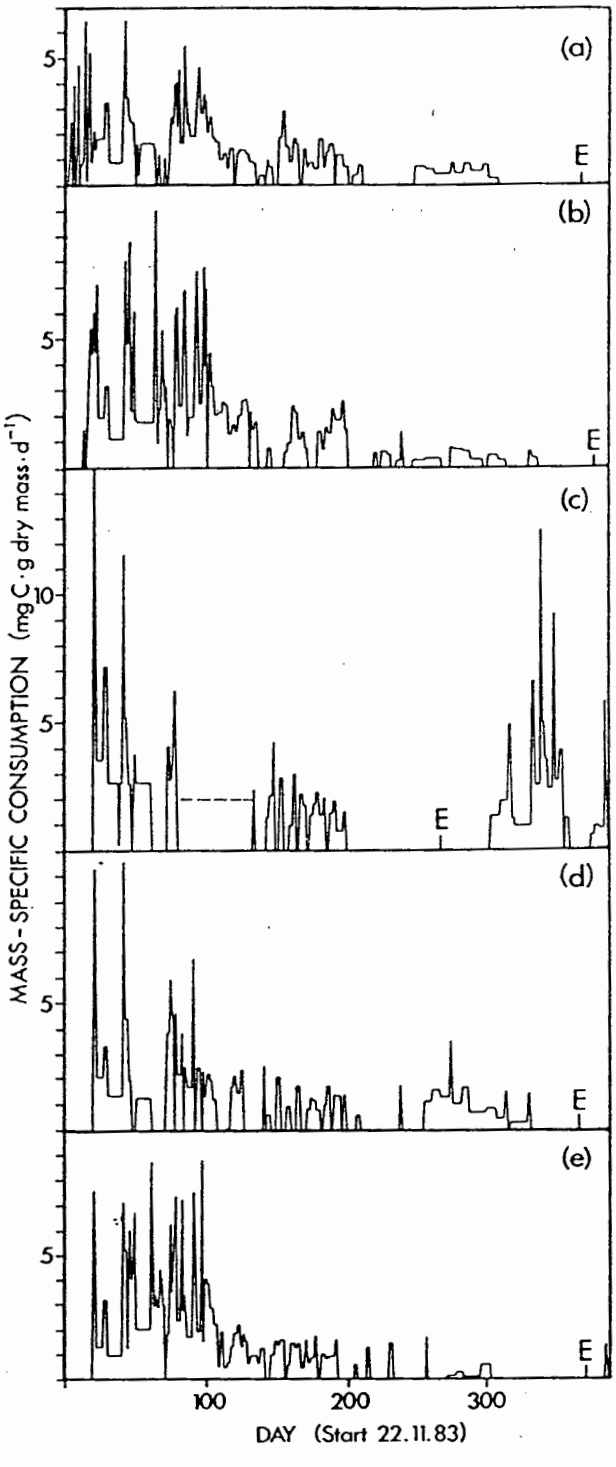

Figure 3.2. Mass-specific consumption of 5 *Jasus lalandii* (A-E). E denotes the day of ecdysis in the moulting cycle

often followed by high intake. This may be a residual pattern of activity from field conditions, where it has been observed that a heavy swell can limit the mobility of *J. lalandii* and in turn its feeding activity. This statement is supported by the observations of local rock-lobster fishermen, who report reduced catches in baited traps when the swell is high or when the current is strong. In the longer term there may be another explanation for this pattern. When feeding on mussels, once a shell has been cracked, the contents will usually be eaten completely. Eating food in units may result in a high intake resulting from the unit size, which may be followed by a day or days without feeding.

Paterson (1969a), observing *J. lalandii* which were fed on a mixed diet (including fish pieces) under aquarium conditions, reported that feeding activity was bimodal, with peaks occurring before sunrise and after sunset. Local West Coast fishermen who deploy baited traps confirm that feeding activity peaks at about dawn and again at dusk. It therefore appears that feeding is crepuscular. Superimposed on that pattern, individual consumption may vary with regard to mass ingested and the interval between meals, as seen in Figure 3.2.

3.3.4. Effects of moulting on consumption

Feeding ceases under the influence of the moult cycle. This can also be seen in Figure 3.2, in which ecdysis is denoted by the letter E. The periods before and after ecdysis during which consumption was zero for thirteen *J. lalandii* (A-M), are evident in Figure 3.3. The pre-ecdysis period had a mean value of 44 d and a range of 20-71 d (n = 8), and the mean post-ecdysis period was 34 d with a range of 10-90 d (n = 13). Therefore, there is a mean annual value of 78 d or 21 per cent of the potential time available for feeding when no food is eaten during the moulting period. In addition to the carbon loss through the removal of exuviae, the need to compensate for the extended period without feeding could in part account for the high rate of consumption recorded in summer.

The mean date of ecdysis was 22 October during the experiment in 1984. Such a date is in agreement with the spring ecdysis peak (September/October) for males recorded by Newman and Pollock (1974b) for both Dassen Island and the Cape Peninsula. Therefore, although the animals were captive, the innate moult cycle does not appear to have been affected.

3.3.5. Annual consumption

The relationship between *J. lalandii* dry mass and carapace length can be expressed by the regression

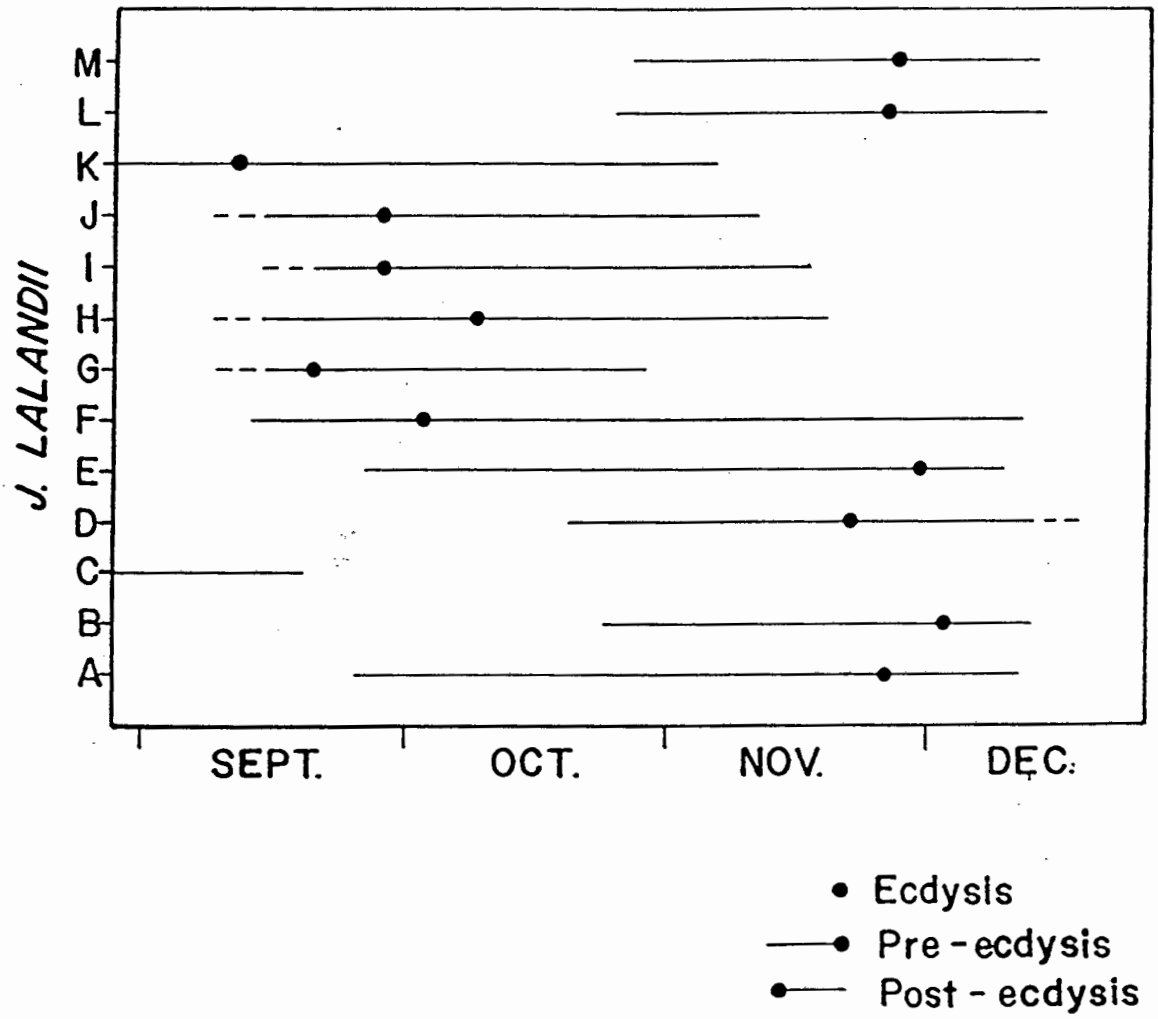

Figure 3.3. Periods before and after ecdysis when consumption was zero

$$DM = 0{,}000274L^{2{,}877} \quad (r^2 = 0{,}99; \quad n = 152), \qquad (3.1)$$

where DM is the dry mass in grams and L is the carapace length in mm.

Summing the monthly means for December to November from Figure 3.1 resulted in a mass-specific consumption figure of 479 mgC.g dry mass^{-1}.yr^{-1}. Therefore, from carapace length via dry mass from Equation 3.1, it is possible to predict the annual consumption of a rock lobster under ideal feeding conditions. For example, the average size of commercially caught specimens in some areas is about 97 mm carapace length (C. J. de B. Beyers, formerly Sea Fisheries Research Institute, pers. comm.), which is equivalent to an annual consumption of 68,3 g C.

3.3.6. Potential environmental impact of *J. lalandii*

In the rock-lobster sanctuary at Oudekraal between depths of 12 and 18 m where regular counts were carried out, the mean population density of *J. lalandii* determined over one year was 0,48 individuals.m^{-2} or 49,75 g dry mass.m^{-2} (Zoutendyk 1987) (Chapter 5). In terms of carbon, the total consumption by rock lobsters would be equal to 23,8 gC.m^{-2}.yr^{-1} or equivalent to the annual removal of 107 *C. meridionalis* of 50 mm shell length from each square metre of hard substratum.

A more detailed interpretation is possible with data from Pollock (1978) for the Robben Island rock-lobster sanctuary. Size frequency counts for depths of 14, 20 and 27 m have been combined. The population figures have been expressed per square metre by applying the overall mean density of 0,81 individuals.m^{-2} (Pollock *op. cit.*). Most rock lobster are of 70-80 mm carapace length, and animals of this size therefore account for the highest rates of consumption of carbon. From the *J. lalandii* size frequency data, the impact of the rock-lobster population at Robben Island would be to remove 35,3 g C from prey populations.$m^{-2}.yr^{-1}$. This is comparable to the figure of 23,8 $gC.m^{-2}.yr^{-1}$ for Oudekraal.

In contrast, Barkai and Branch (1988a) constructed an energy budget to estimate consumption for a population of *J. lalandii* off Malgas Island, a lobster sanctuary 58 naut. miles north-north-west of Cape Town. They recorded a lobster standing stock of 1094 $gDM.m^{-2}$ compared to the 49,75 and 73,7 $gDM.m^{-2}$ for Oudekraal and Robben Island respectively. This value is 15 times higher than the standing stock at Robben Island. Using the mass-specific consumption rate of 479 $\mu gC.gDM^{-1}.\ yr^{-1}$ given above, it is seen that the Malgas population would consume 524 $gC.m^{-2}.yr^{-1}$. Allowing for messy feeding, this is equivalent to the removal of 2 937 *C. meridionalis* of 50 mm shell length, or 60 per cent of the standing stock (875

$gC.m^{-2}$) at nearby Marcus Island which is recorded as having high mussel densities (Barkai and Branch 1988b). The impact of consumption by *J. lalandii* in the nearshore system of Malgas Island is thus extremely high in comparison with the other two lobster sanctuaries discussed above.

The rates of consumption obtained for the experimental animals may be considered as maximal for sedentary rock lobsters at the temperature concerned (*c.* 12°C), because they were all fed *ad libitum*. Consumption rates in the field may not approach these levels if physical conditions are stressful or if food is limiting, as suggested by the results of several field studies (Newman and Pollock 1974a, Pollock and Beyers 1981). On the other hand, energy requirements in the field may be higher than those in the aquarium in order to meet the demands of foraging, mating and the escape from predators. Subject to the availability of food, these higher energy requirements would be met by a higher consumption rate. Temperature could affect consumption both directly and indirectly. Direct effects would include rates of foraging and feeding, while indirect effects would be compensatory, once again subject to food availability, to balance changes in temperature-dependent metabolic rates (Chapter 4). Thus, an increase in daily, seasonal or mean temperature in the presence of available food would result in increased consumption, thereby

modifying the form of Figure 3.1. The converse, with a drop in temperature, would also hold true.

CHAPTER 4

OXYGEN CONSUMPTION BY THE CAPE ROCK LOBSTER *JASUS LALANDII*

4.1 INTRODUCTION

Respiration has been extensively measured and studied from unicells through the major animal phyla. Peters (1983) reviews the rôle of respiration in metabolism and the effect of body mass, where mass-specific respiration decreases with increase in body mass. Temperature also plays an important rôle in respiration. Phillips *et al.* (1980, in Cobb and Phillips), reviews the effects of both temperature and mass in relation to lobsters.

Respiration involves the chemical release of energy and may take place either in the presence or absence of oxygen (aerobic and anaerobic respiration). Oxygen consumption during aerobic respiration is proportional to the heat generated during energy release. However, anaerobic respiration can occur in many organisms, particularly when under stress. In this case oxygen consumption is no longer proportional to the heat generated and its measurement underestimates energy release. Crisp (1984; in Holme and McIntyre 1984) warns of the problems of equating O_2

consumption with energy release and recommends that calorimetry be carried out simultaneously with O_2 measurements. This procedure not only complicates the experimental protocol, but places additional stress on the animals. However, in flow-through respirometry systems, it is reasonable to assume that anaerobic respiration is not a problem if measurements are made over an extended period of time and oxygen is maintained at high levels. Prolonged measurements also smooth any peaks of high energy output where anaerobic processes may have come into play. Many organisms resort to anaerobic respiration when oxygen concentrations fall, for example, some bivalve molluscs. However, aquatic animals frequently maintain their blood oxygen levels over a wide range of water oxygen tensions by regulating the flow-rate over the gills. A large number of decapod crustaceans fall into this category of oxygen regulators. Taylor (1976) showed that the crab *Carcinus maenas* regulates down to levels as low as 39-53 per cent air saturation. Butler *et al.* (1978) have shown in *Homarus vulgaris* that O_2 consumption is independent of O_2 concentration in the water down to levels of mild hypoxia. Hagerman (1982) reported similar regulation in young *Homarus gammarus* and Winget (1969) showed that the spiny lobster *Panulirus interruptus* regulates down to 25-45 per cent air saturation. It is therefore a reasonable assumption that *J. lalandii* is a regulator. However, to keep stress to a minimum, all respiratory measurements on *J. lalandii* took

place with an inflow of oxygen-saturated water and depletion levels did not fall below 85-95 per cent air saturation. Anaerobic respiration is unlikely under these conditions and has been ignored.

Mann (1965) and Carefoot (1976) as quoted in Crisp (*op. cit.*), warn that laboratory measurements of O_2 consumption lead to an underestimation because the animal is constrained, and found it necessary to double the observed respiration loss in order to balance energy budgets. As *J. lalandii* spends much of its time inactive in cracks and caves, O_2 consumption in the field will tend to be low and therefore may approach the standard rate in the laboratory. On balance, however, laboratory results are likely to underestimate rates in the field.

An additional complication is, however, the possibility that activity rhythms will influence metabolism. Kubo and Masuda (1964) reported a bimodal 24-h cycle in the feeding habits of *Panulirus japonicus* corresponding with dawn and dusk. Fielder (1965) observed that the maximum for both locomotor and feeding activity in captive *Jasus novaehollandiae* occurred at dusk. Paterson (1969a) observed pre-sunrise and post sunset peaks in the activity of captive *J. lalandii*, and another peak in the mid-afternoon when the animals were fed.

Changes in habitat temperature are another variable to consider. Generally temperature changes in global seas are gradual and usually seasonal. However, the time scale for temperature fluctuations varies from hours to generations. Changes in temperature involve responses in poikilotherms aimed at maintaining a positive index of energy balance (Newell 1979). These responses are complex and are mainly dependent on the length of exposure time, and may result in a range of adaptations taking place.

When exposure time is short (minutes to hours), the response is acute and no immediate adaptation takes place. When exposure time is measured in days and weeks, enzyme activity is altered to compensate for the temperature change and acclimation occurs (Newell and Branch 1980; Blackstock 1984; Branch *et al.* 1988) In addition to short- and medium-term changes involving enzymes, a number of specialized adaptations may occur in lobsters. These include ventilatory, circulatory and blood chemistry adaptations (Cameron and Magnum 1983).

Longer exposure times result in acclimatization or seasonal adaptation. If the time scale covers several generations, genetic adaptations may result. Ignoring these long-term patterns, *J. lalandii* is subject to rapid changes in temperature during upwelling and downwelling where 5° C variations can occur within a few hours (Zoutendyk, CSIR

unpublished). *J. lalandii* has been a component of the nearshore Benguela system for many thousands of years. One of the questions to be addressed is, what short-term adjustments does *J. lalandii* make to these rapid temperature changes?

However, the primary aims of this chapter are, a) to describe the metabolic rates of a wide size-range of rock lobsters at a range of temperatures covering annual fluctuations and, b) to use this information to estimate metabolic energy demands for a population of rock lobsters in a sanctuary off Robben Island 10 km northwest of Cape Town.

4.2. MATERIALS AND METHODS

4.2.1. Collection and holding of specimens

Lobsters were captured by SCUBA divers in a sanctuary at Oudekraal, south of Cape Town, on the west coast of the Cape Peninsula. The full size range collected for respiration measurements fell between 40 and 187 mm carapace length (CL). Only a limited number of individuals were collected during each dive to fill specific needs and to avoid holding animals for prolonged periods prior to experimentation.

Aquarium facilities consisted of a recirculating system supplying approximately 20 x 100 *l* GRP tanks, each with a continuous through-flow of seawater. Each tank contained a gravel floor-filter operated on the air-lift principle by bubbling compressed air. One to four lobsters were kept per tank, depending on animal size.

Temperature control of the aquarium was accomplished by air conditioning which stabilized the water temperature to ±0,5° C. When two temperature regimes were required, the lower temperature was air controlled for the whole system, while individual tanks were heated and thermostatically held to ±0,5° C. Salinities were checked regularly and deionized water added to compensate for evaporation, thus maintaining a level of *c.* 35°/$_{oo}$.

Illumination was natural but without direct sunlight, and was held at a level of *c.* 35 lux. This is approximately the same as that in the environment at 14-20 m depth at Oudekraal. During nocturnal experiments, lighting was provided by a Kodak safelight equipped with a 1A red filter.

After capture, lobsters were held for a minimum of one week prior to being subjected to respirometry. During that time they were fed black mussels, *Choromytilus meridionalis, ad libitum.* Individuals which did not feed normally or suffered any physical injury were excluded from experiments.

Feeding of experimental animals ceased two days prior to respirometry.

Sound or vibration such as the slamming of the aquarium door, or sudden changes in light intensity, caused a reaction in experimental animals resulting in a marked rise in O_2 consumption. Care was taken to prevent such events happening, but if they did they were noted and any abnormal results were discarded.

4.2.2. Description of respirometer

A flow-through respirometer system was built with a number of features in common with that described by Coulton (1978) (Figure 4.1). Saturated seawater of constant temperature and pressure flowed through the chamber containing the lobster. O_2 concentration was measured at the outflow end. Water flow could also be directed through a chamber bypass by switching glass stopcocks. This enabled O_2 measurement of both pre- and post-chamber water by the same calibrated polarographic oxygen sensor. Flow-rate was controlled by a nozzle inserted into the end of the sump return pipe and was set so that O_2 levels never dropped below 85 per cent of the inflowing water. Nozzles were made from glass tube drawn to different terminal diameters. Each nozzle was calibrated using a measuring cylinder and stopwatch. The nozzles could be used on consecutive runs to ensure repeatable flow rates. Loosely folded plugs of gauze

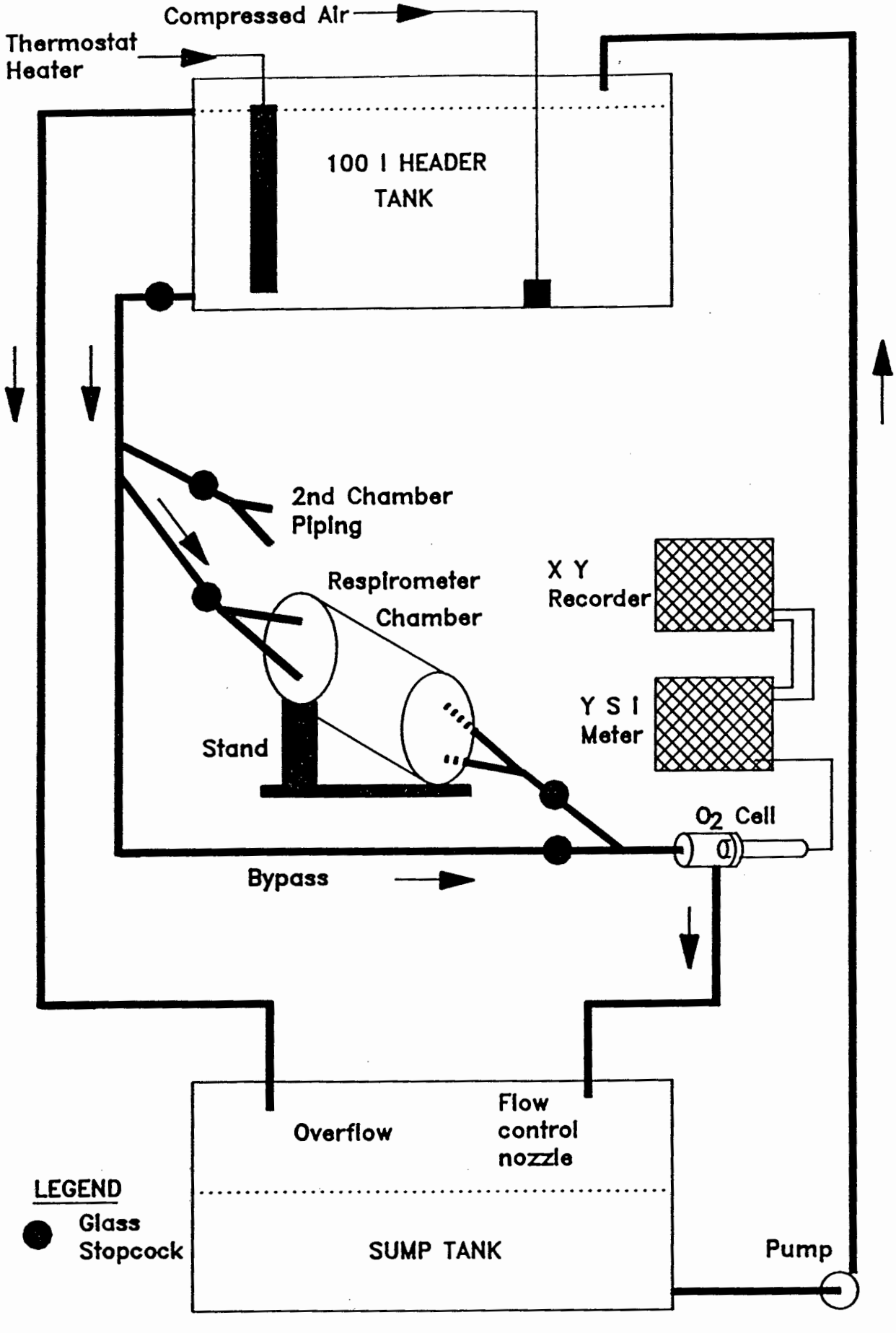

Figure 4.1. Flow-through respirometer system used for O_2-consumption measurements in *J. lalandii*

were inserted into the exit pipes to prevent faeces from reaching either the oxygen sensor or the flow-control nozzle.

Water from the sump tank was returned to the header tank by a CAL 1200 PVC centrifugal pump. Excess water in the header tank returned to the sump via the header overflow pipe. Water in the header tank was kept O_2-saturated by bubbled compressed air, and at a constant temperature by means of a thermostatically controlled heater, when experimental and aquarium temperatures differed.

Three volumes of chamber were used (14,6-*l*, 5-*l* and 0,5-*l*) in order to accommodate the full size range of animals. The system was designed to accommodate two chambers arranged in parallel, thus doubling the number of runs possible in a given time. Chambers were checked for "dead spots" where water could become stagnant. Milk was used as a marker and introduced into the waterflow above the junction of the pair of incoming pipes. Within five seconds of introduction, the total fluid content of the chamber became uniformly discoloured, confirming that complete mixing had taken place and no dead spots were present.

At regular intervals the system was dismantled and sterilized in a solution of calcium hypochlorite to prevent

bacterial build-up which could have affected measurements of O_2.

4.2.3. Measurement of oxygen

Dissolved oxygen concentration was measured by means of a YSI polarographic oxygen sensor connected to a YSI model 57 meter. The meter was modified to include a switch which allowed readings to be made from either of the two probes in the parallel system of chambers. The probe not in use remained on to avoid repolarization and time lag when chambers were alternated. Calibration of the sensors was by the "in-air" method where 100 per cent humidity in a small chamber acted as the reference. Zero oxygen level was checked using a solution of sodium diothionate. Results were verified at regular intervals against Winkler titrations. To incorporate respiration results into the energy flow equation, oxygen values were transformed to their carbon equivalent by applying the stochiometric conversion where 1 ml O_2 = 0,536 mg C.

4.2.4. Choice of temperatures

Sea temperatures at Oudekraal range from 8-14° C in summer and reach 17° C in winter when warmer water moves in (Field *et al.* 1980a). Five temperatures were therefore selected at approximately equal intervals (8, 10, 13, 16 and 19° C), to cover the spectrum encountered by *J. lalandii* under natural conditions. Temperature affects the metabolic

rate of poikilotherms which may be expected to double for every 10° C rise. This can be modified due to an animal's ability to acclimate, which results in a value of <2 (Brafield and Llewellyn 1982). A convenient way of expressing the change in metabolic rate with temperature is by the use of the temperature coefficient Q_{10} as follows

$$Q_{10} = \left[\frac{R_2}{R_1}\right]^{\frac{10}{T_2-T_1}}$$

where R_1 and R_2 equal O_2 consumption rates at temperatures T_1 and T_2 respectively (Newell 1979). Q_{10} values have been calculated for the intervals between the five experimental temperatures stated above.

4.2.5. Running the respirometer system

A single lobster was placed in a chamber which was then filled. A stoppered hole at the top of the chamber allowed the escape of air during filling. For up to six hours after the start of the experiment, animals showed raised levels of O_2 consumption. Only recordings after six hours from time of commencement were used. Runs lasting 8-12 h would therefore have been adequate, but they were extended to 24-48 h as a check. Lack of food during that period should have had no effect on the lobsters as normal healthy animals often go for several days without feeding (Chapter 3).

4.2.6. Interpretation of O_2 consumption recordings

Respiration, O_2 consumption and metabolism form part of a series of processes which have a common end product, the release of energy. For the sake of clarity, as the end product of both O_2 consumption and metabolism is a common energy output, the two terms have been used synonymously.

Basal metabolism is a long-established term used by physiologists and defined as "the sum total of anabolic and catabolic activities of an organism in the resting state providing just enough energy to maintain vital functions" (Lapedes 1978). The term standard metabolism is more loosely defined and usually replaces basal metabolism under normal laboratory conditions. It means that the results are not necessarily minimal, but were obtained under standardized conditions which normally yield low values (Peters 1983).

Output from the oxygen sensor was an analogue trace. Fluctuations in lobster activity within the respirometer were reflected in the recording. Activity levels varied from quiescent, when there was no apparent movement in the lobster, to moments of fairly intense activity when, for example, the lobster attempted to change its position in the chamber. A line was drawn on the graph connecting the trace-troughs, which represented minimal activity. This line has been interpreted as the standard metabolic rate.

4.2.7. Diurnal variations in O_2 consumption

To test if diurnal cycles of activity described earlier influence metabolic rate, the oxygen consumption of nine lobsters in the size range from 406-727 g wet mass (i.e. within the commercial size range) was measured for periods reaching a maximum of 4 days. Six of the animals were held under a light/dark regime, synchronized to normal day, while three were under continuous light, supplied by a 40-Watt tungsten source which gave an incident strength of 44 lux.

4.2.8. Responses to short-term temperature change

Rate of acclimation of *J. lalandii* in response to a 5° C raising or lowering of water temperature was tested in six lobsters with a body mass range of 424-1270 g (Table 4.1). In the first case animals were held in 14° C water for two weeks to allow full acclimation to that temperature. At Time = -2 days (0 = Time of 5° C temperature change) animals were placed in the respirometer chambers and for 48 h their standard rate of O_2 consumption measured. Beginning at Time = 0 the water temperature was dropped over 5 h from 14° C to 9° C. Oxygen recording continued until Time = 9 days. In the second case animals were acclimated for two weeks at 9° C before being introduced into the respirometer at Time = -2. Water temperatures were raised 5° C over 5 h at Time = 0, and the run continued for 9 days.

Table 4.1. Wet mass (g) of *J. lalandii* used in experiments to test temperature responses as reflected by oxygen consumption rates

A	B	C	D	E	F
1270	1000	961	935	744	424

4.3. RESULTS

4.3.1. Diurnal variations in O_2 consumption

In five of the six day/night runs the standard rate of O_2 consumption remained constant throughout, with no discernable difference in frequency or amplitude of the record. In the sixth run during the first 30 h there was a period of low consumption corresponding to the hours of daylight. During the next 24 h a second period of low consumption lasting only 6 h took place during daylight. During the last 24 h the standard rate of consumption remained constant throughout. In the three runs with constant light there was no evidence of any diurnal rhythm reflected by O_2 consumption. Paterson's (1969a) observations on daily activity patterns were therefore not reflected by any recorded changes in O_2 consumption This could lead to an underestimate for field conditions.

4.3.2. Effect of temperature on oxygen consumption

In Figure 4.2 recordings of O_2 consumption are given at 8° C, 13° C and 16° C. During the first six hours there is an increase followed by a decrease, after which the trace levels. The lower region of the trace, after the six-hour stabilization period, has been interpretted as standard rate. At 8° C and 13° C the fluctuations above standard rate are small. At 16° C there is an increase in these fluctuations. However, for less than 5 per cent of the time do activity peaks occur which can be considered an elevated rate (See 4.3.3).

In Figure 4.3 standard rate of oxygen consumption is plotted against lobster wet mass for the five experimental temperatures. The slopes of the regressions are positive and are close to the general value of 0,75 (Hemmingsen 1960, quoted in Brafield and Llewellyn 1982) as seen in Table 4.2. Standard rates of O_2 consumption for a 500 g lobster have been calculated for the five temperatures from the regressions in Table 4.2 and are shown in Figure 4.4 and Q_{10} values for each temperature interval are listed in Table 4.3. The plot has the characteristic sigmoid appearance described by Newell (1979) for some intertidal organisms where temperature sensitivity is reduced and therefore the rate of O_2 consumption is flattened (Q_{10}=1,7), to coincide with the modal habitat temperature.

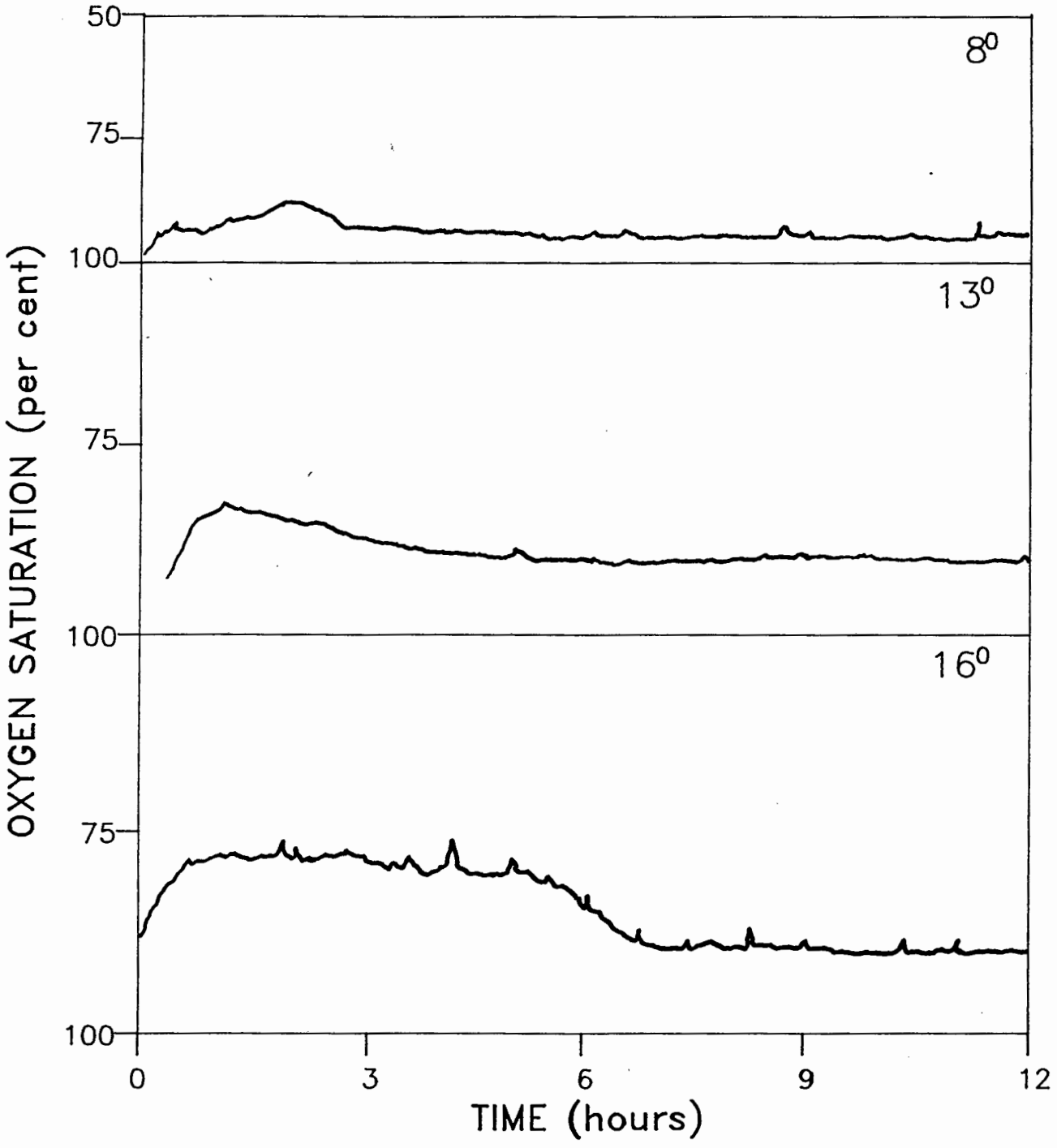

Figure 4.2. Typical recordings of oxygen consumption in *J. lalandii* at 8° C, 13° C and 16° C

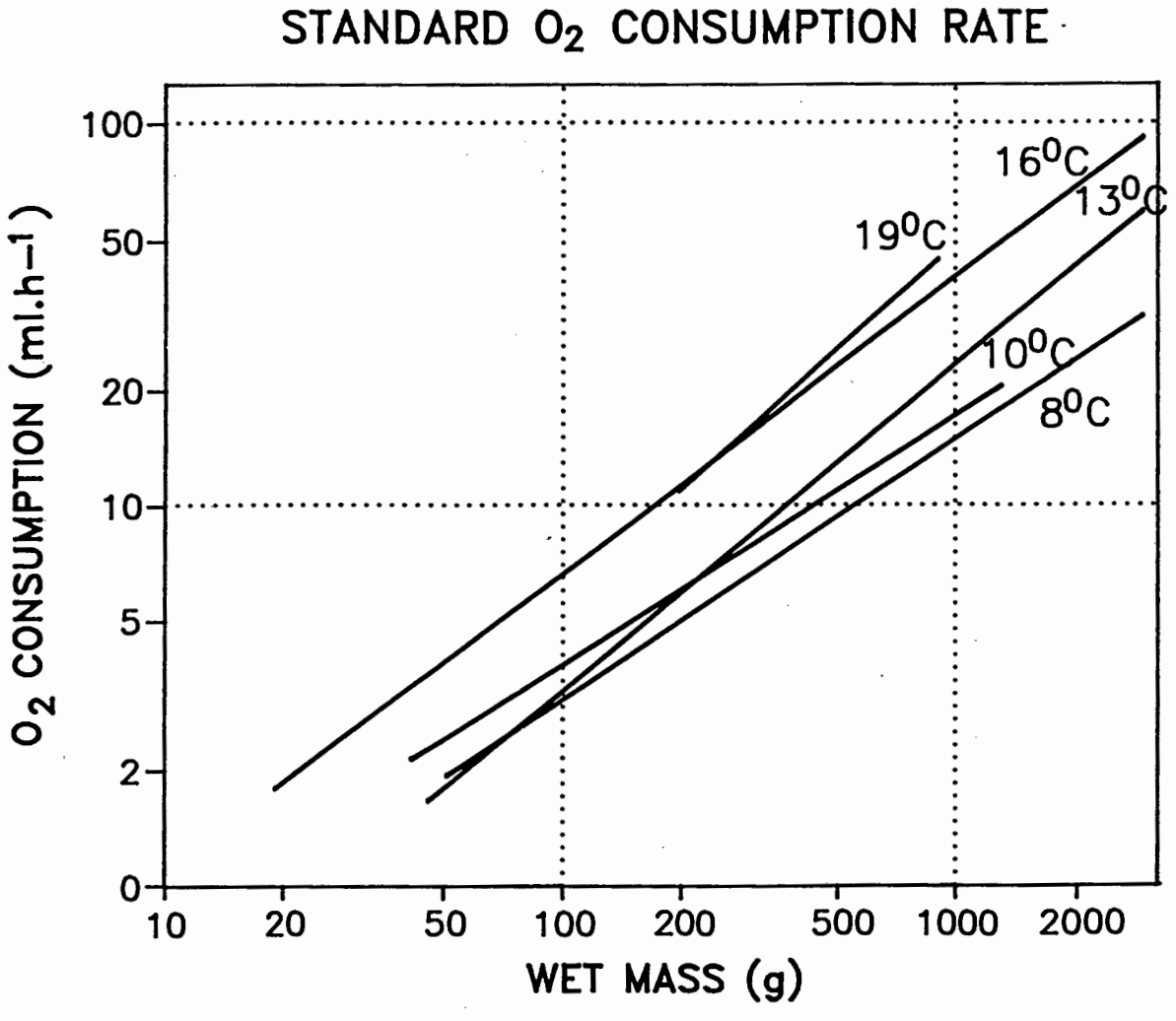

Figure 4.3. Comparison of regressions representing the standard rate of oxygen consumption in *J. lalandii*, at five temperatures

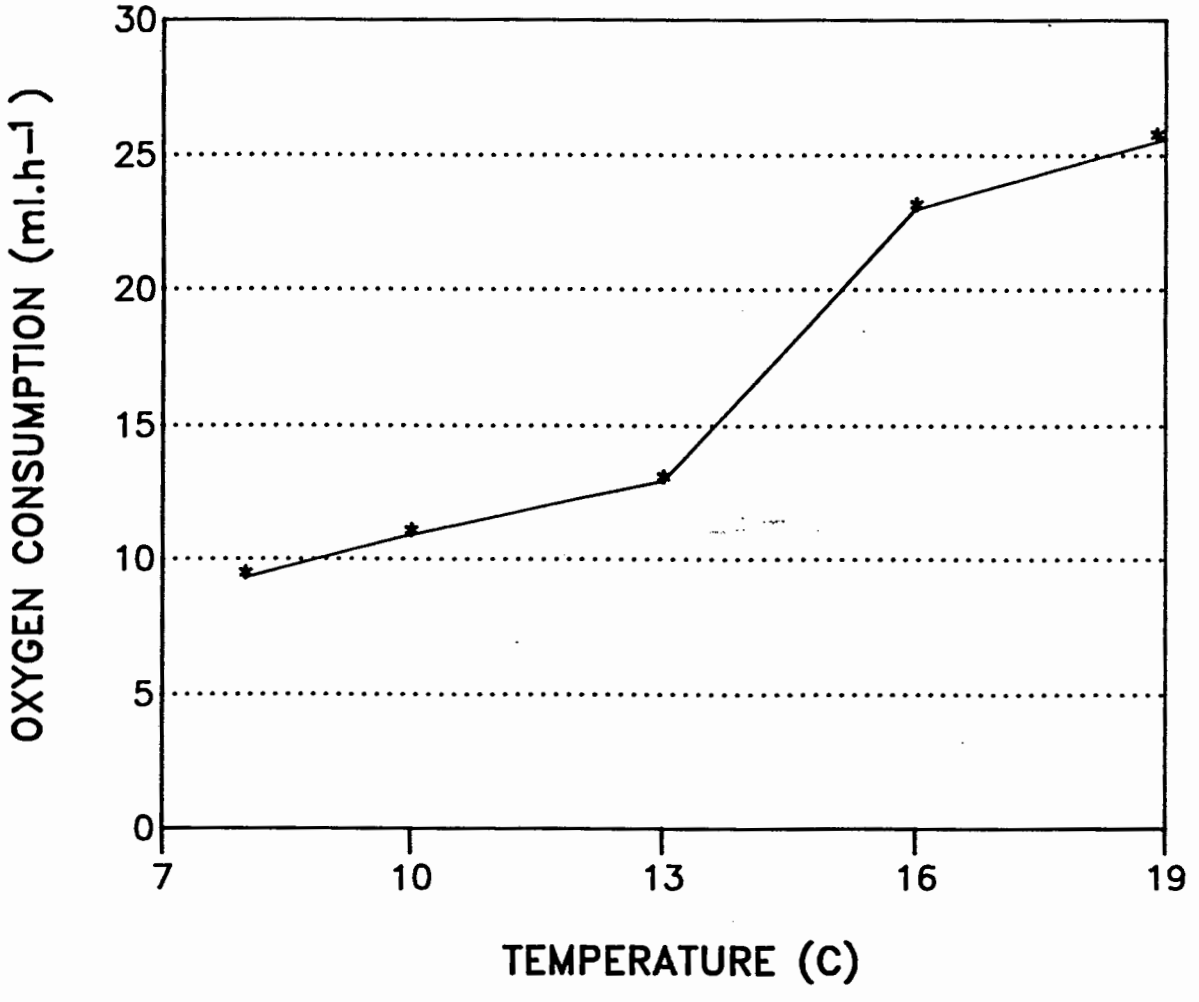

Figure 4.4. Standard O_2 consumption rate for a 500 g *J. lalandii* at 5 temperatures spanning the normal habitat range

Table 4.2. Regressions of oxygen consumption ($ml.h^{-1}$) on lobster wet mass (g), at standard rates for five temperatures, where

O_2 Consumption = a.Wet Mass^b

T° C	a	b	*n*	r^2
8	0,1333	0,6834	18	0,95
10	0,1903	0,6519	18	0,88
13	0,0638	0,8543	11	0,97
16	0,1842	0,7770	20	0,96
19	0,0893	0,9102	11	0,86

Above 13° C there is a sharp increase in O_2 consumption rate, followed by a slackening in rate between 16-19° C. At 19° lobsters appeared stressed as indicated by an increased incidence of small-scale movements. As this temperature is beyond the normal environmental conditions, lobsters were not subjected to higher experimental conditions. However, this slackening in rate may be the fore-runner of a negative slope which follows temperature stress, leading ultimately to coma and death. Although comparable data on lobsters could not be found, this negative slope has been encountered by a number of workers in other taxa. These include Branch *et al.* (1988) investigating the limpet *Patella compressa*, Newell (1969) on the whelk *Littorina littorea*, Newell and Kofoed (1977) on *Crepidula fornicata*, and McMahon and Russell-Hunter (1977) on six species of gastropods.

Table 4.3. Calculated standard oxygen consumption for a lobster of 500 g wet mass at 5 temperatures, together with Q_{10} values for each temperature interval

TEMP.° C	O_2 CNSMTN	Q_{10}
8	9,3	
10	10,9	2,2
13	12,9	1,7
16	23,0	6,7
19	25,6	1,4

4.3.3. Elevated oxygen consumption rates

During measurement of oxygen consumption, peaks reflecting elevated levels of activity were recorded. These usually corresponded with the lobster attempting to change its position in the respirometer. A mean value of the elevated activity peaks was 1,7x standard rate (range = 1,5 to 1,9). Peters (1983) generalizes that the sustained metabolic rate of most animals is approximately ten times the resting rate and that the average realized metabolic rate in poikilotherms is probably between 2-3 times that of standard rate (Bennett and Nagy 1977; Ware 1978; Winberg 1960 as quoted in Peters 1983). In *J. lalandii* the recorded elevated rate at its upper limit approaches the lower end of the range for the average realized rate of Peters (*op. cit.*). As the experimental animals were under no obligation to walk, feed, avoid predators etc. it is reasonable to assume that under field conditions the average realized metabolic rate would be higher and fall within the 2-3 times

standard rate given by Peters (*op. cit.*), although only a limited fraction of the day may be spent in these activities. Newell (1979) states that the routine rate of O_2 consumption is affected by temperature to a greater extent than the standard rate and that the two rates coincide at the extremes of the animal's temperature range, with the envelope between them being the scope for activity. At both 8° C and 19° C *J. lalandii* showed scope for activity which indicates that the temperature extremes lie beyond the range of the experimental temperatures. As these extremes also lie beyond the range of habitat temperature, extension of experimental temperatures, although of interest, is not warranted within the scope of this investigation.

4.3.4. Mass-specific O_2 consumption

Standard O_2 consumption rates were converted to mass-specific rates. Equations for the allometric regressions are listed in Table 4.4. From these equations regressions for standard mass-specific rates were plotted (Figure 4.5). It is seen that the slopes for all temperatures are negative, thus conforming to the general principle summarized by Peters (1983) that mass-specific metabolic rate is inversely proportional to body mass.

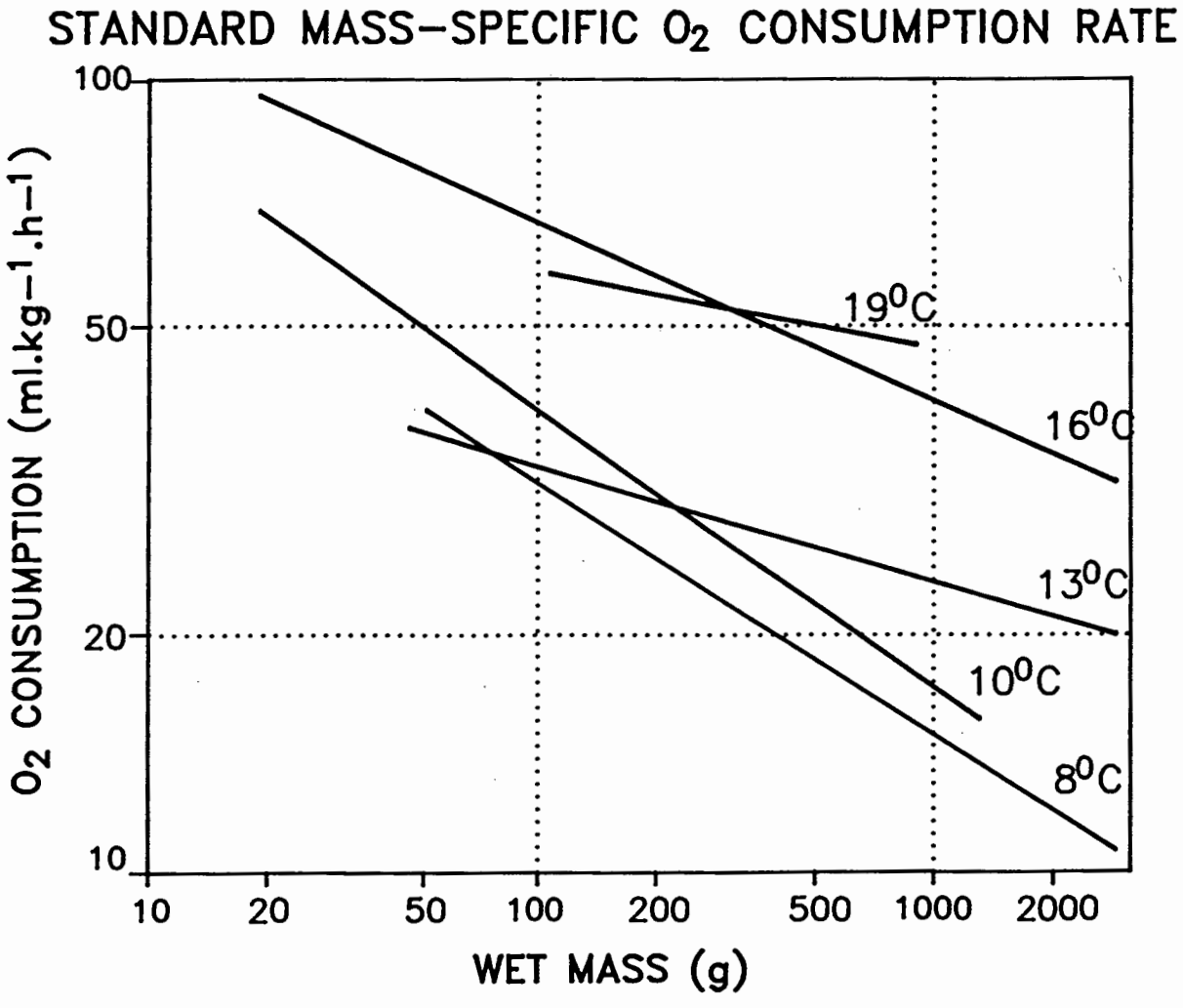

Figure 4.5. Comparison of regressions representing the standard rate of mass-specific oxygen consumption in *J. lalandii*, at five temperatures

4 5 RM·MM

Table 4.4. Regressions of mass-specific oxygen consumption ($ml.kg^{-1}.h^{-1}$) on lobster wet mass, at standard rates for five temperatures, where

Mass-specific O_2 Consumption = a.Wet Mass^b

T° C	a	b	*n*	r^2
8	133,3	-0,317	18	0,80
10	190,3	-0,348	18	0,69
13	63,76	-0,146	11	0,52
16	184,2	-0,223	20	0,69
19	89,53	-0,097	11	0,10

Mass-specific results make comparisons between data sets and between species easier, because the general effect of body mass is reduced, or can even be eliminated by comparing animals of a standard size. In Table 4.5 the results of the present study are compared with the results of other investigators working on lobsters. Eight species are involved in the comparison, with temperatures ranging from 5-27° C. In Figure 4.6 mass-specific oxygen consumption for the listed species has been plotted against temperature for animals with a standard mass of 1 kg. Considering the wide range of species and temperatures and the differences in methods used, the scatter is low. The data points representing *J. lalandii* (filled squares) form an integral part of the trend. However, they lie in the right half of the extended group which means that for a given temperature the O_2 consumption rate is lower. This may be due to the *J. lalandii* data representing standard

Table 4.5. Mass-specific oxygen consumption (ml.kg^{-1}.h^{-1}) obtained by other investigators compared with the present study. Where necessary data have been recalculated to render them comparable

Reference	Species	WM (g)	T° C	QM.
PRESENT STUDY	*Jasus lalandii*	500	8	19
			10	22
			13	26
			16	46
			19	51
BEUSA (1979)	*Panulirus argus*	417	27	74
	Panulirus guttatus	157	27	83
BUTLER, TAYLOR & MCMAHON (1978)	*Homarus vulgaris*	220-510	15	27
MCLEESE (1964)	*Homarus americanus*	380-520	12	44
		"	15	56
		"	20	80
		"	25	88
MCLEESE & WATSON (1968)	*Homarus americanus*	*c.* 500	5	30
PENKOFF and THURBERG (1982)	*Homarus americanus*	250	9-10	26
THOMAS (1953)	*Homarus vulgarus*	*c.* 500	6	25
		"	10	31
		"	16	62
WIENS and ARMITAGE (1961)	*Orconectes immunis*	8	16	68
	Orconectes nais		16	66
WINGET (1969)	*Panulirus interruptus*	200-600	13	34
		200-600	16	48
		200-600	19-20	66

Legend: QM = ml O_2.kg^{-1}.h^{-1}.

rate, whereas the rates for many of the other data are not specified and therefore could lie anywhere between standard and active rates.

4.3.5. Summary of standard metabolism

Figure 4.7 summarizes the effects of increasing temperature and lobster mass on the rate of O_2 consumption. The pattern described for the standard 500 g lobster in section 4.3.2 applies over the full size range of lobsters. Superimposed upon this is the mass-specific effect where the rise in metabolic rate with body mass eases progressively.

4.3.6. Responses to short-term temperature change

From the data shown in Table 4.2, predicted rates of O_2 consumption can be calculated for 9° C and 14° C. These are superimposed on Figures 4.7 and 4.8 and can be used to assess the response of animals to acute temperature changes.

Figure 4.8 illustrates the change in standard metabolic rate when lobsters acclimated to a 14° C environment are subjected to a drop of 5° C in water temperature. The response reflected in the rate of oxygen consumption is rapid. In lobsters B, C and D O_2 consumption rates dropped rapidly during the first six hours from Time = 0. Thereafter O_2 consumption stabilized with only minor fluctuations being recorded. In lobsters A and E, due to equipment malfunction, the first 24 h of recordings were

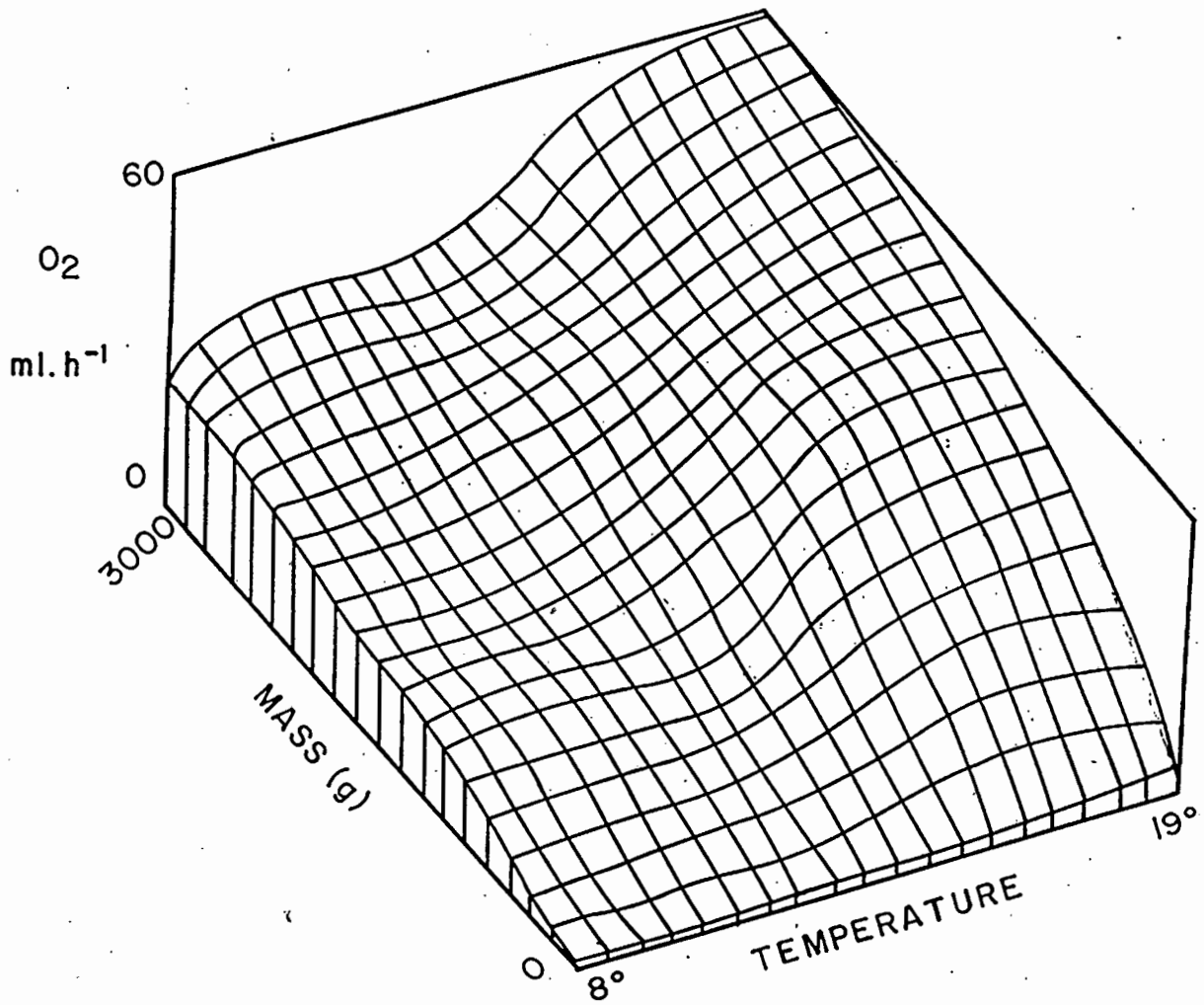

Figure 4.7. A surface response plot for standard rate of oxygen consumption in *J. lalandii* for a wide temperature and mass range

lost. However it appears that the pattern was the same as for lobsters B, C and D. Lobster F had a slower response than those of B, C and D on the first day, but thereafter the pattern was similar.

Figure 4.9 illustrates the response of the standard metabolic rate when animals are acclimated to 9° C and then exposed to a 5° C elevation of temperature. In all five animals the initial response was a rapid increase in O_2 consumption resulting in an overshoot (Newell 1979) between days 0.5-1,5, thereafter decreasing to day 3. From day 3, with the exception of lobster A, O_2 consumption rate stabilized in the region of the predicted respiration rate, with only minor low-amplitude fluctuations occurring.

In summary, *J. lalandii* responds to a drop in temperature by a rapid decrease in O_2 consumption rate with no overshoot occurring, thereafter maintaining its low value with no suggestion of acclimation taking place. With an increase in temperature the acute response is also rapid, but it results in an overshoot, followed by a gradual return to the predicted rate over 2-5 d. Because of its relatively short duration this stabilization period should not be interpreted as one of acclimation.

J. lalandii's responses to temperature change are well adapted to the nearshore Benguela system where upwelling can

lead to substantial decreases in temperature (up to 8° C) in a matter of hours. Conversely, downwelling occurs at only one third of the rate of upwelling (Andrews and Hutchings 1980) and the resulting elevation of temperatures takes place over several days (Field *et al.* 1980). This may be reflected in the longer period of stabilization for raised temperatures described above.

4.3.7. Respiration at population level

Rate of oxygen consumption can be affected by both extrinsic and intrinsic cycles which play an integral part in the lives of lobsters. Extrinsic cycles include diurnal and seasonal photoperiodicity, and short-term, seasonal and long-term environmental temperature fluctuations. In addition, variations in swell height and period, and strengths of bottom currents may affect levels of activity. Added to this are non-cyclic events which also affect activity levels, such as predator avoidance, contact with low oxygen water (Bailey *et al.* 1985; Pollock and Shannon 1987), or the effects of floods (Branch in press 1989).

Intrinsic cycles which are often linked to extrinsic fluctuations, include reproductive (Chapter 8), moult (Chapter 7) and feeding (Chapter 3) cycles. All three may have the effect of raising oxygen consumption rates above the normal standard rate; for example in berried females (Buesa 1979) or in a moulting individual at the point of

ecdysis (Penkoff and Thurberg 1982), or during feeding. Not only does feeding raise oxygen consumption as a result of increased activity, but an elevated rate of oxygen consumption persists for some hours because of the specific dynamic action resulting from deamination and digestion among other processes. At the other end of the scale the standard metabolic rate may be depressed over long periods (days to weeks) during normal periods of starvation (Chapter 3). McLeese (1964) recorded a metabolic rate for non-feeding *H. americanus* which was 56 per cent of the rate exhibited by fed animals.

To add to the complexity, at population level, variations in rates of oxygen consumption occur between individuals of differing age, sex and body mass. To quantify the effects of all the above factors at either individual or population level is impractical, perhaps even impossible. Mean monthly surface temperatures for Table Bay lie between 13-14° C throughout the year (Taunton-Clark and Kamstra 1988). It is assumed therefore that the mean annual temperature at 20 m depth off near-by Robben Island will therefore be close to 13° C. Standard metabolic rate, although possibly a low estimation, at a mean environmental temperature of 13° C has therefore been taken as representative of a *J. lalandii* population at Robben Island, and converted to an area of 100 m^2 (Chapter 6). This will underestimate field metabolism by an unknown factor because

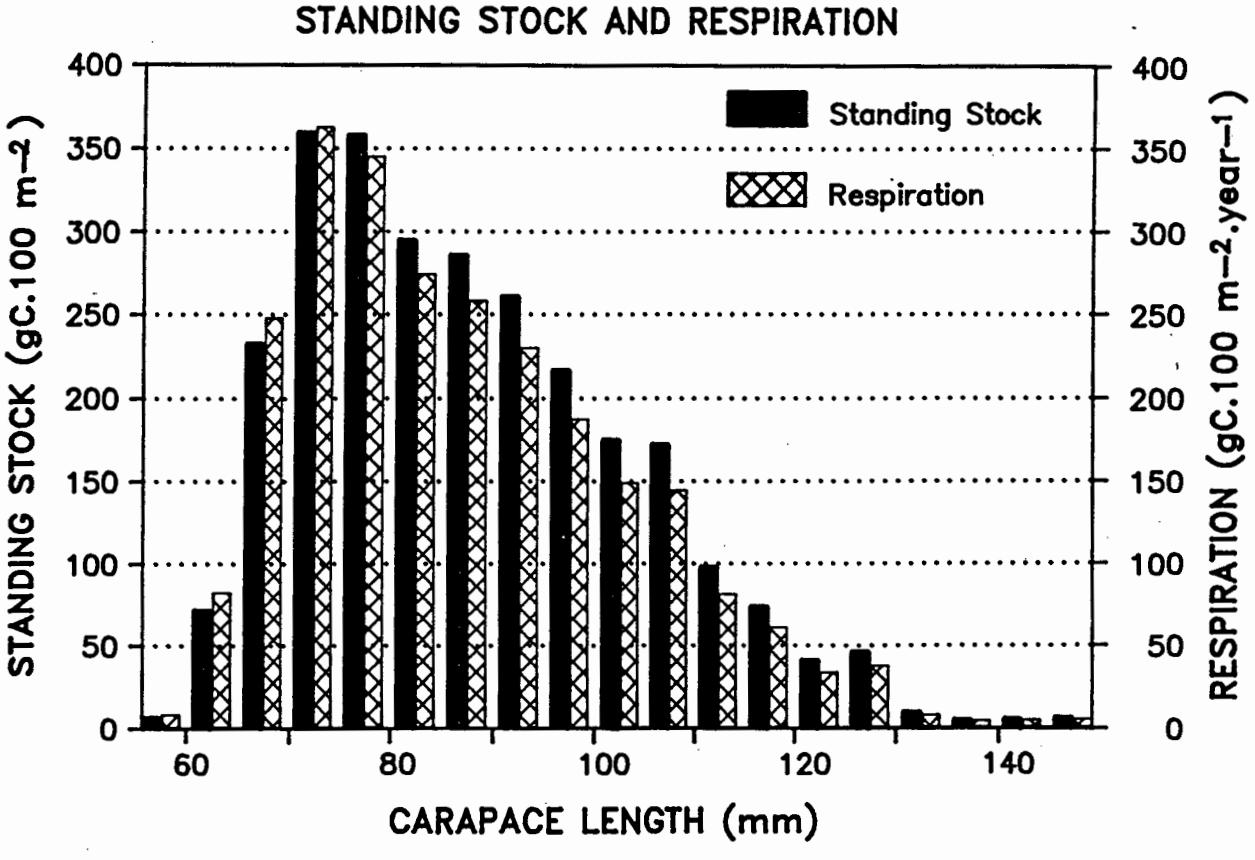

Figure 4.10. Standing stock of carbon representing a population of *J. lalandii*, and the carbon respired at standard rate by the same population in one year, from an area 100 m² off Robben Island

it ignores activity. In the absence of field activity budgets no realistic conversion can be applied between standard and field rates of metabolism.

Figure 4.10 illustrates the standing stock of carbon represented in the *J. lalandii* Robben Island population, and the carbon metabolized by the same population ($yr^{-1}.100\ m^2$). Standard rate of respiration was calculated from Table 4.1 for the mean seawater temperature of 13° C. Animals between 70-80 mm carapace length metabolize approximately the equivalent of their own mass of body carbon per annum, while smaller lobsters metabolize more and larger ones less, as predicted from the negative slope for mass-specific respiration. As the end products of metabolism are heat and carbon dioxide, respiration therefore represents an irreversible energy loss to the biotic community, equivalent to the oxidation of 2.6 kg carbon $100\ m^{-2}.yr^{-1}$.

CHAPTER 5

NITROGEN EXCRETION BY THE CAPE ROCK LOBSTER *JASUS LALANDII* AND ITS POSSIBLE CONTRIBUTION TO THE INSHORE BENGUELA SYSTEM.

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5.1. INTRODUCTION

The Cape rock lobster *Jasus lalandii* is a top carnivore in the kelp-bed system along the west coast of southern Africa. It supports a major fishing industry and reaches densities of 0,81 individuals per square metre (Pollock 1979a). In this paper, an energy budget approach is adopted to determine the quantity of nitrogen excreted (U_N) and voided as faeces (F_N). This contribution is then evaluated relative to the nitrogen requirements of primary producers in a West Coast kelp bed.

In lobsters, nitrogen excretion follows two main pathways to the environment. The first pathway is via the antennal glands. For *Jasus edwardsii*, Binns and Peterson (1969) have shown that urine nitrogen accounts for 11,6 per cent of the total nitrogen excreted. The second and more

important pathway in lobsters is via the gills and possibly the integument (Burger 1957).

Of the total nitrogen excreted by marine organisms, ammonia is for many species the main form. It amounts to 69,6 per cent in the Atlantic menhaden (Durbin and Durbin 1981) and 72 per cent in the spiny lobster *J. edwardsii* (Binns and Peterson 1969). In euphausids, nitrogen excretion in the form of ammonia amounts to 80-85 per cent (Jawed 1969, Mayzaud 1973).

Crisp (in Holme and McIntyre 1984) formulates several equations for describing energy budgets in animals. The terms are either in carbon or kJ units. However, it is possible to use similar equations where nitrogen is the currency. It should be noted that respiration is limited to the context of protein catabolism when, for example, the animal is starved.

The pathways followed by nitrogen through *J. lalandii* are shown in Figure 5.1. They can be expressed by the formula

$$C_N = P_N + G_N + U_N + F_N \ , \qquad (5.1)$$

where C, P, G, U and F refer to consumption, production, reproduction, excretion and faeces (Crisp, in Holme and

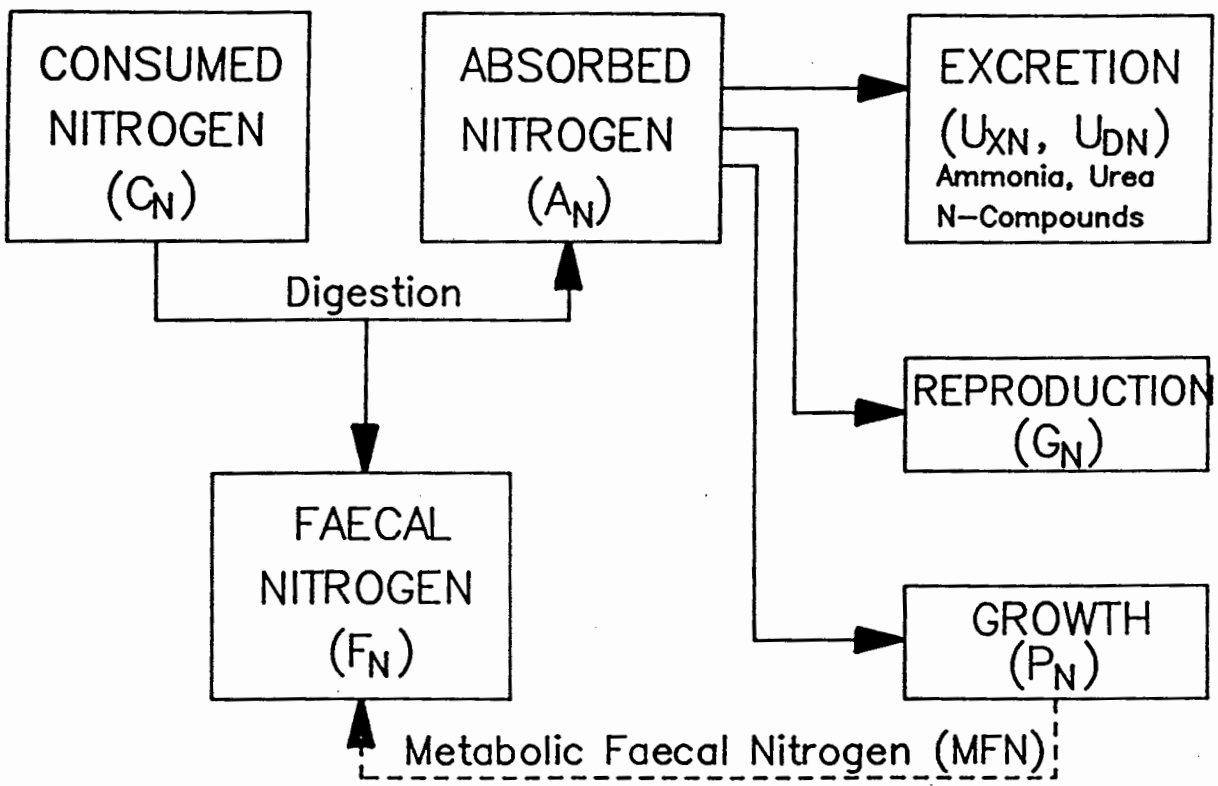

Figure 5.1. Nitrogen pathways through *J. lalandii*

McIntyre 1984). The terms P, U and G represent the fraction absorbed (Ab) after digestion, and it can be expressed by

$$Ab_N = P_N + U_N + G_N \quad . \qquad (5.2)$$

Therefore $Ab_N = C_N - F_N$.

From Equations 5.1 and 5.2, the percentage absorption efficiency can be defined as

$$\frac{Ab_N}{C_N} \cdot 100 \quad .$$

From Figure 5.1 it may be seen that faeces nitrogen has been derived from two sources, the major being the non-absorbed fraction of consumption. The second source is that of metabolic faecal nitrogen (MFN), derived from digestive enzymes plus cells abraded from the walls of the alimentary canal (Maynard *et al.* 1979).

In some crustaceans an additional contribution to MFN comes from the secretion used to encapsulate faecal pellets. However, for *Palaemon serratus* in which this does occur, Forster and Gabbott (1971) have shown that MFN from this source does not form a significant fraction of the total faecal nitrogen. In *J. lalandii*, in which faeces do not appear to be encapsulated, secretions of this type as a source of nitrogen have been ignored.

J. lalandii may make a significant contribution to the nitrogen budget of the inshore region. If the quantitative and qualitative ingestion of food is known and the quantity of nitrogen-containing wastes excreted in the form of ammonia and urea are measured together with the nitrogen loss through faeces, a nitrogen budget can be constructed. In addition it becomes possible to estimate the contribution in terms of recycled nitrogen that *J. lalandii* makes available to both plant and bacterial populations within the inshore Benguela system. A series of experiments was designed to yield results which would put into perspective the quantities of nitrogen made available by *J. lalandii* compared with the annual requirements of both kelps and phytoplankton.

5.2. MATERIALS AND METHODS

All experimental animals and field data were obtained from Oudekraal on the west coast of the Cape Peninsula, a locality within a rock-lobster sanctuary. It is assumed that both plant and animal populations here represent a system where Man's influence is minimal. The area is described by Velimirov *et al.* (1977).

During 1977 and 1978, regular belt counts of *J. lalandii* numbers were made in an area of 180 m^2 in the depth range 12-18 m. Individuals were visually assessed as small

(carapace length <90 mm), medium (90-120 mm) and large (>120 mm). Representatives of each size class were collected, and mean sizes and wet and dry masses were calculated.

In the early summer of 1985, 20 *Jasus lalandii* were caught by SCUBA divers and held in a recirculating seawater aquarium. Three specimens of commercial size (carapace length 110-130 mm) were selected for experimentation on the basis of their consistent feeding. They were placed in separate glass tanks containing 8 *l* of aged seawater which had been held animal-free for four months prior to use. The water had been filtered through 5-µm mesh, to remove large particles, and UV sterilized to minimize bacterial activity. A fourth tank contained seawater only and acted as a control. The four tanks were held at 12° C in a constant temperature room for the duration of the experiment.

Some 30 minutes after the start of the experiment each animal was fed one large *Choromytilus meridionalis*, which constituted a known ration of food that amounted approximately to the rock lobster's daily requirement (Zoutendyk 1988b) (Chapter 3). The food content of the shell was established from a power curve regression of shell length against dry flesh mass (Equation 2.1). Flesh from a representative sample of *C. meridionalis* was dried to constant mass at 60° C. After grinding to a fine powder, part was fired in a ballistic bomb calorimeter to establish

the energy value in terms of kJ.g dry mass^{-1}, and another part was analyzed in a Carlo Erba 1106 CHN elemental analyzer, standardized to acetanilide. Full details of the procedures used are described in Chapter 2.

Feeding in all but one case was complete after three hours. Water was changed, with the replacement conforming to the standards described above, to remove both the build-up of dissolved organic nitrogen (DON) leached from the mussel flesh during ingestion and the particulate organic nitrogen (PON) of the same origin.

At the start of the experiment, duplicate sets of 5-m*l* water samples were collected from each tank for both urea and ammonia analyses. Similar sets of samples were taken at the completion of feeding, and then at hourly intervals for the ensuing 10 h. Thereafter samples were taken at 24-h intervals for two days. The experiment was repeated a second time with three experimental animals over 72 h to determine longer-term excretion of endogenous nitrogen.

All water samples were deep frozen at -20° C. Urea and ammonia were later analyzed according to modified versions of the methods of Grassoff *et al.* (1983).

Faeces were removed from the water by filtration through 44-µm mesh, followed by a second filtration through

Whatmans GFC paper of 3,2-µm mesh. The retained particles were subjected to elemental analysis. An estimate of the dissolved fraction was made from figures for dissolved organic carbon (Chapter 2) and a C:N ratio of 5,9:1 (n = 18, SD = 1,1).

5.3. RESULTS AND DISCUSSION

5.3.1. Nitrogen content of food

In the field, *J. lalandii* feeds on both *C. meridionalis* and *Aulacomya ater*, but laboratory feeding tests were carried out with *C. meridionalis* only. The more abundant of the two mussels at Oudekraal is *A. ater* (Velimirov *et al.* 1977). Results of elemental analysis of the two mussels are given in Table 5.1. To test whether the nitrogen content of the flesh of the two species differed significantly, the original data were transformed by means of an arcsine transformation (Zar 1974), and a Student's t-test of the difference in means was applied. The result shows that nitrogen values of the two species are not significantly different at a level of p = 0,05. Therefore, a nitrogen budget drawn up with *C. meridionalis* as food may be assumed to be similar to one in which *A. ater* is preyed upon, although the shell of *A. ater* is tougher to crack (Griffiths and Seiderer 1980).

Table 5.1. A comparison of *Choromytilus meridionalis* and *Aulacomya ater* flesh subjected to elemental analysis

Prey species	*n*	Percentage of unit mass					
		Nitrogen		Carbon		Hydrogen	
		Mean	S.D.	S.D.	S.D.	S.D.	S.D.
C. meridionalis	4	10,24	0,48	38,73	0,87	5,98	0,31
A. ater	3	10,93	0,19	40,64	0,50	6,67	0,38

5.3.2. Nitrogen loss through messy feeding

Nitrogen values from elemental analysis of food particles remaining after feeding are given in Table 5.2. As the C:N ratio of 3,6:1 is the same for both particles and the original mussel flesh it is assumed that the C:N ratio of the fraction released is also similar. From measured values of dissolved organic carbon release and a conversion factor of 3,6, values for dissolved organic nitrogen (DON) can be estimated. Thus, by combining values for particulate and dissolved fractions, a total of 14,1 per cent of the original nitrogen is being returned directly to the environment without being ingested by *J. lalandii*.

5.3.3. Nitrogen loss through faeces

From total faecal nitrogen and ingested nitrogen in Table 5.2 the percentage nitrogen loss through faeces can be calculated. The mean of five runs on each of the three animals is 13,8 per cent (n = 15). This figure represents

Table 5.2. Fate of food nitrogen in *J. lalandii* determined from the means of five runs

Animal	Food (mg)				Faeces (mg)		Absorption		Excret.(mg)		Balance for use
	Start Mean	PON loss	DON loss	Ingst N	PON loss	DON loss	N (mg)	Effic %	Urea N	NH_4 N	
A	209,9	18,7	16,1	172,1	15,8	10.4	145,9	84,8	3,66	15,46	126,8
B	182,3	8,6	11,6	162,1	8,0	11,5	142,6	88,0	3,26	11,89	127,5
C	167,0	8,7	15,0	143,3	11,2	9,2	122,9	85,8	2.32	10,06	110,5
Mean	185,4	12,0	14,23	159,2	11,7	10,4	137,1	86,2	3,08	12,47	121,5
%	100	14,1		85,9	11,9		73,9		6,67	0,38	65,5

the proportion of the ingested food returned to the environment from within a few hours of feeding to several days later.

5.3.4. Absorption efficiency of nitrogen

From Table 5.2 it can be seen that the mean absorption efficiency of nitrogen in *J. lalandii* is 86,2 per cent. This is relatively high when compared with 72,7 per cent in farm animals (Maynard *et al.* 1979). However, even higher values have been recorded for other marine taxa. Durbin and Durbin (1981), after feeding the Atlantic menhaden *Brevoortia tyrannus* a diet of zooplankton, recorded a mean nitrogen assimilation efficiency of 93,9 per cent.

Durbin and Durbin (1981) also show that the C:N ratio in faeces of *B. tyrannus* is higher than that of the food, a finding similar to that for *J. lalandii*, for which the C:N ratio in tank-collected faeces is 5,8:1 compared to the 3,6:1 of *C. meridionalis* flesh ingested as food. For *J. lalandii* the mean absorption efficiency of nitrogen is 6,7 per cent higher than that of carbon (Chapter 2). It therefore appears that a selective absorption of nitrogen results in a higher absorption efficiency for nitrogen when compared with that for carbon.

5.3.5. Exogenous nitrogen excretion

Exogenous nitrogen excretion is associated with ingestion and the period immediately following it. Durbin and Durbin (1981) showed that, for *B. tyrannus*, 90 per cent of the total exogenous nitrogen excretion was complete within 2,4 h of the end of feeding. In *J. lalandii* a similar pattern has emerged, and this is reflected in the analyses of both urea and ammonia nitrogen.

Figure 5.2 shows that peaks of urea nitrogen excretion occur 5-9 h after the commencement of feeding in all three experimental animals. Figure 5.3 shows that the mean maximum excretion occurs 7 h after the commencement of feeding. Twelve hours after the start, urea nitrogen excretion drops to a low level, typical of the period between meals.

Exogenous nitrogen excreted as ammonia shows superficially a similar pattern. However, two main differences exist. A peak of excretion follows immediately after feeding ceases. In Animals A and B, a second peak occurs 3-4 h later (Figure 5.4), and in Animal C the same occurs, but during the 72 h test only (Figure 5.5). This double peak is clearly seen in the mean values shown in Figure 5.3. It appears therefore that the excretion of exogenous nitrogen in the form of ammonia is pulsed.

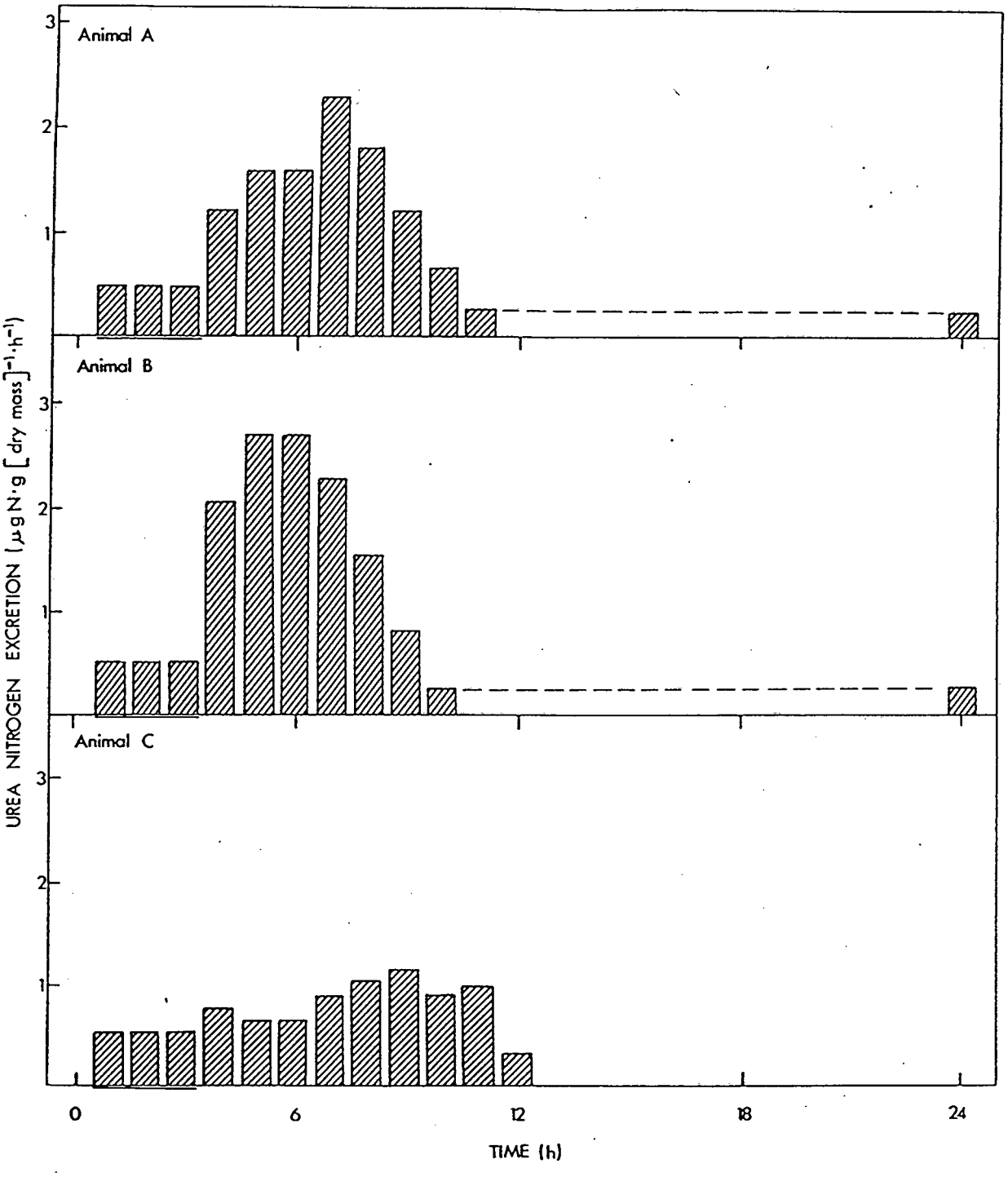

Figure 5.2. Urea nitrogen excretion by Animals A, B and C during and after a 3-hour feeding period

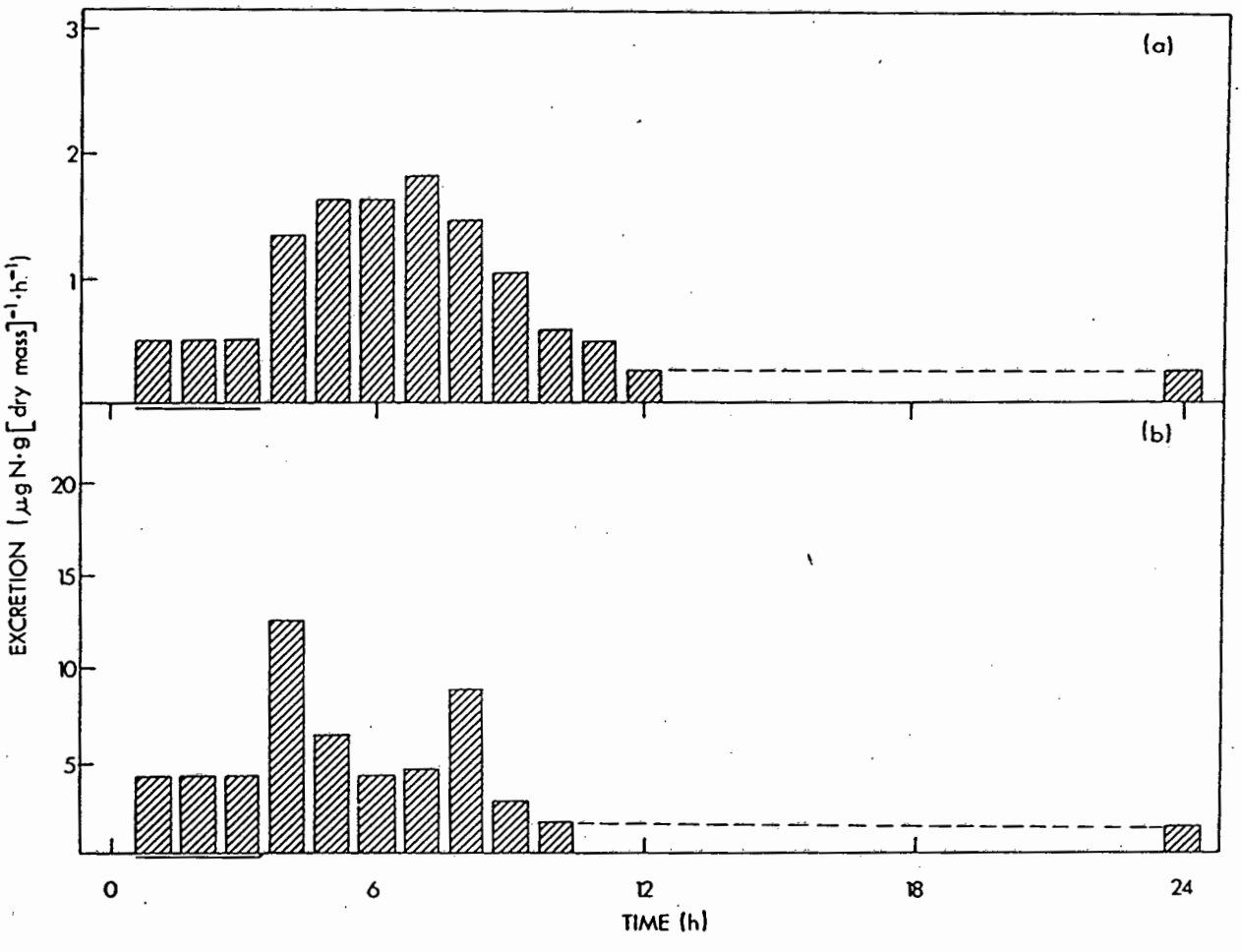

Figure 5.3. Mean values of (a) urea and (b) ammonia nitrogen excreted by *J. lalandii*

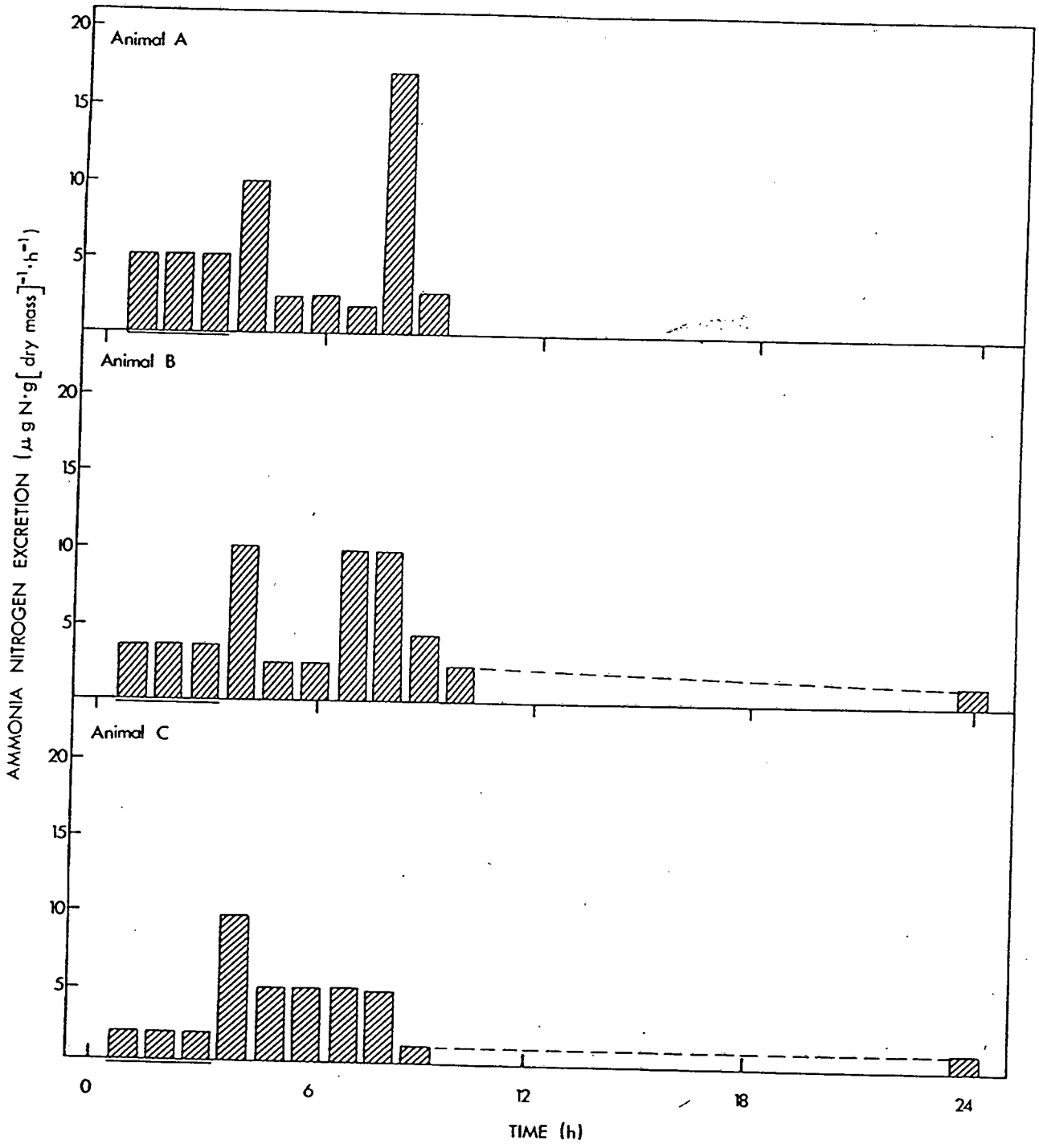

Figure 5.4. Ammonia nitrogen excretion by *J. lalandii* during and after a 3-hour feeding period

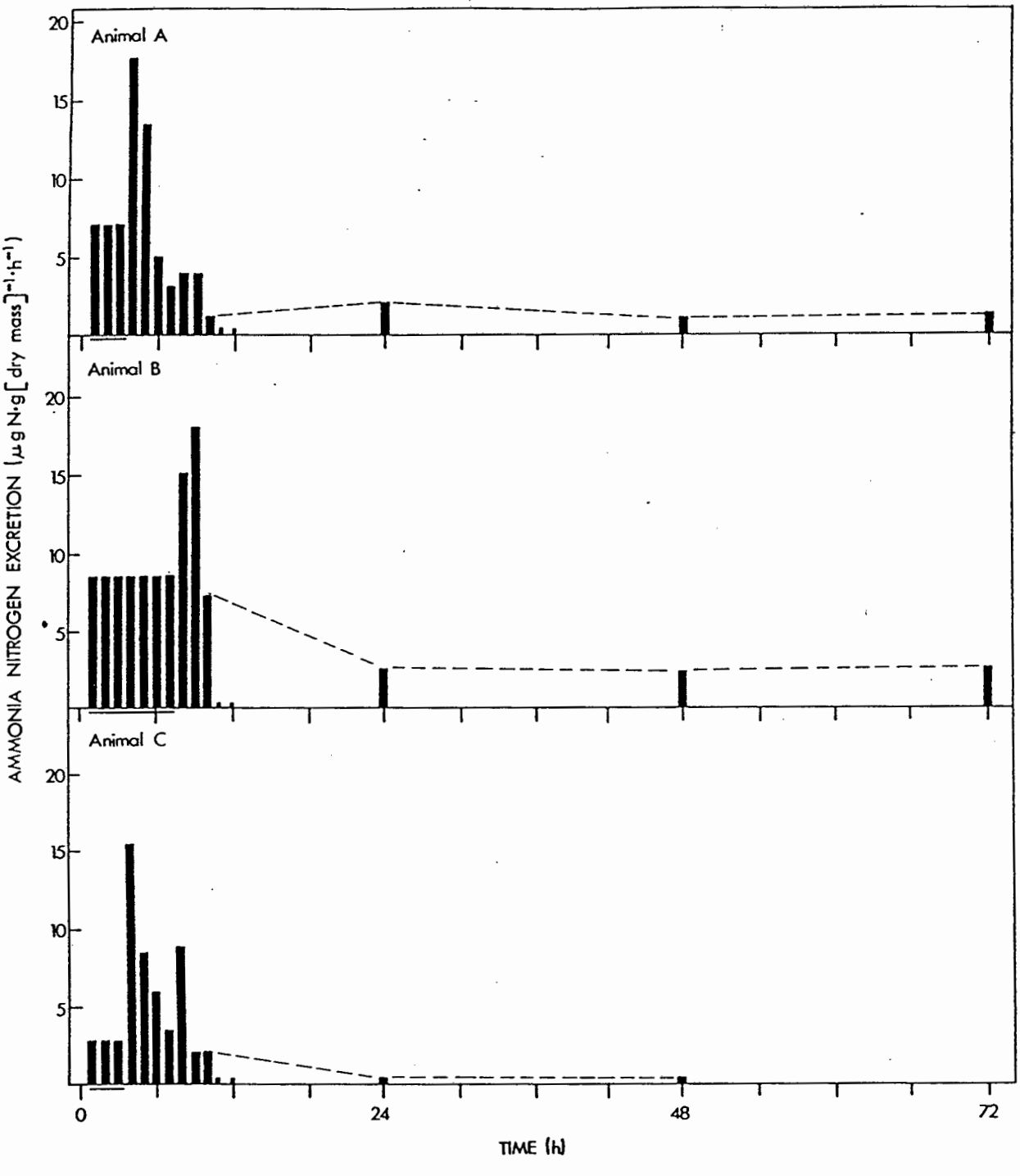

Figure 5.5. Ammonia nitrogen excretion during and after a 3-hour feeding period monitored for 72 hours

Similar pulsing of ammonia excretion has been described for juvenile American lobster by Hawkins *et al.* (1986).

Table 5.3. Summary of nitrogen excretion during and after feeding

Parameter	Value
Mean exogenous N excretion	9,7 per cent of ingested N
Mean exogenous urea N	8,7 µg.g(dry mass)$^{-1}$.meal^{-1}
Mean exogenous ammonia N	45,6 µg.g(dry mass)$^{-1}$.meal^{-1}
Mean endogenous urea N	0,27 µg N.g(dry mass)$^{-1}$.h^{-1}
Mean endogenous ammonia N	1,63 µg N.g(dry mass)$^{-1}$.h^{-1}
Exogenous ammonia N : Exogenous urea N = 5,2 : 1	
Endogenous ammonia N : Endogenous urea N = 6,0 : 1	

Table 5.3 shows that the mean total of exogenous nitrogen excreted as urea is 8,7 µg.g (dry mass)$^{-1}$.meal^{-1}, compared with the value of 45,6 for ammonia. This gives an ammonia N:urea N ratio of 5,2:1, and therefore the ammonia pathway for the excretion of exogenous nitrogen appears the more important of the two.

5.3.6. Excretion of endogenous nitrogen

Catabolism, either as general tissue breakdown or specifically as the oxidation of protein reserves during respiration, is an on-going process. It results in a continuous low-level excretion of endogenous nitrogen. This is in the form of both urea and ammonia, as seen in Figures 5.2-5.5. Dotted lines link data points after the

elimination of exogenous nitrogen is complete. From Table 5.3 it is seen that six times more nitrogen is excreted as ammonia than urea. This nitrogen, together with ammonia and urea of exogenous origin, could be of particular importance to the phytoplankton in kelp beds where, according to Probyn and McQuaid (1985), both forms of nitrogen are absorbed preferentially over nitrates.

5.3.7. Biomass of *J. lalandii* at Oudekraal

Figure 5.6 illustrates the results of belt counts made over a period of 20 months. The size structure of the population is typically pyramidal, in which most of the individuals are in the small size class. Counts indicate a stable population with no obvious seasonal pattern. The peak and subsequent trough in July and August respectively in 1977 are artefacts of weather, conditions for the July count being exceptionally good, but followed by adverse diving conditions the next month. Rock lobsters are affected by swell and move in and out of shelter accordingly, and this has an effect on the accuracy of belt counts. The mean density of *J. lalandii* for the period under consideration was 0,48 individuals.m^{-2}. This is the equivalent of 49,75 g (dry mass).m^{-2}.

5.3.8. The rôle of *J. lalandii* in inshore nitrogen requirements

At Oudekraal the ribbed mussel *A. ater* has a mean biomass of 1,151 kg dry mass.m^{-2} (Velimirov *et al.* 1977).

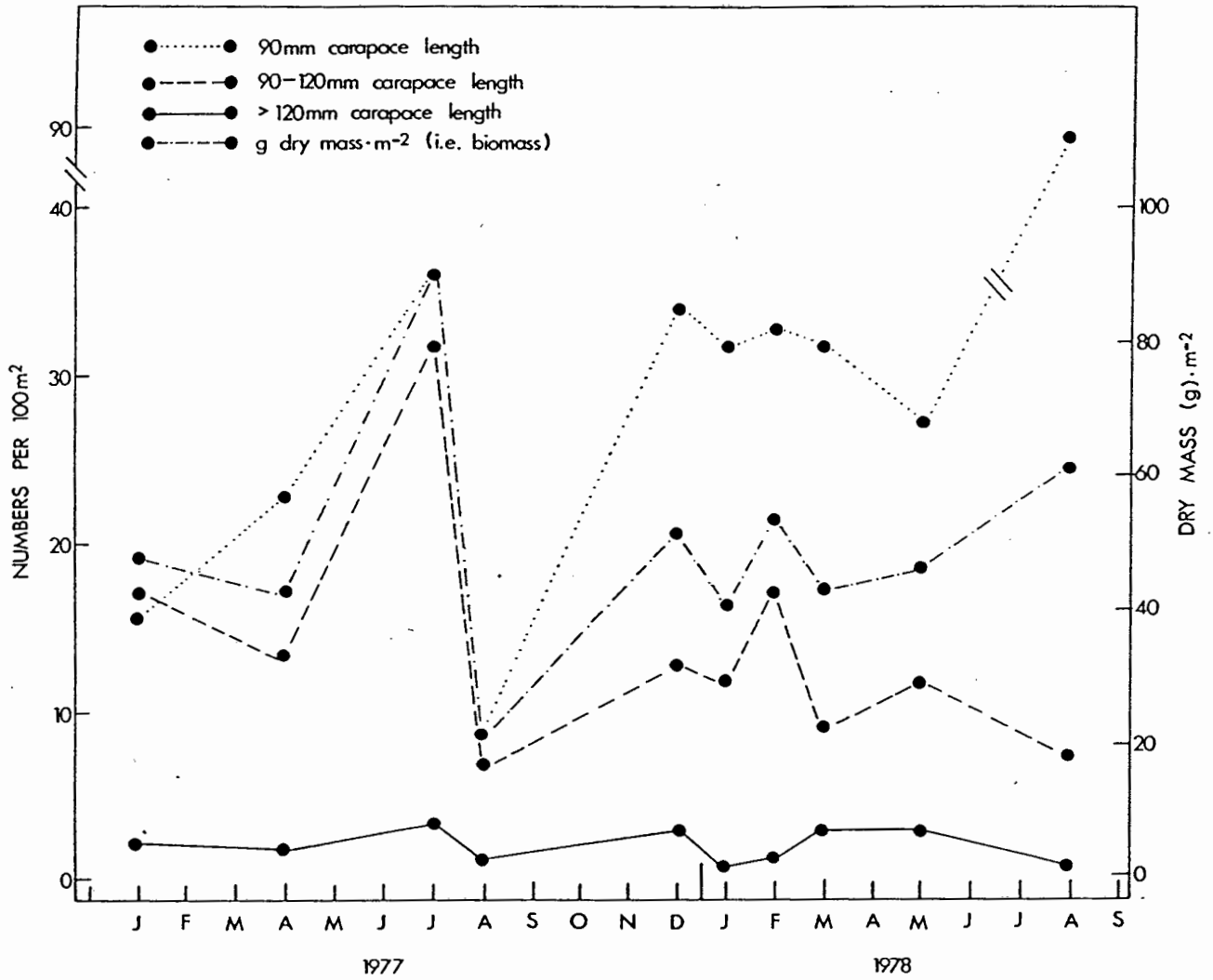

Figure 5.6. Small, medium and large *J. lalandii* at Oudekraal from the results of belt counts carried out during 1977/78

From the conversion factor of Field *et al.* (1980a) and the results of bomb calorimetry and elemental analysis, this represents 21,0 g $N.m^{-2}$. The mussel *C. meridionalis* has a P/B ratio of 3:1 (derived from Griffiths 1981). If the same ratio is used for *A. ater*, 63 g $N.m^{-2}$ are available, which is well in excess of the annual requirement of 6,3 g $N.m^{-2}$ for the resident lobster population, inspite of only a portion being accessible (Griffiths and Seiderer 1980). Nitrogen values were calculated from carbon values (Chapter 3) using the conversion factor of 0,38 (derived from Table 5.1).

What then is the significance of regenerated nitrogen to the plants in the system? To permit such analysis, one approach is to utilize figures of new nitrogen advected into the inshore area. However, due to the site-specific nature of upwelling (Chapman and Shannon 1985), it is difficult to estimate how much nitrogen is available via this channel. This is further complicated by the rate of water turnover in the nearshore environment where it can vary from 3 to 7 times 24 h^{-1} (Field *et al.* 1981). An alternative approach is to estimate how much nitrogen is required by the primary producers annually. Jarman and Carter (1981) estimate kelp production as 1,17 $kgC.m^{-2}.yr^{-1}$. From the C:N ration 15:1 (Probyn and McQuaid 1985) for kelp, this is equivalent to an annual requirement of 78,0 $gN.m^{-2}.yr^{-1}$. Probyn and McQuaid (*op. cit.*) have estimated the uptake of nitrogen in *Ecklonia*

maxima on a seasonal basis and, calculated on the basis of their data, the annual requirement would by 75,5 g $N.m^{-2}$.

Carter (1982) estimated that phytoplankton in open water associated with kelp beds had an annual production of 1,13kg$C.m^{-2}$. From his C:N ratio of 6,5:1, the annual requirement would be 174 g $N.m^{-2}$. However, in the kelp beds, shading occurs which reduces nitrogen uptake to 5 per cent of that in open water (Borchers and Field 1981). On this basis, phytoplankton in the kelp beds would require only 8,7 g $N.m^{-2}.yr^{-1}$. Similarly, from the data of Probyn and McQuaid (1985) for phytoplankton nitrogen uptake in kelp beds, a value of 0,8 g $N.m^{-2}.yr^{-1}$ is obtained.

At the upper end of the scale, and from the data of Jarman and Carter (1981) and Carter (1982), the total annual requirement of kelp and phytoplankton is 86,7 g$N.m^{-2}.yr^{-1}$. The lower estimate of 76,4 g $N.m^{-2}.yr^{-1}$ from the data of Probyn and McQuaid (1985) is in close agreement. Newell and Field (1983a,b) constructed diagrams for carbon and nitrogen flows through a typical Cape Peninsula west-coast kelp bed, with the emphasis of the availability of these two elements to filter-feeders and bacteria. Their estimate of nitrogen directed into this channel from primary producers amounted to 145 g $N.m^{-2}.yr^{-1}$, and is higher than the two estimates above due to a factor of 50 per cent being applied to the

shading effect of kelp on phytoplankton (c.f. 5 per cent applied above) and the incorporation of understorey algae.

In summing up, Figure 5.7 illustrates the relative quantities, pathways and compartments through which nitrogen moves as a result of *J. lalandii* feeding on *C. meridionalis*. As seen earlier, *J. lalandii* is responsible for recycling 6,3 g $N.m^{-2}.yr^{-1}$ at Oudekraal. This amounts 7,2-8,2 per cent of the kelp and kelp-bed phytoplankton annual requirements, the possibility exists that it may be an overestimate in the light of Newell and Field's (*op cit.*) work. Such provision of nitrogen could be of particular significance to the primary producers during static conditions or weak downwelling, when the availability of new nitrogen is limited.

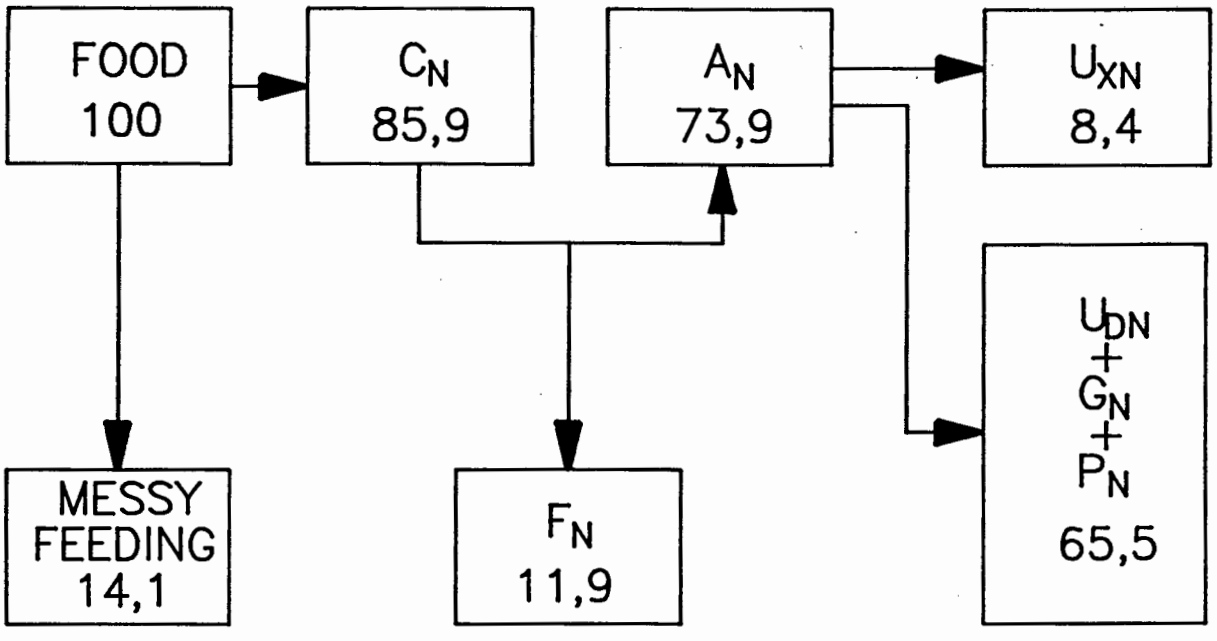

Figure 5.7. Pathways and compartments through which nitrogen moves as a result of *J. lalandii* feeding on *C. meridionalis*

CHAPTER 6

PRODUCTION IN THE CAPE ROCK LOBSTER *JASUS LALANDII* IN TERMS OF CARBON AND NITROGEN ALLOCATED TO GROWTH

6.1. INTRODUCTION

Growth is a fundamental characteristic of life and implies a change in size with time. Production is more specific than growth and is mainly used in conjunction with energy budgets and fisheries management. Phillipson (1975) defines production as the "energy content of the biomass of materials digested during a specified time interval... less that respired or rejected". Crisp 1984 (in Holme and McIntyre 1984) narrows the definition to "that part of assimilated food or energy which is retained or incorporated into the biomass of the organism, but excluding reproductive bodies released...", and can be expressed by the following equation:

$$\text{Production (P)} = Ab - (R + G + U) , \qquad (6.1)$$

where Ab = absorption, R = respiration, G = gonadal output and U = excreta, including exuviae. Production in *J. lalandii* is discussed within the limits of Equation 6.1.

The ratio of production to biomass (P/B) provides an insight into the dynamics of an organism within an ecosystem and, if the organism is of commercial importance, a measure of what yield may be expected from a specified biomass over a specified period of time (usually one year). In *J. lalandii* both aspects are of importance. In this paper biomass and growth estimates have been converted into units of carbon and nitrogen, contributing to the solution of Equation 6.1. In addition, production has been quantified and expressed in terms of carbon and nitrogen, as well as wet mass and numbers of individuals, to facilitate comparison.

6.2. MATERIALS AND METHODS

Carbon and nitrogen values for 15 whole *J. lalandii* which had previously been dried, milled and homogenized were measured in a Carlo Erba 1106 elemental analyzer standardized to acetanilide. Dry mass (DM of lobster) was calculated from carapace length (mm) using the formula

$$\text{Dry Mass} = 0{,}000274\,\text{Carapace Length}^{2{,}877}$$

($r^2 = 0{,}99$; $n = 152$).

Dry mass was converted to organic carbon and nitrogen using the relevant values listed in Table 6.1.

Table 6.1. Mass conversions and elemental analyses of 15 whole *J. lalandii*. Energy (kJ), elemental percentages and C:N ratios are all related to dry mass

TISSUE	WM	DM	AFDM	O.C%	I.C%	N%	H%	*n*	kJg^{-1}	C:N
WHOLE *JASUS*	3,10	1	0,74	35.51	2,01	9,90	6,35	3	16,94	3,59

Legend WM = wet mass, DM = dry mass, AFDM = ash-free dry mass, O.C = organic carbon, I.C = inorganic carbon, N = nitrogen, H = hydrogen, *n* = number of replicates.

Data from Pollock (1978) have been used to illustrate growth and production in *J. lalandii* at population level (Chapter 3). Size-frequency counts for 14, 20 and 27 m depths were combined and standardized per 100 m^2 by applying the mean density of lobsters at Robben Island i.e. 0,81 m^{-2} (Pollock *op. cit.*).

6.3. RESULTS AND DISCUSSION

6.3.1. Growth

Pollock (1973 as quoted in Pollock 1978) has shown that male and female *J. lalandii* have similar growth rates until a carapace length of approximately 60 mm is reached. Females become sexually mature after 60 mm when the increment in carapace length at moulting drops. This

implies that a portion of the carbon previously used in growth of juveniles is allocated to egg production in mature females.

In Figure 6.1 the growth of males and females is compared. Both sets of data are taken from Pollock (1978). The data are empirically described by normal distribution curves and can be expressed by the following non-linear equations which apply only to lobsters >60 mm CL:

$$\text{Male Increment} = 8{,}131e^{-0{,}0006516(CL-96{,}884)^2} \qquad (6.2)$$

$$\text{Female Increment} = 2{,}568e^{-0{,}002155(CL-60)^2} \qquad (6.3)$$

where measurements are in millimetres and CL represents carapace length prior to moulting.

The male increase in carapace length at moulting continues to rise until a maximum is reached between 90 and 100 mm, after which it drops steadily, finally reaching zero at the asymptotic length of 190 mm. The latter length coincides with the maximum length found in extensive surveys in Table Bay by Zoutendyk (unpub. data).

6.3.2. Biomass and total production

Production was calculated for 5-mm size-classes for a combined population of male and female lobsters using

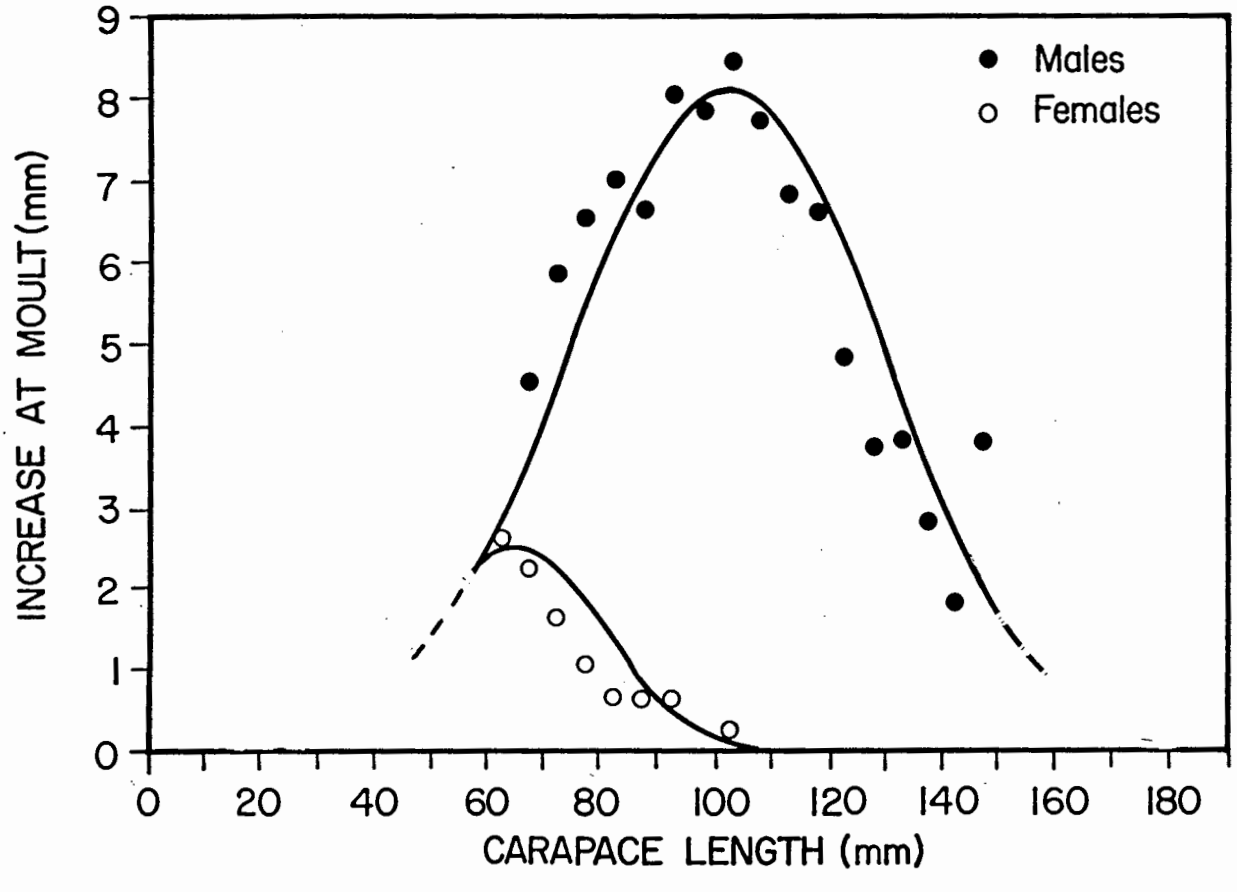

Figure 6.1. A comparison between male and female *Jasus lalandii* growth: increase in carapace length after moulting, in relation to pre-moult carapace length. (Data from Pollock 1978)

Equation 3.1 (Chapter 3) in conjunction with Equations 6.2 and 6.3, and Equation 6.4 as follows:

$$\text{Production (gDM)} = DM_{T1} - DM_{To} \qquad (6.4)$$

where DM = Dry Mass, DM_{To} = Dry Mass at initial measurement and DM_{T1} = Dry Mass 1 year and 1 moult later.

In Figure 6.2 standing stock and production have been expressed in terms of carbon, which has been derived from dry mass using the factors in Table 6.1. The standing stock was skewed to the left with the highest values being recorded in the size range of 70-80 mm. Robben Island is a lobster sanctuary and the population structure may therefore be looked upon as representing a natural unexploited stock. It is thus of interest that this peak in standing stock should occur 10-20 mm below the commercially exploitable size of 89 mm, a feature which would be expected in a population subjected to fishing pressure. Production, in contrast, follows a normal distribution, with the highest rate taking place from 70-110 mm carapace length. Under-estimation of the smallest size classes may have occurred as a result of undersampling young lobsters.

The total standing stock at Robben Island was 2,617 kg carbon.100 m^{-2}, while the annual production amounted to 435 gC. Equivalent nitrogen values can be derived from carbon using the C:N ratio of 3,59 from Table 6.1. Lobster biomass

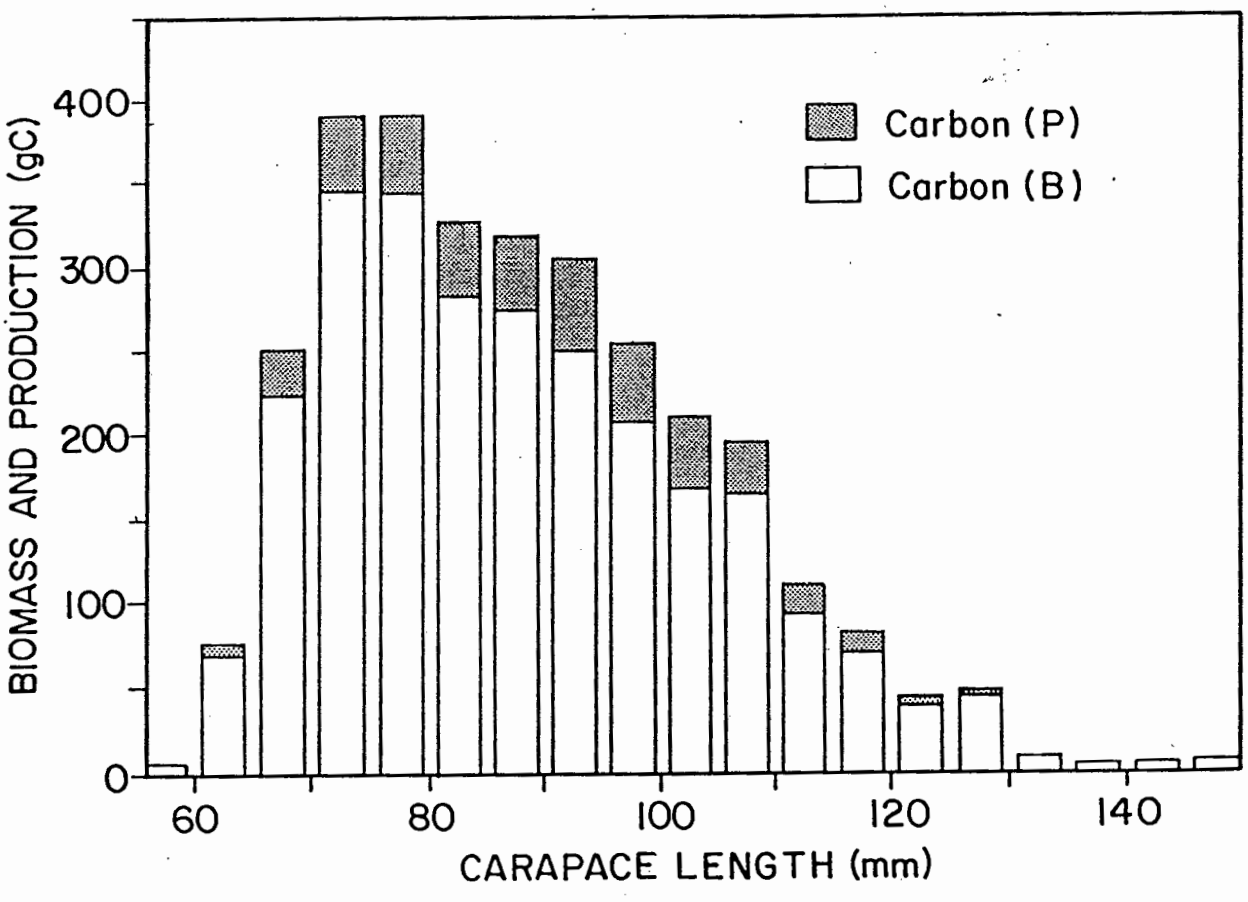

Figure 6.2. Biomass and production (gC.100 m^{-2}) per size class of a population of *Jasus lalandii* off Robben Island. B = biomass; P = production per annum

contained 729 g nitrogen with an annual net production of 121 g per year. By comparison the cost of moulting in the same population amounted to an annual loss of 53,7 g nitrogen (Chapter 7) which is equal to 44 per cent of the production as defined in Equation 6.1.

6.3.3. Production differences between sexes

Annual production in the lobster population off Robben Island is illustrated separately for males and females in Figure 6.3. In the smaller size classes, carbon production by females exceeds that of males due to the population structure. However, after reaching a maximum at 65-75 mm, production in females drops rapidly. In males it continues to increase until a maximum is reached between 90-95 mm, after which it decreases rapidly. More notable are the absolute production figures. Annual production by males is 380 $gC.100^{-2}.yr^{-1}$ compared to female-production of 55,4 $gC.100^{-2}.yr^{-1}$. Thus female-production amounts to only 12,7 per cent of total carbon production. If female-production is viewed in terms of lobsters >90 mm (subjected to commercial exploitation), their annual production amounts to only 0,6 $gC.100\ m^{-2}$ compared to a figure of 213,7 $gC.100\ m^{-2}$ for males >90 mm. Therefore, in this size category, females contribute only 0,3 per cent of the total production.

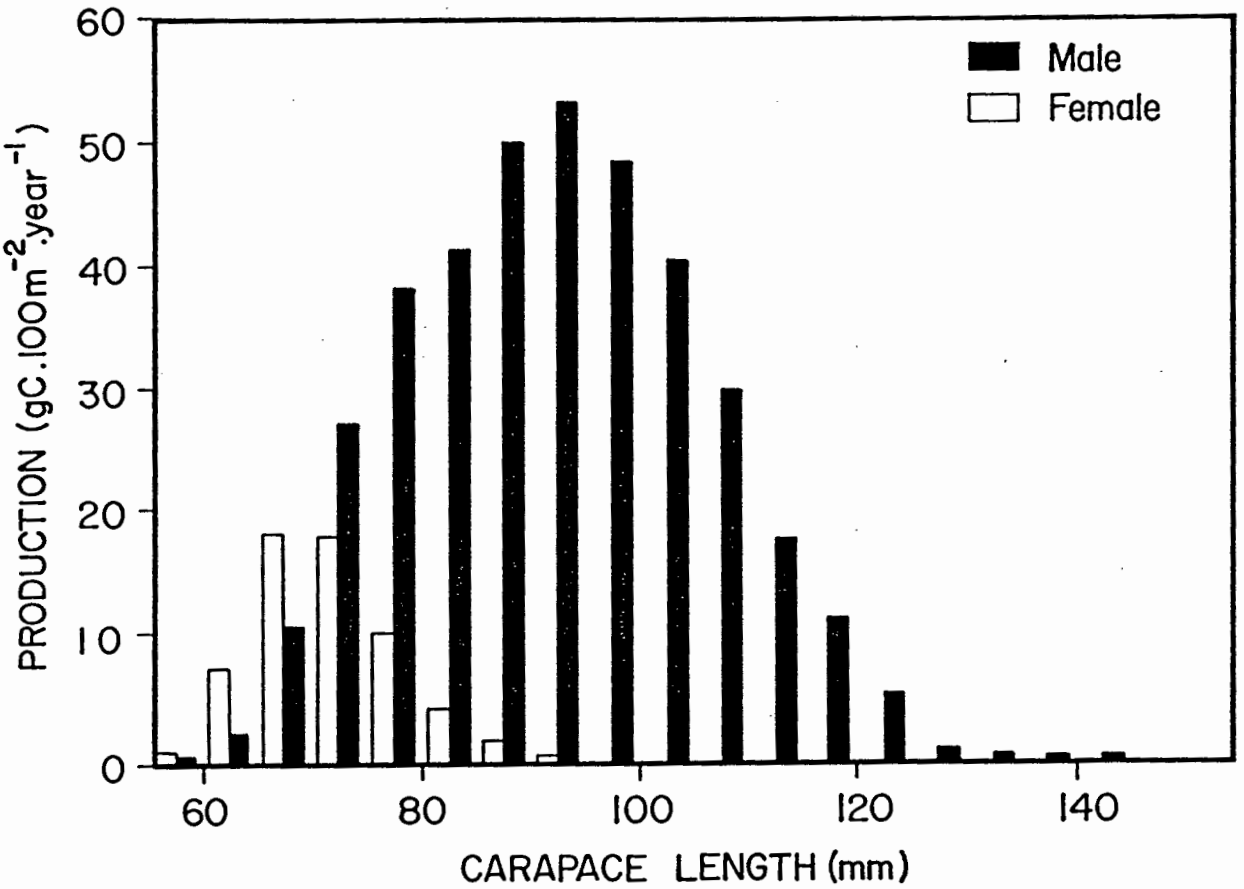

Figure 6.3. Annual carbon production for a population of *Jasus lalandii* off Robben Island, expressed separately for the two sexes

6.3.4. P/B ratios

In Figure 6.4 the P/B ratios for Robben Island lobsters have been plotted against carapace length for males and females separately. As production is linked to growth, the form of the plots follows closely the growth curves in Figure 6.1. In the observed range (55-150 mm carapace length), the female P/B ratio is close to that of males at the lower limit. However, the two diverge rapidly with females dropping to below 0,01 at 85-95 mm, while at this length males reach their maximum with a value of 0,27. For the Robben Island population the mean P/B ratio for males and females combined is 0,166. In contrast, Berry and Smale (1980) reported high P/B ratios with similar values for males and females of 0,43 and 0,42 respectively, for the warm-water lobster *Panilirus homarus*.

In Figure 6.5 data from Saila, Annala, McKoy and Booth (1979), on the closely related lobster *Jasus edwardsii* off North Island, New Zealand, have been expressed as P/B ratios. In large animals it is seen that P/B ratios for the two species are similar. However in *J. lalandii* the males have a higher P/B in the larger size classes, and in females of *J. lalandii* the P/B ratios are all smaller than in *J. edwardsii*. There is thus a greater contrast in production capabilities between sexes in *J. lalandii* when compared with *J. edwardsii*. It appears therefore, that *J. lalandii*

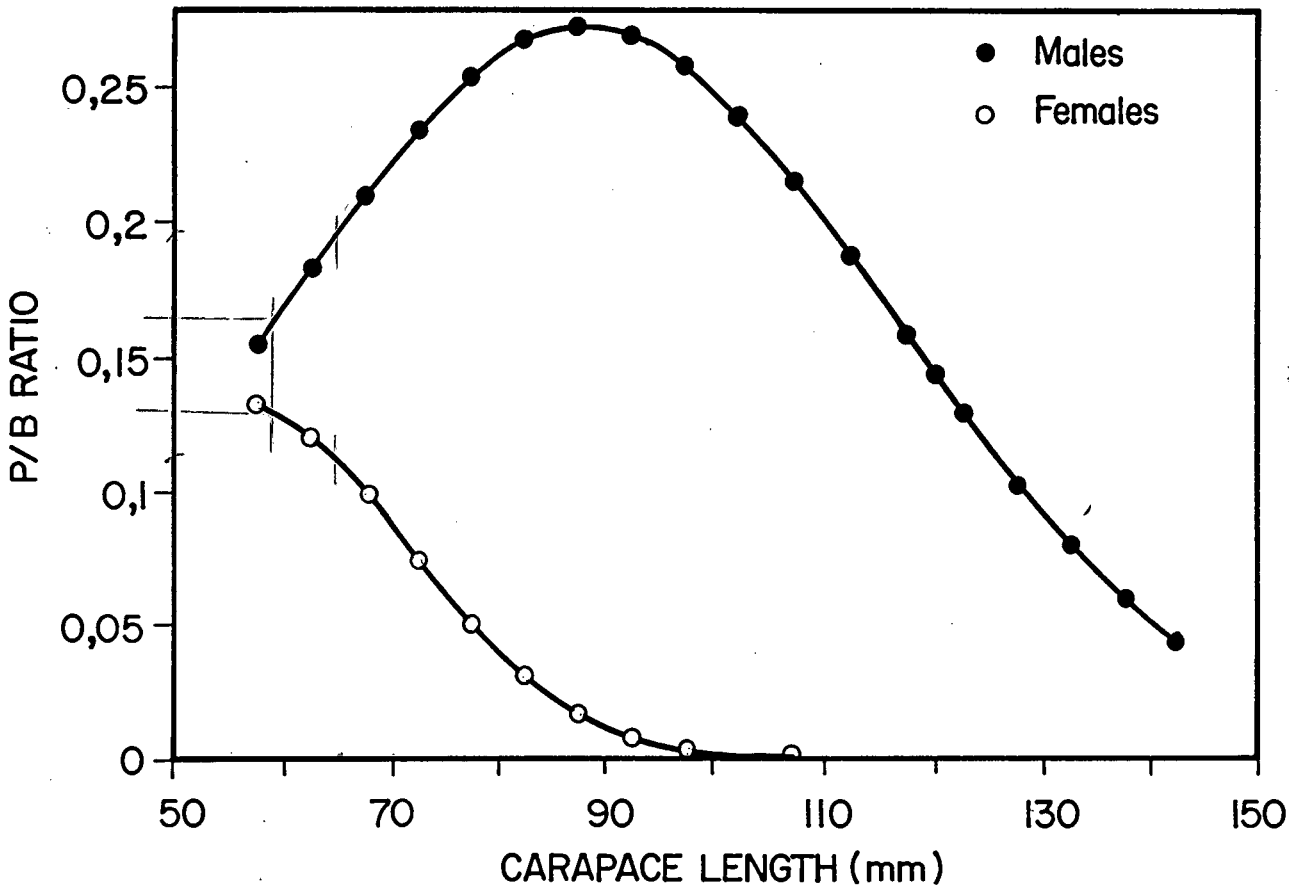

Figure 6.4. P/B ratios for male and female *Jasus lalandii* off Robben Island

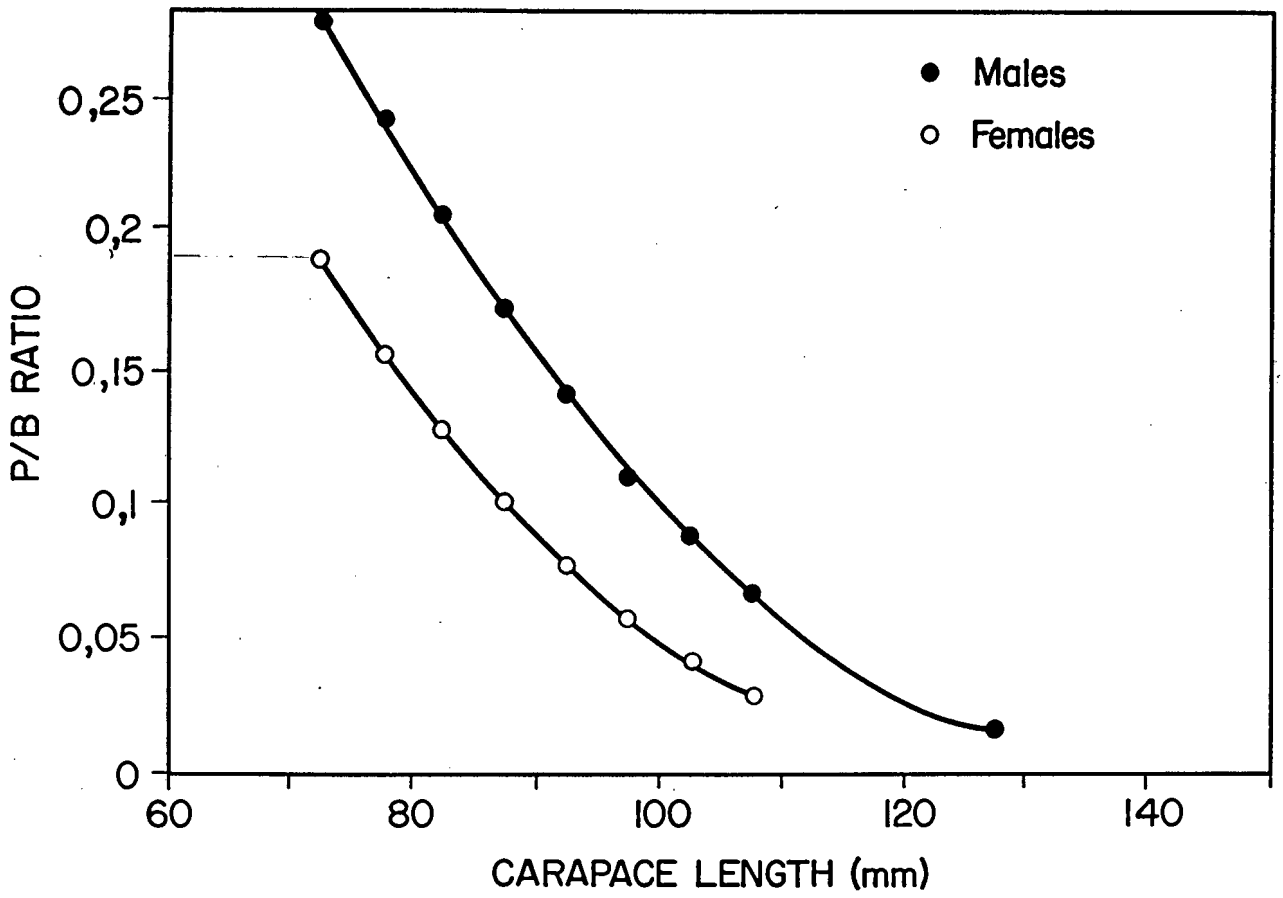

Figure 6.5. P/B ratios for male and female *Jasus edwardsii* (data from Saila *et al.* 1979)

diverts more energy into egg production at a smaller size, which results in a reduced growth rate in females.

6.3.5. Conversion efficiencies

Growth or production can be calculated per unit of ingested ration to give a measure of food conversion efficiency (Windell 1978). This is affected by body size, acclimation temperature and availability of ration (Newell 1979). Gross growth efficiency (K_1) has been calculated as follows:

$$K_1 = \frac{\text{Production}}{\text{Consumption}}$$

where production includes both somatic and reproductive growth. Somatic production for males and females has been calculated from Equation 6.4, and reproductive production as set out in Chapter 8. Consumption has been calculated from dry mass where Consumption ($gC.yr^{-1}$) = 0,479DM (Chapter 3). Figure 6.6 shows the gross growth efficiencies at 12° C for a size-range of mature male and female *J. lalandii*. Somatic and reproductive growth efficiencies for females have been plotted separately, in addition to their combined values. Female somatic growth efficiency decreased steeply with increase in size, while there is only a small decrease in reproductive growth efficiency. When the two are combined, the female growth efficiency has a maximum of *c.* 0,2 at 55 mm carapace length. Males reflect a similar pattern, but the curve is offset to the right with a maximum occurring at

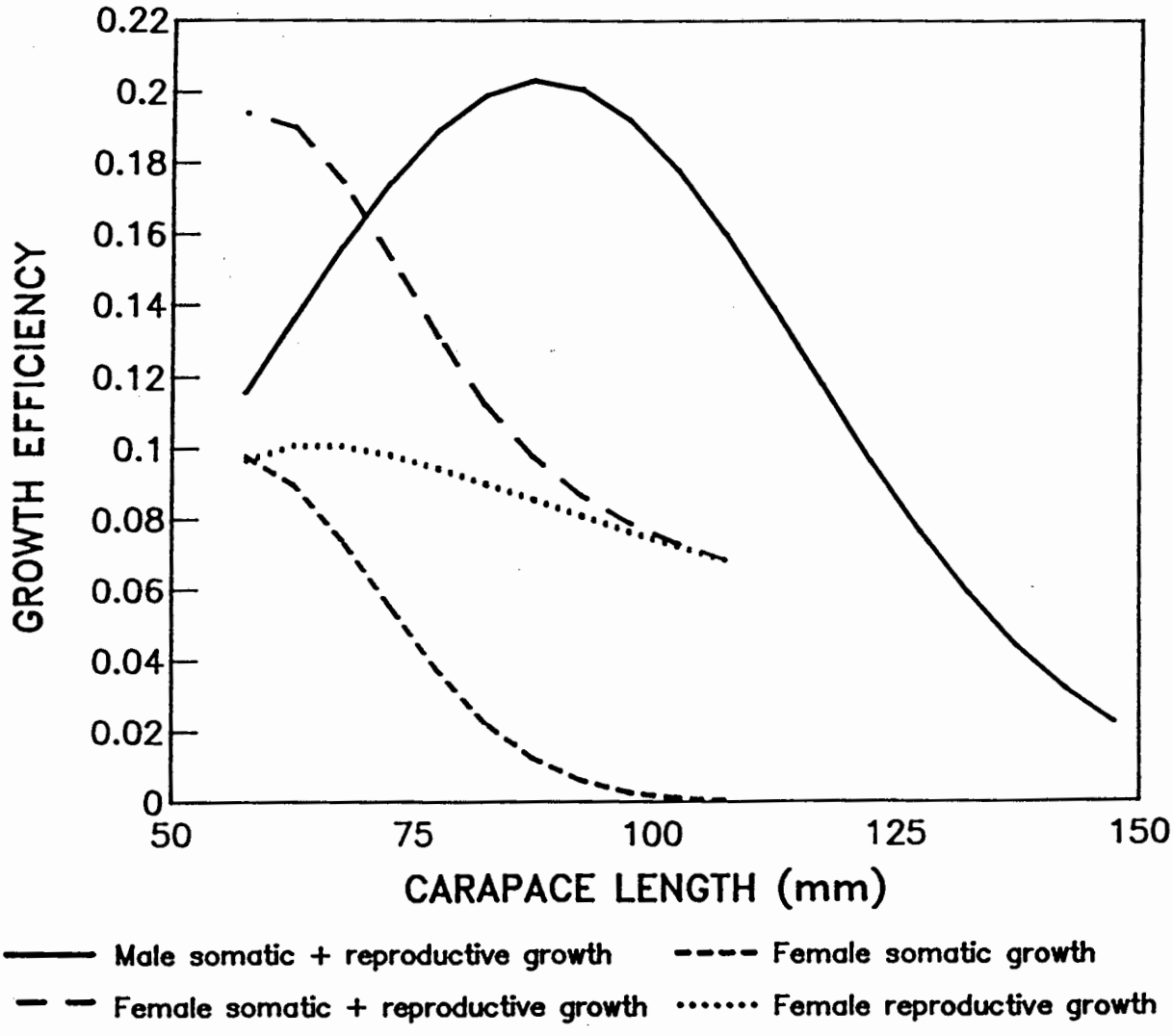

Figure 6.6. Growth efficiencies at 12° C for mature male and female *J. lalandii*

90 mm CL. The maximum K_1 value of *c.* 0,2 is close to the predicted value of 0,219 for poikilotherms of equivalent mass calculated from the formula of Peters (1983) where $K_1 = 0,21WM^{-0,05}$. At population level the mean value for *J. lalandii* at Robben Island is 0,16 which is lower and outside the range of 0,236-0,207 predicted for individuals by Peters (*op. cit.*). But at population level a lower energy efficiency is predicted (Bradfield and Llewellyn 1982) and *J. lalandii* therefore conforms to the general poikilotherm pattern.

In conclusion, in the unexploited population of lobsters at Robben Island, annual production per 100 m^2 amounts to 435 g carbon and 121 g nitrogen. This is equivalent to a yield of 3,798 kg live lobster 100 m^{-2} or 11,4 individuals of 97 mm carapace length - the mean size of commercially caught lobsters in many areas (Beyers SFRI, pers. comm.). Within a stable unexploited population, these quantities of carbon and nitrogen are therefore returned to the ecosystem annually in the form of natural mortality due to death by disease and old age, or predation by major predators such as the striped catshark *Poroderma africana*, (Pheiffer, Kelp Products pers. comm.), the South African fur seal *Arctocephalus pusillus* (David 1987), and the bank cormorant *Phalacrocorax neglectus* (Cooper 1985).

CHAPTER 7

CARBON AND NITROGEN LOSSES THROUGH MOULTING IN THE CAPE ROCK LOBSTER *JASUS LALANDII*

(Published in: *S. Afr. J. Zool.* 23: 173-175. 1988)

7.1. INTRODUCTION

It is axiomatic that an exoskeleton has survival value to the individual. However, there are distinct disadvantages to this structure when the necessity for growth is considered. In *Homarus* the pre-moult phase may last several months (Aiken 1980). In the spiny lobster, *Jasus lalandii* this phase is similarly long and is associated with a cessation of feeding (Chapter 3). After ecdysis, feeding can only be resumed when the exoskeleton has hardened sufficiently, which may take several weeks (Chapter 3). Possibly even more costly to lobsters than the disruption of feeding or susceptibility to predation during moulting, is the physical loss of the exoskeleton including the elements carbon and nitrogen. In this investigation these latter losses have been quantified and the results are discussed in relation to carbon and nitrogen budgets at the population level.

7.2. MATERIALS AND METHODS

Specimens of *J. lalandii* were collected by SCUBA divers from a depth of 8-15 m in a rock-lobster sanctuary at Oudekraal on the west coast of the Cape Peninsula. Details of the research area are given by Velimirov *et al.* (1977).

Nineteen post-moult male rock lobsters in the size range of 80-135 mm carapace length were collected in early summer of 1983. They were used in feeding and respirometry experiments for a 400-d period (Chapter 3). A further 18 male rock lobsters in the same size range were collected in August 1984 prior to moulting. In this size range lobsters moult once per annum (Pollock 1978).

Specimens were kept singly in 100 *l* seawater tanks at 12° C and a salinity of 35°/$_{oo}$ in a recirculating system. Illumination is an important factor in the control of moulting. Lipcius and Herrnkind (1982) and Quackenbush and Herrnkind (1983), working on *Panulirus argus* discuss the profound effect that light has on the moulting cycle. Similarly, Nelson *et al.* (1983) reported that moulting in *Homarus americanus* was controlled by hours of daylight. *J. lalandii* tanks were illuminated by indirect daylight at a level of 35 lux which is close to the level experienced at 15 m water depth at Oudekraal. The animals were thus

subjected to both diurnal and seasonal photoperiodicity under intensities as close to natural as possible.

Normal moulting can also be affected by food consumption. Hagerman (1983) observed that moulting decreased in *Homarus gammarus* when the quality of food deteriorated. To prevent this happening, mussels (*Choromytilus meridionalis*) which may form a dominant component in their diet (Pollock 1979a) were presented to each lobster in quantities exceeding their daily requirements. Their feeding rate subsequently was monitored regularly 5-7 times per week. When moulting occurred, the exuviae were carefully lifted from the tank and excess moisture removed by gentle tapping on paper towel.

Whole intermoult male lobsters and exuviae were oven dried at 60° C until constant mass was reached (up to 5 d). Small samples of intermoult exoskeletal material were oven dried following Lovegrove (1966). All samples were weighed and subsequently ground using a Wiley mill for large material or a Kinematica hammer-cutter mill fitted with a 0,5 mm screen for small samples. Subsamples were analyzed according to the following protocol. One fraction was heated in a muffle furnace to 450° C for 4 h in order to oxidize the organic carbon while not affecting the calcium carbonate remaining in the ash (Bligh *et al.* 1984). Elemental analyses using a Carlo Erba 1106 instrument

standardized to acetanilide, were carried out on a second fraction of the powder as well as on the ash for total carbon, hydrogen and nitrogen. The difference between the dry mass carbon and ash carbon measurements resulted in an organic carbon value. The factor of 47,70 $kJ.gC^{-1}$ after Platt and Irwin (1973) was used to convert carbon values to kiloJoules.

Exuvial dry mass can be derived from Equation 3.1, where Lobster Dry Mass = $0.000274 Carapace\ Length^{2,877}$, combined with the equation in Figure 7.1, to give

$$Exuvial\ Dry\ Mass = 0,12191^{0,168} Lobster\ Dry\ Mass. \quad (7.1)$$

In order to interpret results in terms of a natural population, data of Pollock (1978) were used from the lobster sanctuary at Robben Island. Size frequency counts for 14, 20 and 27m depths have been combined. Population figures have been expressed per 100 m^2 by applying the overall mean lobster density of 0,81 m^{-2}.

7.3. RESULTS AND DISCUSSION

In Table 7.1 comparative analyses of exuviae, fresh exoskeletons and whole *J. lalandii* are listed. The high wet mass of exuviae in relation to that of fresh exoskeletons is due to water retention in the legs and endophragmal system.

Table 7.1. Analyses of fresh exoskeleton, dry exuviae and whole *J. lalandii*. Energy (kJ) and elemental values are expressed in terms of dry mass

TISSUE	WM	DM	AFDM	O.C%	I.C%	N%	H%	*n*	kJg^{-1}	C:N
EXOSKELETON	1,49	1	0,46	17,34	5,71	3,88	3,45	7	8,27	4,47
EXUVIAE	3,6	1	0,33	12,47	6,21	2,95	2,21	3	5,95	4,23
WHOLE *JASUS*	3.1	1	0,74	35,51	2,01	9,90	6,35	3	16,94	3,59

Legend: WM = Wet Mass; DM = Dry Mass; AFDM = Ash-free Dry Mass; O.C = Organic Carbon; I.C = Inorganic Carbon; N = Nitrogen; H = Hydrogen.

A better correlation of exuviae to exoskeleton exists between their respective dry masses and should be used for comparative purposes. Figure 7.1 shows the power curve regression of exuvial dry mass against carapace length.

The ash content of exuviae constitutes 67 per cent of the dry mass. By comparison, Du Preez and Mclachlan (1983) recorded an exuvial ash content for the swimming crab, *Ovalipes punctatus* of 92,11 per cent. The living exoskeleton of *J. lalandii* contains only 54 per cent ash, but has an organic carbon content 28,1 per cent higher than exuviae, suggesting that reabsorption of carbon occurs prior to ecdysis.

Inorganic carbon content was similar in both tissues. If all the inorganic carbon is bound as calcium carbonate it represents 47,6 per cent of the fresh exoskeleton and 51,8 per cent of the exuviae. This small difference between the two tissues suggests that little transfer of calcium carbonate occurs prior to ecdysis. Nitrogen declined by 24 per cent from exoskeleton to exuviae, a similar percentage to carbon, suggesting that one is not reabsorbed preferentially to the other. The similar C:N ratios corroborate this.

In Figure 7.2 exuvial dry mass has been plotted against lobster dry mass. Throughout the observed size range,

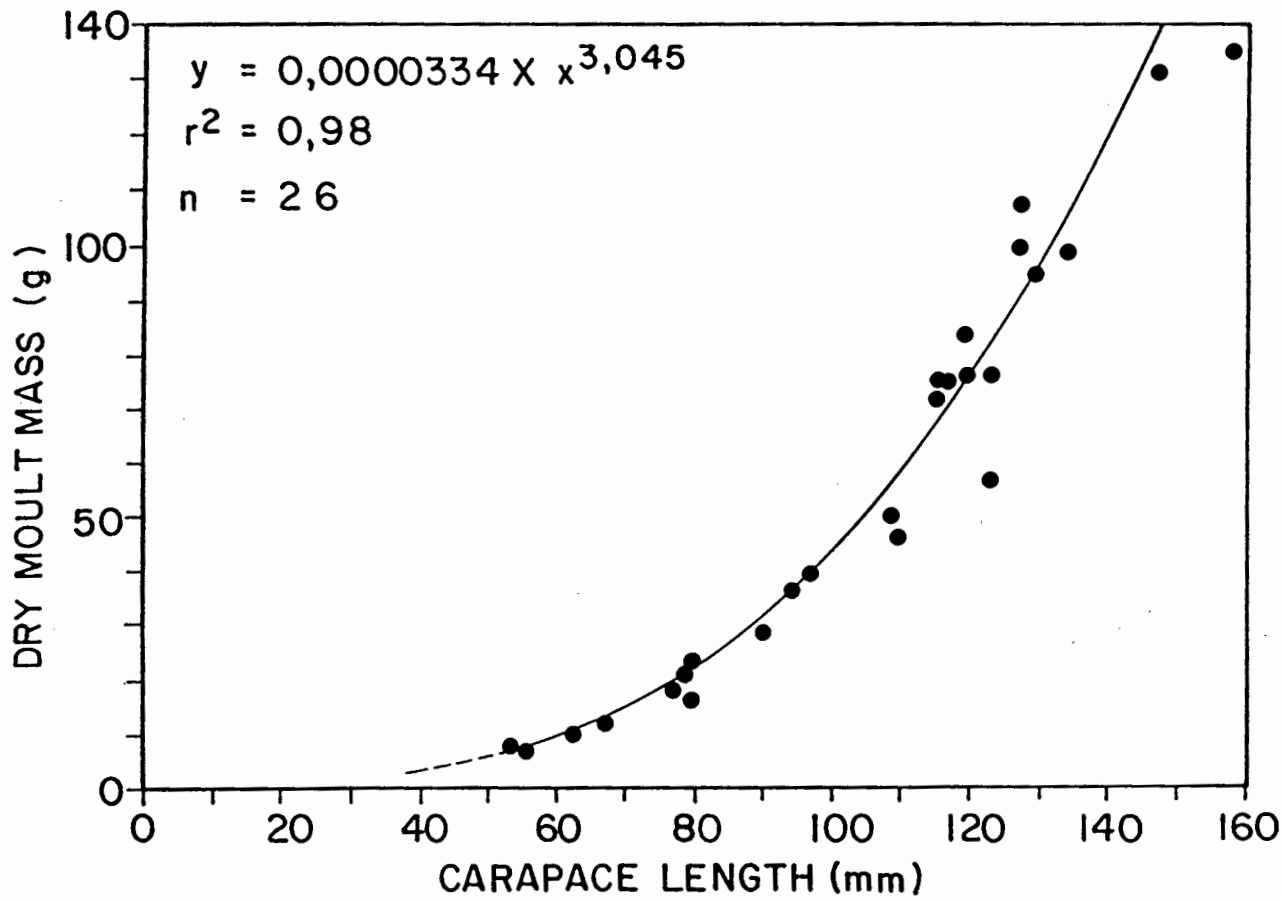

Figure 7.1. Exuvial dry mass regressed against carapace length

exuvial mass is linearly related to body mass. From the slope of the regression for Figure 7.2, the mean annual exuvial loss in *J. lalandii* may be accepted as approximately 27 per cent of animal dry mass.

Figure 7.3 illustrates by size class the proportion of the total dry mass which is lost annually through moulting in a population of *J. lalandii* from 100 m^2 at Robben Island. Greatest losses occur in the 70-80 mm carapace lengths where biomass is highest. The overall annual population loss amounts to 1,83 kg DM.100 m^{-2} or 18,3 g $DM.m^{-2}.yr^{-1}$, or an energy loss of 109 $kJ.m^{-2}.yr^{-1}$.

Under aquarium conditions exuviae have been observed to be consumed by other lobsters, even when the latter were fed *ad libitum*. Consumption of exuviae also occurs under field conditions (Heydorn 1969, Pollock 1978, Barkai and Branch 1988a). The remainder of the exuvial material is probably broken down by waves and remineralized through microheterotroph action.

Lobsters lose 8.7 per cent of their total body carbon and 7.4 per cent of their body nitrogen annually. This amounts to 228 g carbon and 53,7 g nitrogen per 100 m^2. The carbon probably has little environmental impact and the calcium carbonate contained in the exuviae even less where barnacle or bivalve shells are abundant (Velimirov *et al*

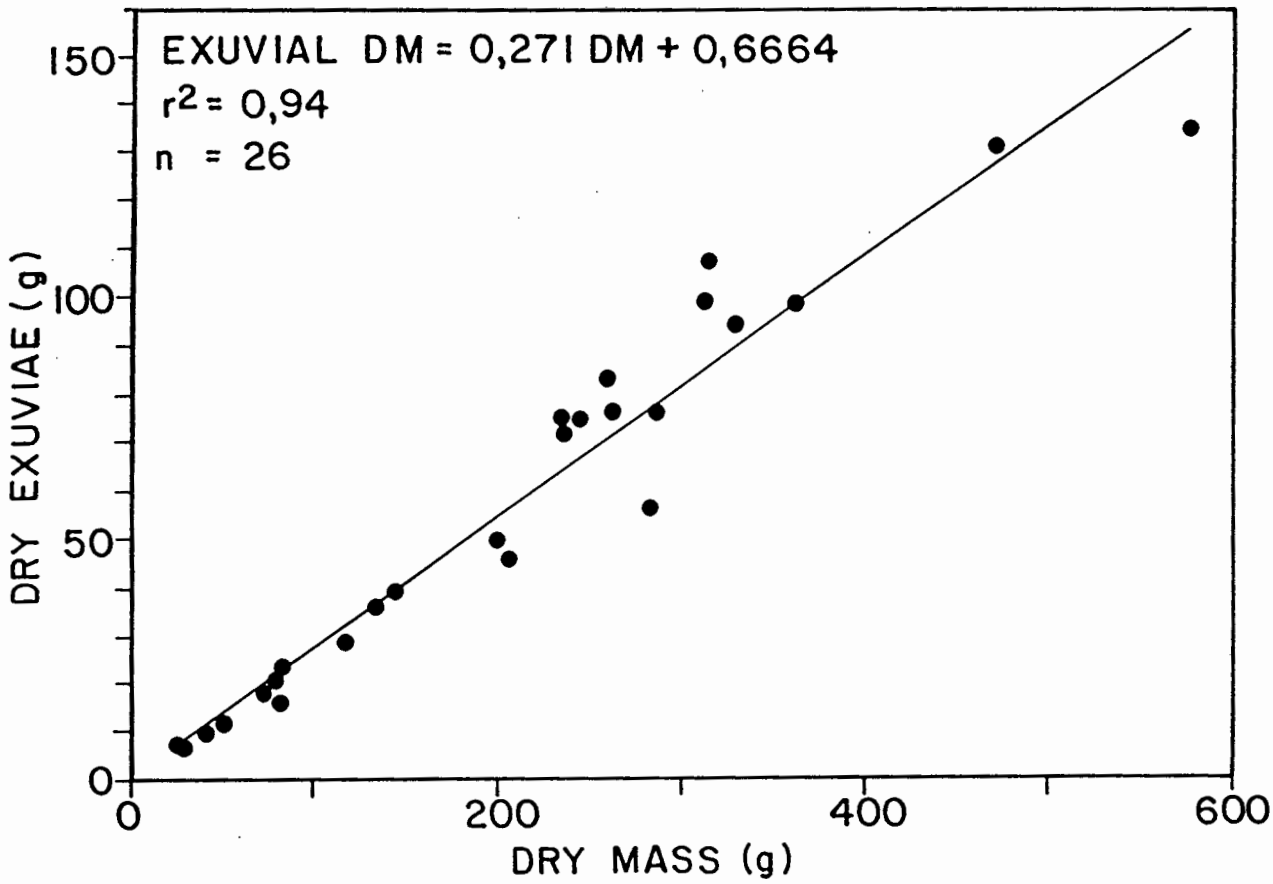

Figure 7.2. Exuvial dry mass regressed against whole lobster dry mass

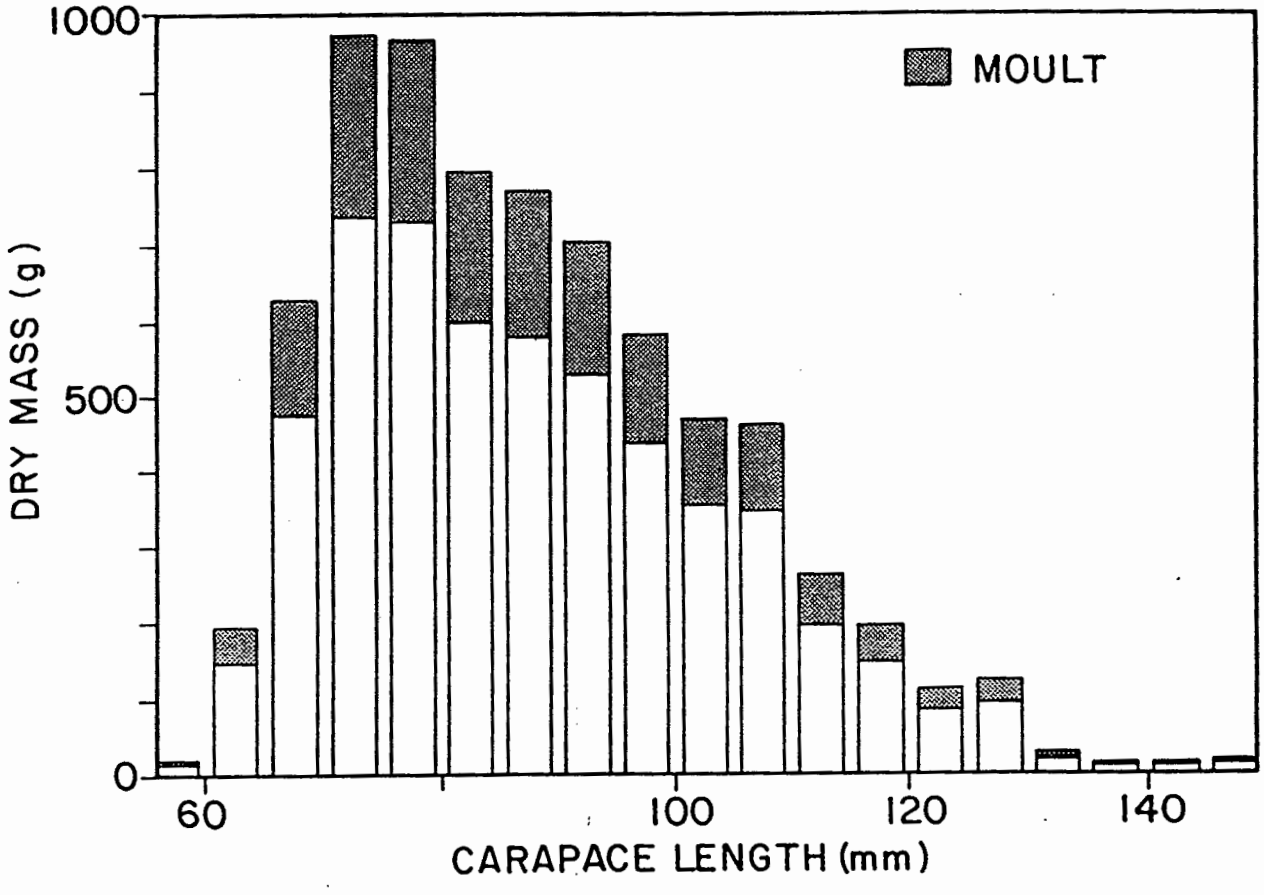

Figure 7.3. The proportion of the total dry mass lost annually through moulting in a population of *J. lalandii* from 100 m² off Robben Island

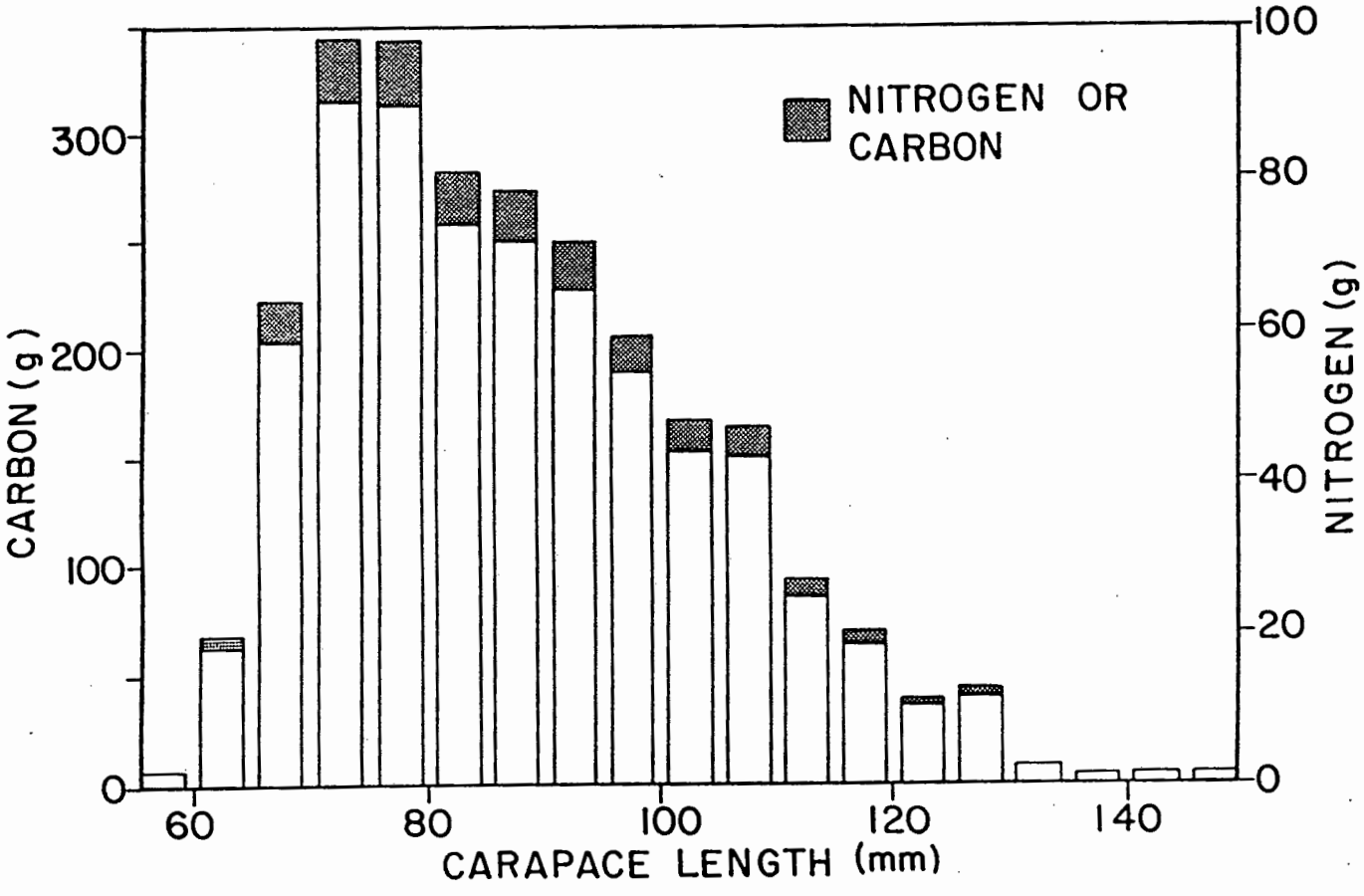

Figure 7.4. The proportion of the organic carbon and nitrogen lost annually through moulting in a population of *J. lalandii* from 100 m² off Robben Island

1977, Pollock 1979, Barkai and Branch 1988). The input of nitrogen to coastal water from exuviae amounts to 0,7 per cent of that required by the inshore primary producers (Chapter 5 based on Probyn and McQuaid 1985) and the impact is therefore also small. However, the annual cost of moulting to *J. lalandii* in terms of exuvial mass, which includes carbon and nitrogen, is considerable when viewed in terms of lost production (Chapter 6).

CHAPTER 8

GONAD OUTPUT IN TERMS OF CARBON AND NITROGEN BY THE CAPE ROCK LOBSTER *JASUS LALANDII*

8.1. INTRODUCTION

In general, reproductive biology in both clawed and spiny lobsters is well documented in the literature (Aiken and Waddy 1980a,b, Berry 1970, Chittleborough 1976, Farmer 1974, Gregory *et al.* 1982, Street 1969, Sutcliffe 1952, Templeman 1940). Berry and Smale (1980) estimated the energy content of gonad output at population level in the palinurid lobster *Panulirus homarus*. With regard to *Jasus lalandii* the anatomical, histological and, to a lesser extent, the functional aspects of reproduction are covered by Von Bonde (1936), Fielder (1964), Heydorn (1965, 1969), Paterson (1968, 1969b), Berry and Heydorn (1970), and Silberbauer (1971a,b). Reproductive biology in this species has also been studied in relation to fisheries management by Matthews (1962), Heydorn (1965, 1969), Newman and Pollock (1974b), Matthews and Smit (1979) and Beyers and Goosen (1987). There is, however, a marked gap in knowledge in relation to energetic cost of reproduction to the individual

and the output of energy from the population in the form of reproductive products.

Fecundity studies yield useful data regarding breeding costs to female lobsters. Matthews (1962) gives fecundity figures for *J. lalandii* from South West Africa/Namibia, while Heydorn (1965) gives a general account of biometrics of berried females along the west coast of South Africa. More recently Beyers and Goosen (1987) have made comparisons of female fecundity between ten major South African lobster grounds, while Barkai and Branch (1988a) have estimated the energy cost of ova production for female lobsters off Malgas Island, 58 naut. miles NNW of Cape Town. Heydorn (1965) used vas deferens mass per mille body mass in male *J. lalandii* as an index of reproductive potential. Due to the comprehensive nature of the published material, further collection of gonadal data was not necessary: by re-evaluating published data in the light of elemental analyses, it was possible to calculate the fluxes of reproductive carbon and nitrogen through *J. lalandii* at both individual and population levels, and to assess their impact on the ecosystem.

8.2. MATERIALS AND METHODS

Adult male and female *J. lalandii* were collected by SCUBA divers in the rock-lobster sanctuary at Oudekraal and

returned to the laboratory where the specimens were weighed, measured and chemically analyzed. Ova were removed from berried females, and testes, including vasa deferentia, were dissected from males. Wet to dry mass conversions were derived from the results of oven-drying at 60° C until constant dry mass was reached. Ash-free dry mass was determined by heating the samples to 450° C in a muffle furnace for 4 h after the method of Bligh *et al.* (1984). Carbon and nitrogen were determined in a Carlo Erba 1106 elemental analyzer standardized to acetanilide.

Data from Pollock (1978) have been used to illustrate the costs of reproduction in terms of carbon and nitrogen in *J. lalandii* for a population off Robben Island. Size-frequency counts for 14, 20 and 27 m depths were combined and standardized per 100 m^2 by applying the mean density of lobsters present i.e. 0,81 m^{-2} (Pollock *op. cit.*).

8.3. RESULTS AND DISCUSSION

8.3.1. Fecundity in *Jasus*

Because an ovum represents a biological unit as opposed to expressing fecundity in terms of mass, authors usually express results as numbers of eggs. The relationship between the number of eggs carried by a female and her size (carapace length (CL)) is best represented by an allometric equation of the type seen in Table 8.1.

Table 8.1. Constants (a) and coefficients (b) for regressions of ova numbers or wet mass on carapace length (CL) calculated from data of Heydorn (1965) for *J. lalandii* and Kensler (1968) for *J. edwardsii*.

Ova (No. or Wet Mass) = a.Carapace Length^b

NO.	REGRESSION	a	b	*n*	r^2
1	*J. lalandii* Ova No. on CL (mm)	0,0136	3,58	8	0,93
2	*J. lalandii* Ova WM on CL (mm)	0,000392	2,593	10	0,73
3	*J. edwardsii* Ova No. on CL (mm)	0,692	2,685	14	0,94

In Figure 8.1 regressions of egg numbers on carapace length have been plotted for *J. edwardsii* (data *ex* Kensler 1968), and for *J. lalandii* (data *ex* Beyers and Goosen 1987 (1) and Heydorn 1965 (2)). Regression (1) for *J. lalandii* by Beyers and Goosen (*op. cit.*) is for Robben Island where lobsters enjoy a high level of available food, as opposed to the general level represented by (2). It can be seen that for a set CL, Robben Island females may carry up to 84 per cent more eggs than predicted by Regression (2). When developing the concept of gonad production in terms of carbon and nitrogen, it is important to remember that Robben Island female lobsters exhibit a substantially higher fecundity than females in other regions.

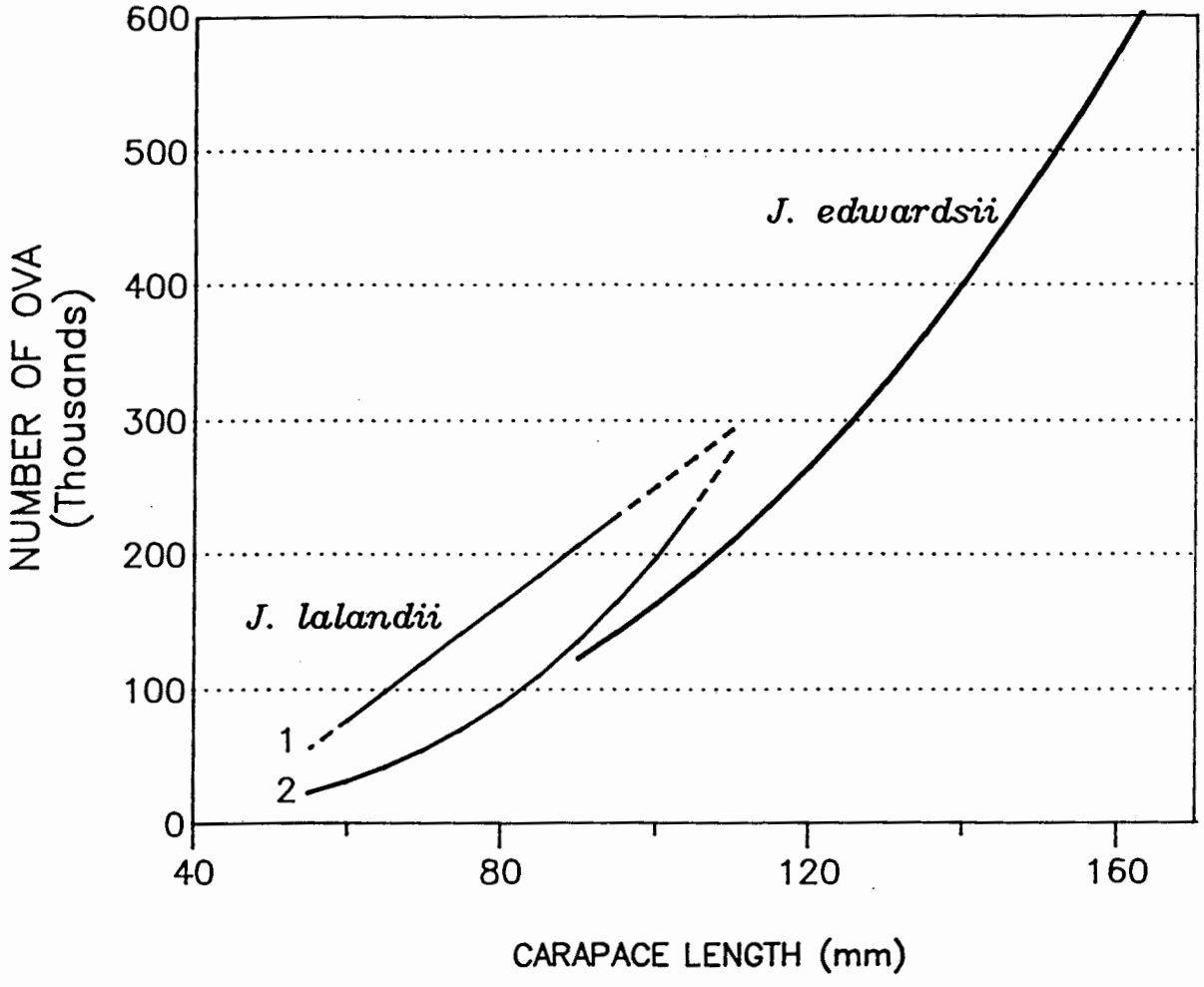

Figure 8.1. Comparison of regressions of ova numbers on carapace length in *J. lalandii* from the formula of (1) Beyers and Goosen (1987) where Ova No.=4312.CL-181932, and the data of (2) Heydorn (1965), and in *J. edwardsii* from data of (3) Kensler (1986). (See Table 8.1 for other equations)

8.3.2. Ova counts in terms of mass

Table 8.2 lists the mean and range for ovum mass from a number of sources for the genus *Jasus*. Ovum mass exhibits a wide range inter-specifically from a minimum of 0,112 µg in *J. verreauxi* to a maximum of 0,507 µg in one of the estimates for *J. lalandii*. The intra-specific range for *J. lalandii* is somewhat less (0,213-0.507 µg), but is still surprisingly high. Variability in range may occur as a function of lobster size as in *J. verreauxi*, with smaller lobsters laying larger ova (Kensler 1967), or as a function of ovum age where shrinkage occurs with time.

Table 8.2. Mean ovum mass for *J. lalandii* compared with *J. edwardsii* and *J. verreauxi*

	SPECIES	NO. OVA $g^{-1}$of eggs	MEAN MASS µg.OVUM^{-1}	RANGE OVA (µg)
A	*J. lalandii*	2621	0,381	0,306-0,507
B	*J. lalandii*	4541	0,221	0,213-0,228
C	*J. edwardsii*	4412	0,227	0,200-0,282
D	*J. verreauxi*	7388	0,135	0,112-0,155

Legend: A = Data ex Heydorn (1965). B = Data ex present study. C = Data ex Kensler (1968). D = Data ex Kensler (1967)

However, range may also be the result of an artefact in measurement, where sub-sampling and the presence of interstitial water can lead to imprecise prediction of egg mass. Ovum wet mass in Table 8.2 was derived from predicted ova numbers and mass shown in Figures 8.1 and 8.2, and from

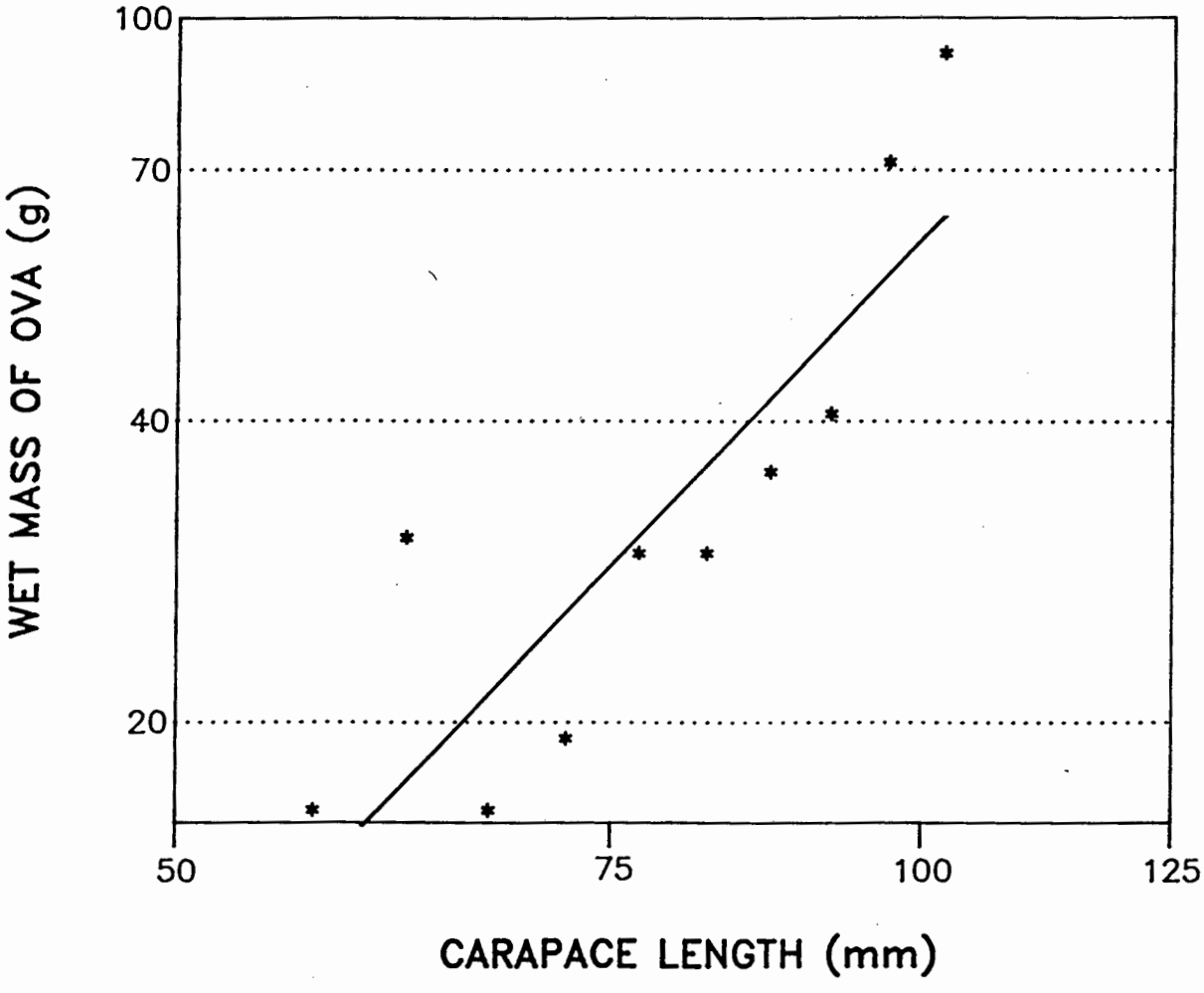

Figure 8.2. Regression of ova wet mass on carapace length in *J. lalandii* from data of Heydorn (1965). (See Table 8.1 for equation.)

the relevant formulae in Table 8.1. The wide range of predicted ova mass may in part be due to the scatter of data which has a low r^2 value of 0,73 (Table 8.1). For this reason it was decided to use the mean ovum value of (B) in Table 8.1 (Data from present study) for further prediction of berry mass from ova counts. This does not, however, imply that superior methods were employed in deriving this value.

8.3.3. Seminal fluid

Estimation of female fecundity is readily open to direct mensuration, whereas estimation of annual output by the testes in the form of spermatophores and/or seminal fluid is more difficult to determine. Although direct measurements would be ideal, available literature provides sufficient evidence upon which to base reasonable assumptions about both the female and male reproductive output. Firstly, mature female *J. lalandii* undergo only one moult and reproductive cycle per annum (Heydorn 1969). Observations by Gilchrist (1913) and von Bonde (1936) confirm that mating takes place after ecdysis and before the new exoskeleton hardens. Aiken and Waddy (1980a) suggest that female moulting, mating and egg extrusion in *J. lalandii* may take place within a few days as is the case in *J. edwardsii* described by Sorensen (1969). Multiple matings have been recorded by Berry (1970) for *Panulirus homarus*. However, in the absence of similar evidence for male *J.*

lalandii during the female post-moult soft phase, and with an approximately equal sex ratio (Pollock 1978), it has been assumed that mating therefore occurs on an average only once per mature male per annum.

Heydorn (1965) uses the combined mass of the two vasa deferentia to give a measure of reproductive potential. In males of CL=150 mm, at the upper end of the size range, the vasa deferentia make up approximately 0,3 per cent of body mass. If half of this mass consists of seminal fluid and mating only takes place once a year, then the annual loss would be only 0,15 per cent of body mass. Seminal fluid loss can thus be estimated from Figure 8.3 where vas deferens mass has been plotted on CL for a size range of mature *J. lalandii* (Data *ex* Heydorn 1965).

8.3.4. Cost of reproduction in terms of C and N

Table 8.3 summarizes mass conversions and elemental analyses of seminal fluid and ova for *J. lalandii*. Using these values it is possible to express wet mass of both male and female products in terms of carbon and nitrogen. In Figure 8.4 equations from Table 8.2 and Figure 8.3 have been combined with factors from Table 8.3 to convert wet mass of ova and seminal fluid to carbon and nitrogen and to plot them per size class for *J. lalandii*. As expected from the allometric equations used, the increase in ova carbon and nitrogen is exponential, reaching 5,6 g carbon and 1,3 g

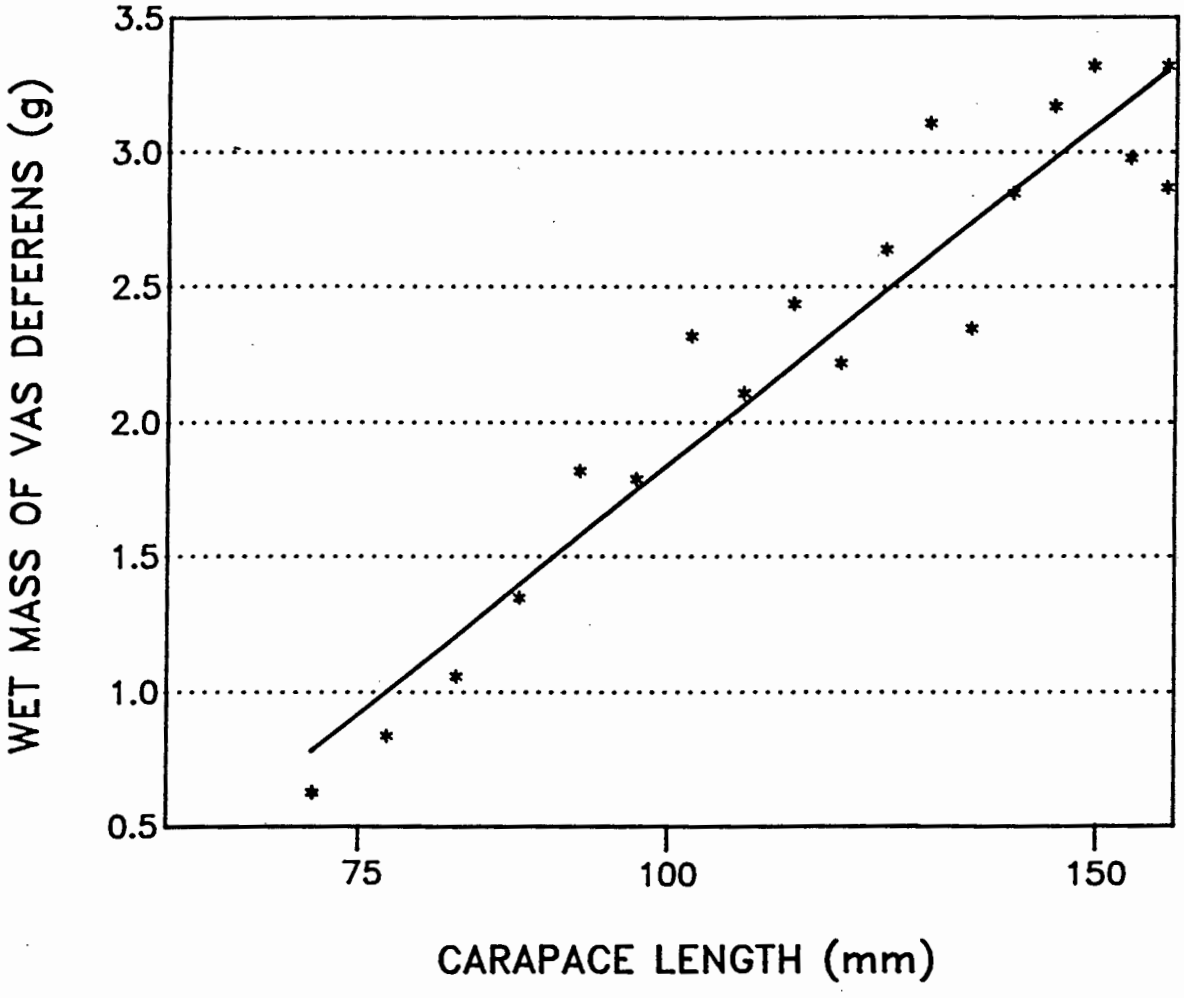

Figure 8.3. Regression of vas deferens wet mass on carapace length for *J. lalandii* where

Vas deferens WM (g) = 7,414.LogCL - 12,983

(n = 18; r^2 = 0,90)

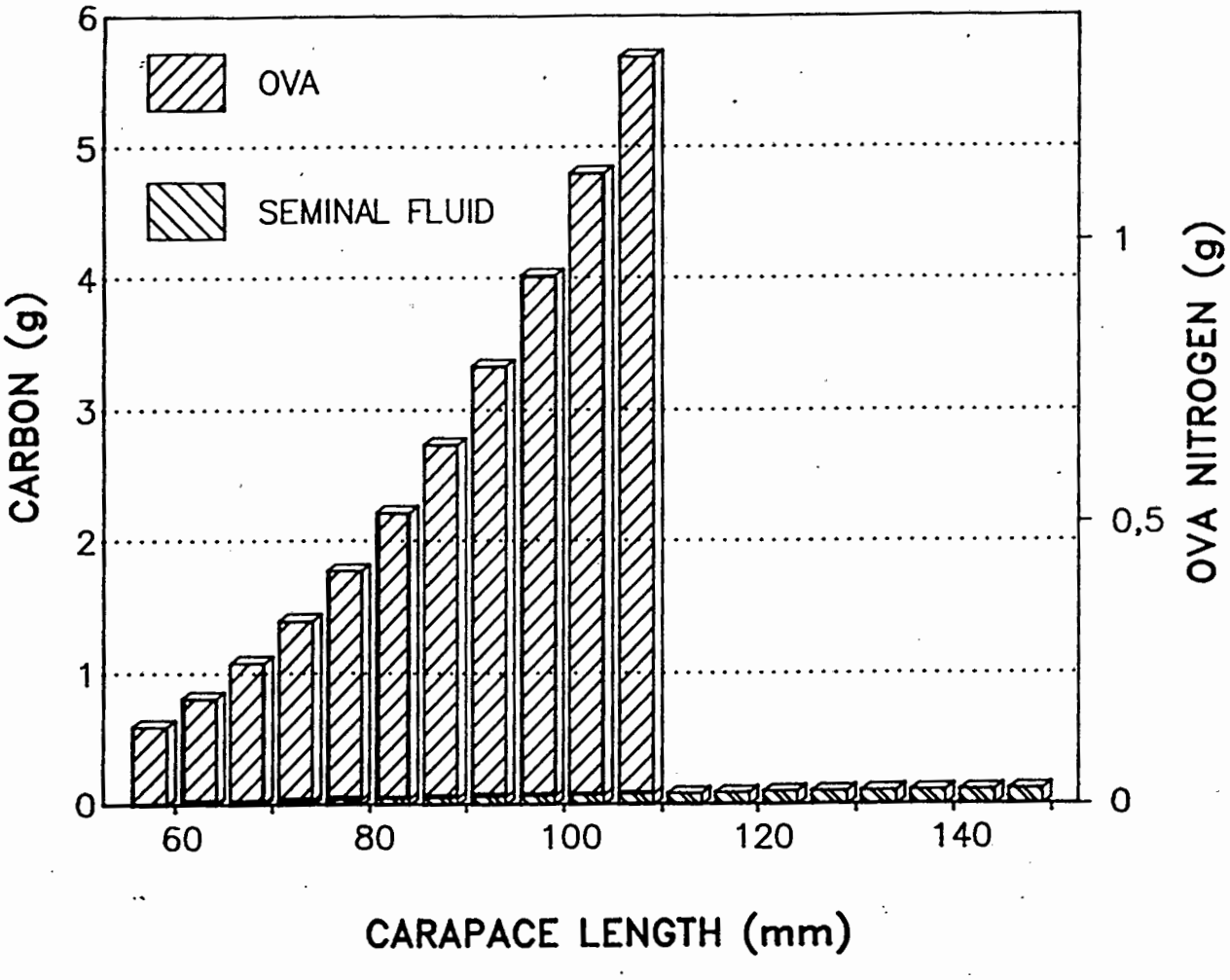

Figure 8.4. Costs in terms of carbon per size class of male and female *J. lalandii* and of nitrogen for females. (Size-class values calculated from equation (2), Table 8.2 and from Figure 8.3)

nitrogen in the 105-109 mm CL size class. Up to a size of 110 mm CL ova account for 98-99,6 per cent of combined male and female reproductive carbon. There are no data for egg-bearing females >110 mm CL, but females above this size are rare (Pollock 1978) and so, in terms of population energetics, the contribution of ova from females above this size will be non-existent or insignificant.

Table 8.3. Mass conversions, energy content and elemental analyses of dried seminal fluid and ova of *J. lalandii*

	WM	DM	AFDM	O.C%	I.C%	N%	kJ.gDM^{-1}	C:N
SF	5,25	1	0,83	40,11	0,06	10,70	19,43	3,75
OVA	4,83	1	0,91	48,32	0,03	11,20	20,36	4,31

Legend: SF = Seminal fluid; O.C = Organic carbon; I.C = Inorganic carbon

In males the amounts of carbon and nitrogen in the seminal fluid are small, but increase slowly as CL goes up, reaching 0,12 and 0,032 g respectively in the 145-149 mm CL size class.

8.3.5. Differences between sexes in reproductive and somatic production

Although small differences in consumption rates between male and female lobsters of the same size may exist as a result of reduced foraging by females while in berry, it is assumed that these differences are not significant. The

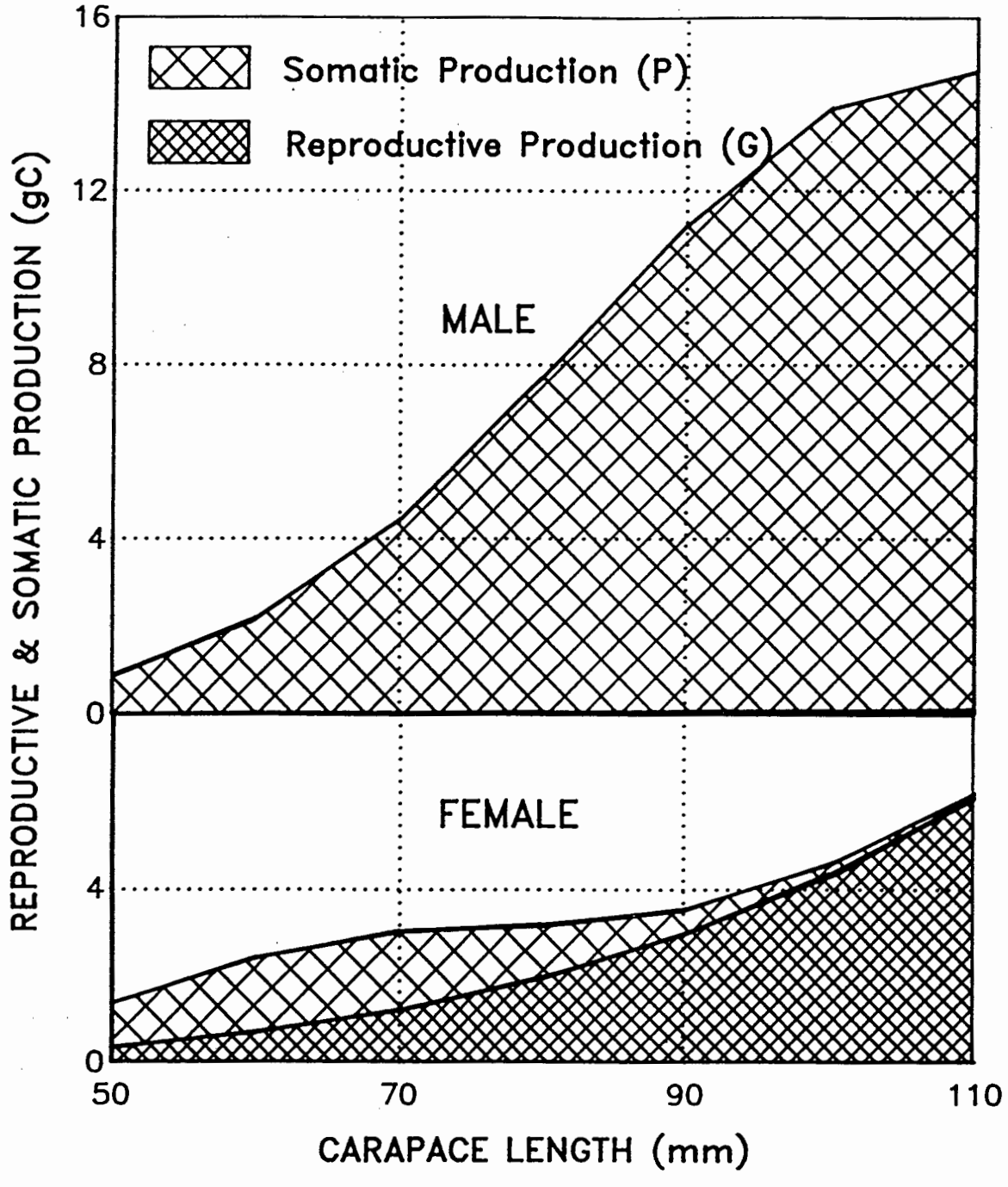

Figure 8.5. A comparison of reproductive and somatic production ($gC.yr^{-1}$) between male and female *J. lalandii* for the size range of mature females. (Ova carbon mass calculated from Equation 1 in Table 8.1; Male reproductive production is so small it is scarcely detectable at this scale)

question arises whether reproductive and somatic production when taken together, are similar for mature male and female lobsters. Figure 8.5 shows the reproductive and somatic production for both sexes within the size range of mature females. Differences in rates and the aportionment of production are marked. Up to 60 mm CL the somatic production in males and females is similar. Thereafter the rate of male somatic production accelerates while that of females first levels then declines.

Combined somatic and reproductive production in males exceeds that of females, with 99 per cent being contributed by somatic growth. In females as reproductive output increases, so there is a decrease in somatic growth, which approaches zero at 110 mm CL. The average combined reproductive and somatic growth in females is only 43 per cent that of males. Why is it that female gross production does not parallel that of males? Possibly it is wrong to assume that males and females consume equal quantities of food, but a more feasible explanation may be that females expend more energy in ova ventilation and maintenance during the three-month incubation period. This is substantiated by Beusa (1979) who has shown for a berried female *Panulirus argus*, where the ova constitute 12 per cent of the total lobster mass, the metabolic rate is 1,6 times higher than an equivalent unberried female. This aspect warrants further investigation. In any event, it no longer appears possible

to attribute the difference between male and female growth rates to egg production alone. The magnitude of the difference greatly exceeds that explainable by the diversion of energy and materials into the production of eggs.

The partitioning of carbon between somatic and reproductive production can be explored in another way. Grahame and Branch (1985) in their review of reproductive patterns of marine invertebrates state that the relative amount of resource channelled into reproduction in many organisms increases with age. This is true of *J. lalandii* as seen in Figure 8.6, where the mass of carbon allocated to reproduction increases relative to lobster size (age) over the full range of carapace length, while that allocated to growth reaches a maximum followed by a decline, which approaches zero at 110 mm CL in females. Using the formula where

$$\text{Reproductive Effort} = \frac{\text{Gonad (C)}}{\text{Gonad (C)} + \text{Growth (C)}} \times 100$$

it is seen that reproductive effort increases with size in both sexes, but the percentages differ markedly. In males it reaches two per cent at 150 mm CL while in females it is 99,6 per cent at 110 mm CL. Therefore in both sexes reproductive effort increases with size (age) as the chance of individual survival drops.

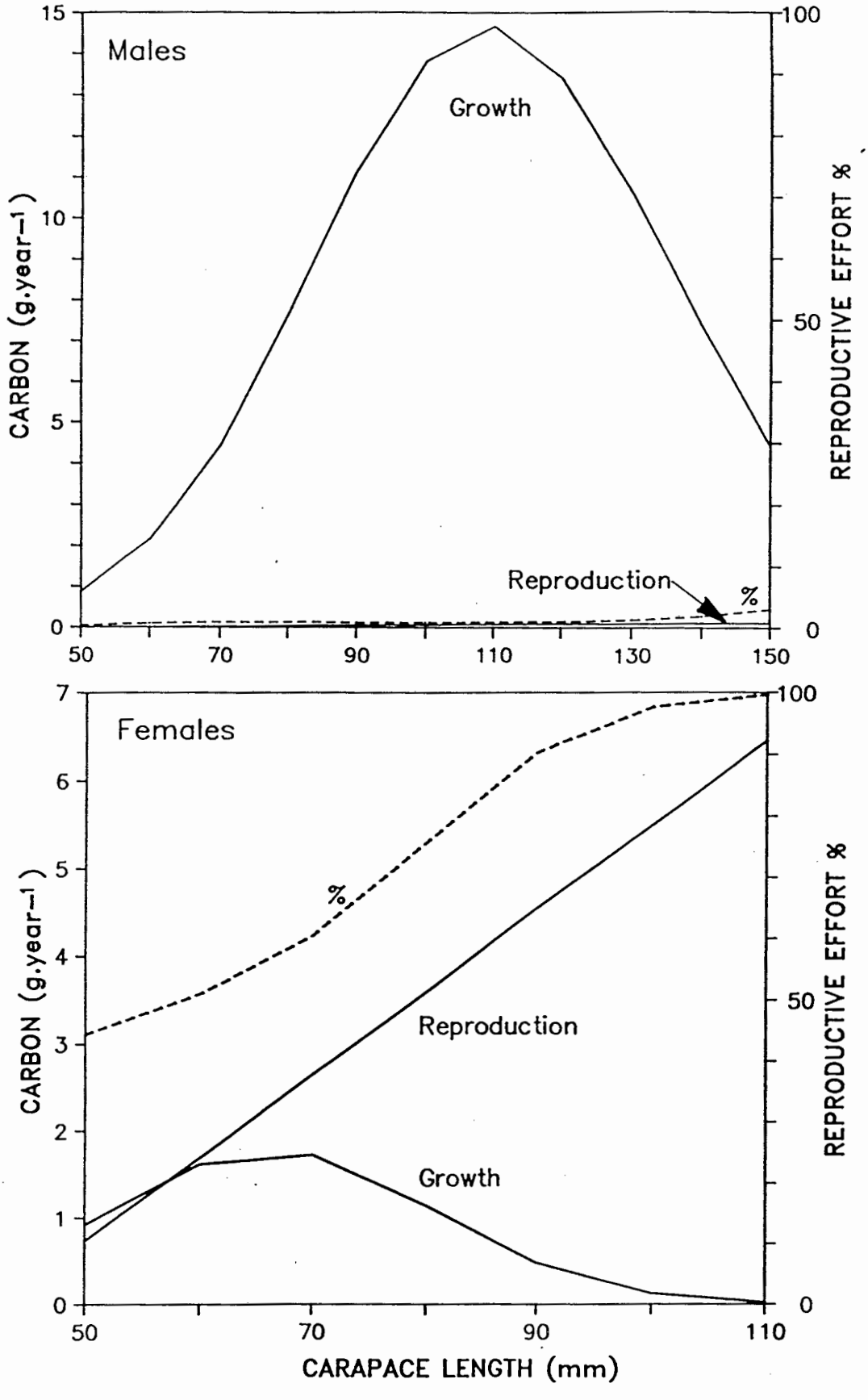

Figure 8.6. Cabon allocated to reproduction and growth, and reproductive effort in male and female *Jasus lalandii*

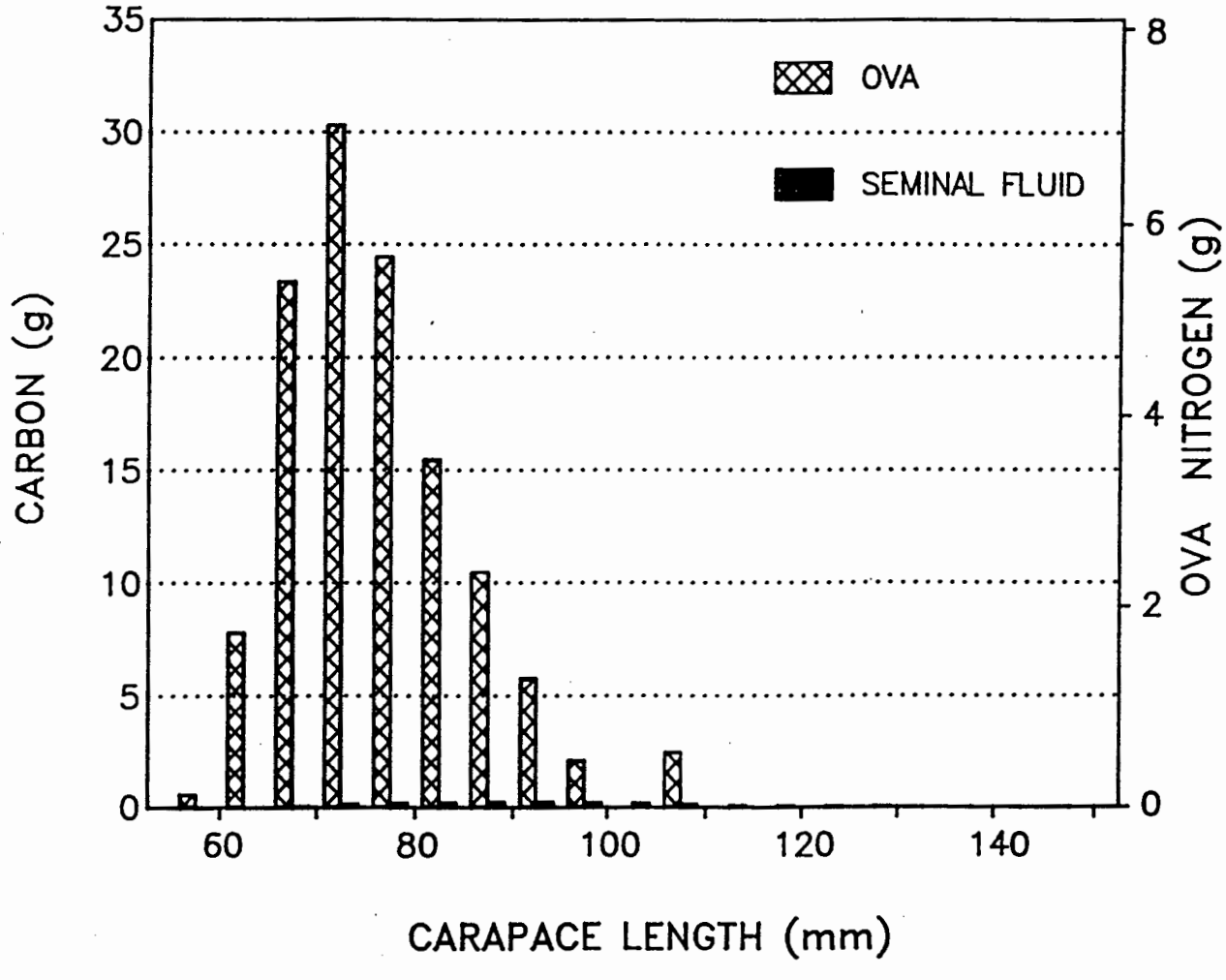

Figure 8.7. Carbon released annually as reproductive products by a population of *J. lalandii* in 100 m² area off Robben Island

8.3.6. Reproduction costs at population level

Figure 8.6 illustrates the cost of reproduction per annum in a rock lobster population occupying 100 m^2 off Robben Island. The peak of ova carbon and nitrogen mass is skewed to the left, with the maximum output occurring in the 65-85 mm CL size classes, while in males the maximum output of seminal fluid, which is very small, occurs between 80-105 mm CL. This amounts to only 2,113 g carbon and 0,56 g nitrogen. In total, 123 g carbon and 28,5 g nitrogen are produced by females 100 $m^{-2}.yr^{-1}$ off Robben Island. This represents $5,58x10^6$ ova. In contrast Berry and Smale (1980) reported for females of the warm-water lobster *Panulirus homarus*, only 36,6 g carbon 100 $m^{-2}.yr^{-1}$ on a shallow reef off Durban. This lower value is a consequence of population density rather than fecundity.

J. lalandii larvae after hatching become part of the plankton. Field *et al.* (1980a,b) have shown that in the nearshore Benguela system water can turn over 3-7 times 24 h^{-1} during upwelling. As hatching takes place in spring when the south-east wind is dominant, it is expected that a large proportion of the larvae will be exported from the nearshore system. Thus the loss to the ecosystem, through reproduction with ova hatching, can be as high as 123 g carbon and 28,5 g nitrogen 100 m^{-2}. The reproductive output of *J. lalandii* can therefore play only a minimal rôle in the system as it is lost through export.

CHAPTER 9

DISCUSSION

9.1. Ecosystem energetics

Ecosystem energetics involves quantifying rates and establishing the pathways of energy flow within individuals and between populations in a defined area (the ecosystem). The energy source is usually of solar origin and in the form of visible radiation which is transformed into chemical energy by autotrophs. The rate of transfer of energy within an ecosystem depends on the efficiency with which populations exploit their food and convert it to biomass. The ultimate fate of the original radiant energy input is heat output to the environment as the end product of respiration.

At ecosystem level the impact of lobsters has been investigated by Breen and Mann (1976) and Mann (1977), among others, in the Canadian east-coast kelp beds. In the infraorder Astacidea some work has been done on the freshwater crayfish *Orconectes*, which has emphasized their feeding habits and effects on plant communities (Lorman and Magnuson 1978), and their rôle in the regulation of benthic production in relation to fish (Momot and Gowing 1978). In

the spiny lobsters Pollock (1979) looked into the predator-prey relationship between *J. lalandii* and the ribbed mussel *Aulacomya ater* off the west coast of South Africa. Robles (1987) studied the effects of foraging by *Panulirus interruptus* on populations of the mussel *Mytilus californianus* off the coast of California and, recently, work by Barkai and Branch (1988) has highlighted the utilization of alternative food resources by *J. lalandii*. General models quantifying energy flow through the nearshore Benguela system have been constructed by Newell *et al.* (1982), Newell and Field (1983), and Wulff and Field (1983). However, little work has been done on the quantification and flux of energy or elements through lobster populations in relation to the ecosystem.

9.2. The nearshore Benguela system

The importance of the Benguela current along the west coast of southern Africa in determining the extensive fish stocks and the nearshore biotic communities, has been recognized for a considerable time. Origin of the water masses which constitute the current and the forces regulating its dynamics have been the subjects of intensive research. Clowes (1950) synthesized much of the early work which resulted in the first over-view of the physical features of the current. Hart and Currie (1960) described regional differences in the current linked to meteorological conditions. Recently Shannon (1985) has given a

comprehensive review of the physical aspects of the Benguela current, while Chapman and Shannon (1985) have reviewed the chemistry and related processes. The presence of low-oxygen water, which holds particular significance for rock lobsters, has been described by Bailey *et al.* (1985) and Pollock and Shannon (1987).

The nearshore Benguela system is characterized by extensive kelp beds which are dominated by the macrophytes *Ecklonia maxima* and *Laminaria* spp., thriving in the cool (8-16° C) nutrient-rich upwelled waters. Heavy Atlantic swells are attenuated by these kelps which create an environment which supplies food and shelter for many organisms. This kelp-bed ecosystem was the focus of an intensive multi-disciplinary research programme carried out during the second half of the nineteen seventies and the beginning of the eighties. Field *et al.* (1977) gave an overview of the interaction between physical and biological elements of the system. Variations in structure and biomass at a number of sites along the south-west Cape coast were described by Field *et al.* (1980a), while Velimirov *et al.* (1977) elaborated on the biotic associations within the system. Field *et al.* (1980b,c) quantified rates of interchange between kelp beds and the adjacent water mass, showing that residence time of water in the kelp beds during upwelling was short and varied from 3 to 8 hours. An overview of the nearshore Benguela system covering the coastal zone, which

is essentially linked to the kelp-bed system, is comprehensivly covered and documented by Branch and Griffiths (1988).

9.3. The rôle of *J. lalandii* in the nearshore Benguela system

It is into this nearshore Benguela or kelp-bed ecosystem that *J. lalandii* fits as a predator and omnivorous consumer. Pollock (1978) has described from stomach contents the range of food taken. This is represented diagrammatically in Figure 9.1, where inputs into the apex occupied by *J. lalandii* are transferred by feeding from other levels of the inverted pyramid. Recently Barkai and Branch (1988a) have shown that *J. lalandii* off Malgas Island, 58 naut. miles NNW of Cape Town, is capable of exploiting a range of alternative food resources, including the barnacle *Notomegabalanus algicola*.

The base of the pyramid in Figure 9.1 resides in the sun-lit zone where solar energy is fixed by macrophytes and phytoplankton. At the opposite end, the extreme apex represents the annual yield harvested by the fishing industry, currently 3 860 tonnes yr^{-1}.

The present study has examined energy flow through *J. lalandii* at three levels; the individual, the population and the ecosystem. Understanding the first two makes interpretations in terms of the third possible. Table 9.1

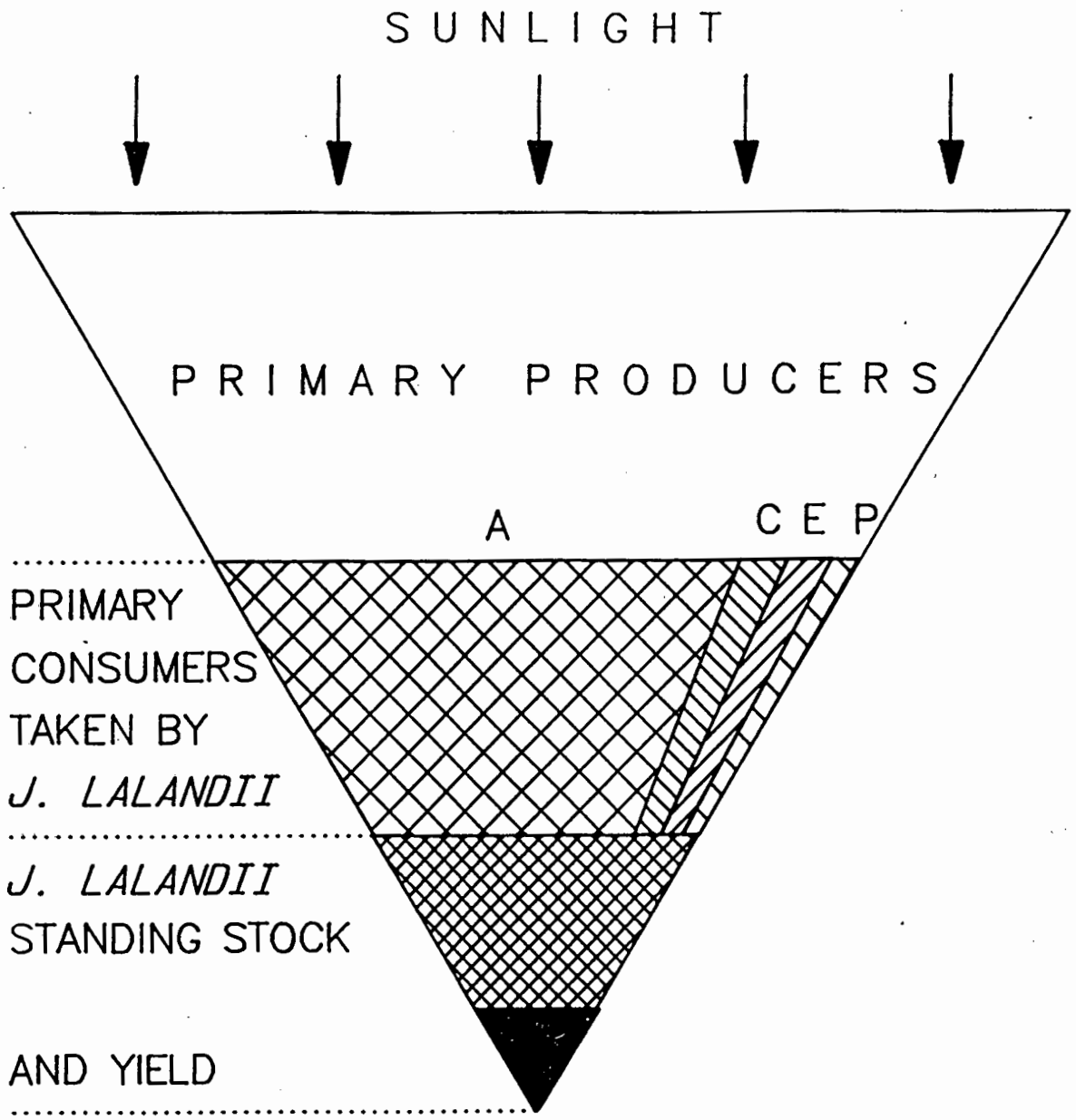

Figure 9.1. A schematic view of the position of *J. lalandii* in the nearshore Benguela system. *Jasus* feeding is from percentage food occurrence in stomach contents, from data by Pollock (1978). Cannibalistic input has been omitted. Legend: A = *Aulacomya ater*; C = Crustacea; E = echinoderms; P = polychaetes

Table 9.1. Summary of formulae used to calculate carbon and nitrogen values from carapace length (CL) in millimetres, for the components of the energy flow equation. All mass measurements are in grams and for rates the period is one year

COMPONENT	FORMULA	SOURCE
JASUS whole		
Wet Mass	$WM = 0,0008494CL^{2,877}$	3&7
Dry Mass	$DM = 0,000274CL^{2,877}$	3
Ash-Free DM	$AFDM = 0,0002028CL^{2,877}$	3&7
Carbon	$C = 0,0000973CL^{2,877}$	3&7
Nitrogen	$N = 0,00002713CL^{2,877}$	3&7
FOOD		
Total	$T_C = 0,5984DM$	3
	$T_N = 0,1579DM$	3
Messy Feed. (loss)	$MF_C = 0,1193DM$	2
	$MF_N = 0,03185DM$	2
CONSUMPTION (C)	$C_C = 0,479DM$	3
	$C_N = 0,1264DM$	3

Table 9.1 (continued)

COMPONENT	FORMULA	SOURCE
PRODUCTION (P)	$P_{MC} = 0,0000973(CL+8,131e^{-0,0006516(CL-96,844)^2})^{2,877}-C$	6
	$P_{FC} = 0,0000973(CL+2,568e^{-0,002155(CL-60)^2})^{2,877}-C$	6
	$P_{MN} = 0,279P_{MC}$	6
	$P_{FN} = 0,279P_{FC}$	6
FAECES (F)	$F_C = 0,0982DM$	2
	$F_N = 0,0176DM$	2
RESPIRATION (Standard) (R)	8° C; $R_C = 0,6259WM^{0,6834}$	4
	10° C; $R_C = 0,8935WM^{0,6519}$	4
	13° C; $R_C = 0,2996WM^{0,8543}$	4
	16° C; $R_C = 0,8649WM^{0,777}$	4
	19° C; $R_C = 0,4193WM^{0,9102}$	4
GONAD (G)	$G_{MC} = 0,283LogCL-0,496$	8
	$G_{FC} = 0,0953CL-4,021$	8
	$G_{MN} = 0,267G_{MC}$	8
	$G_{FN} = 0,232G_{FC}$	8

Table 9.1 (continued)

COMPONENT	FORMULA	SOURCE
EXCRETA (U)	$U_{XN} = 0,01235DM$	5
U-Exogenous U-Endogen.	$U_{DN} = C_N-P_N-G_N-U_{EN}-F_N$	5
U-Exuviae	$U_{EC} = 0,00000416CL^{3,045}$	5
	$U_{EN} = 0,236U_{EC}$	5

Legend: Subscripts- $_C$ = Carbon; $_D$ = Endogenous; $_E$ = Exuviae; $_F$ = Female; $_M$ = Male; $_N$ = Nitrogen; $_X$ = Exogenous; Source = chapter numbers

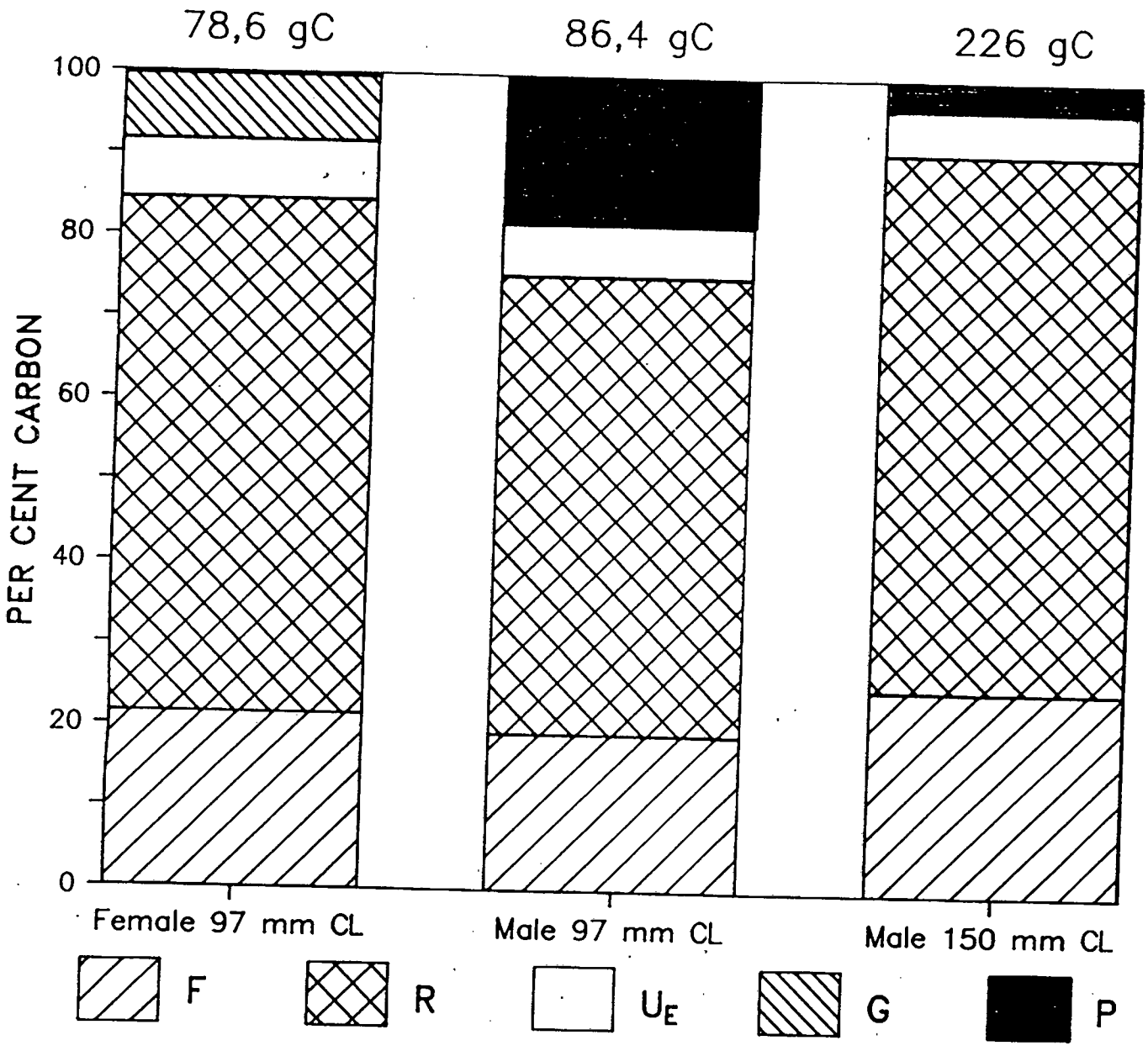

Figure 9.2. Carbon budgets for male and female *J. lalandii* of moderate size (97 mm CL) and for a large male (150 mm CL), expressed as percentages of their annual requirements

Legend: F = faeces, G = gonad, P = production, R = respiration, U_E = excretion (exuviae).

efficiency (A/C) is directly linked to faecal production and has a mean value of 79,5 per cent (Chapter 2). This is very close to the average value of 80 per cent for carnivores given by Bradfield and Llewellyn (1982).

Moulting results in a mean loss of 27 per cent of body dry mass per year of which 8,7 per cent is organic carbon (excluding carbonate carbon). The relationship of exuvial DM to body DM is linear and is not mass dependent (Chapter 8). During the moult cycle feeding ceases for an average of 78 d. In this period production is negative due to the demands of metabolism. Moulting therefore has a marked effect on production and may largely be responsible for the lower-than-average value of 0,16 per annum in *J. lalandii* when compared with the mean value of 0,22 for poikilotherms predicted by Brafield and Llewellyn (1982). Ecdysis, followed by the "soft-shelled" condition, results in increased susceptibility to predation (Chapters 6 and 8).

Respiration represents the largest component of the budget with 56-66 per cent of the carbon being committed in this way. Respiration rate is mass dependent which results in large lobsters metabolizing at a relatively slower rate per unit body mass compared to small individuals. The rate of respiration is affected by the environmental temperature, which, with a Q_{10} value of 2.5 over the temperature range of

8-19° C, can result in a wide variability of carbon consumption rates during a year (Chapter 4).

Important differences exist in the proportions of carbon channelled into gonad output and growth. In the female, not only is the combined somatic production and gonadial output less than half that of a male of same size, but the proportions of production and gonadial output are reversed. As discussed in Chapter 6, the additional carbon devoted to growth in males far exceeds the carbon channelled into ova by females, so that the enhanced growth exhibited by males cannot be explained solely by their lower reproductive costs. From evidence by Beusa (1979), the difference may be accounted for by the higher respiration rate in females during the three-month incubation period (see Chapter 6). Reproductive effort increases with size in both sexes, but the percentages differ markedly. In males it reaches two per cent at 150 mm CL while in females it is 99,6 per cent at 110-mm CL. Therefore in both sexes reproductive effort increases with size (age) as the chance of individual survival drops.

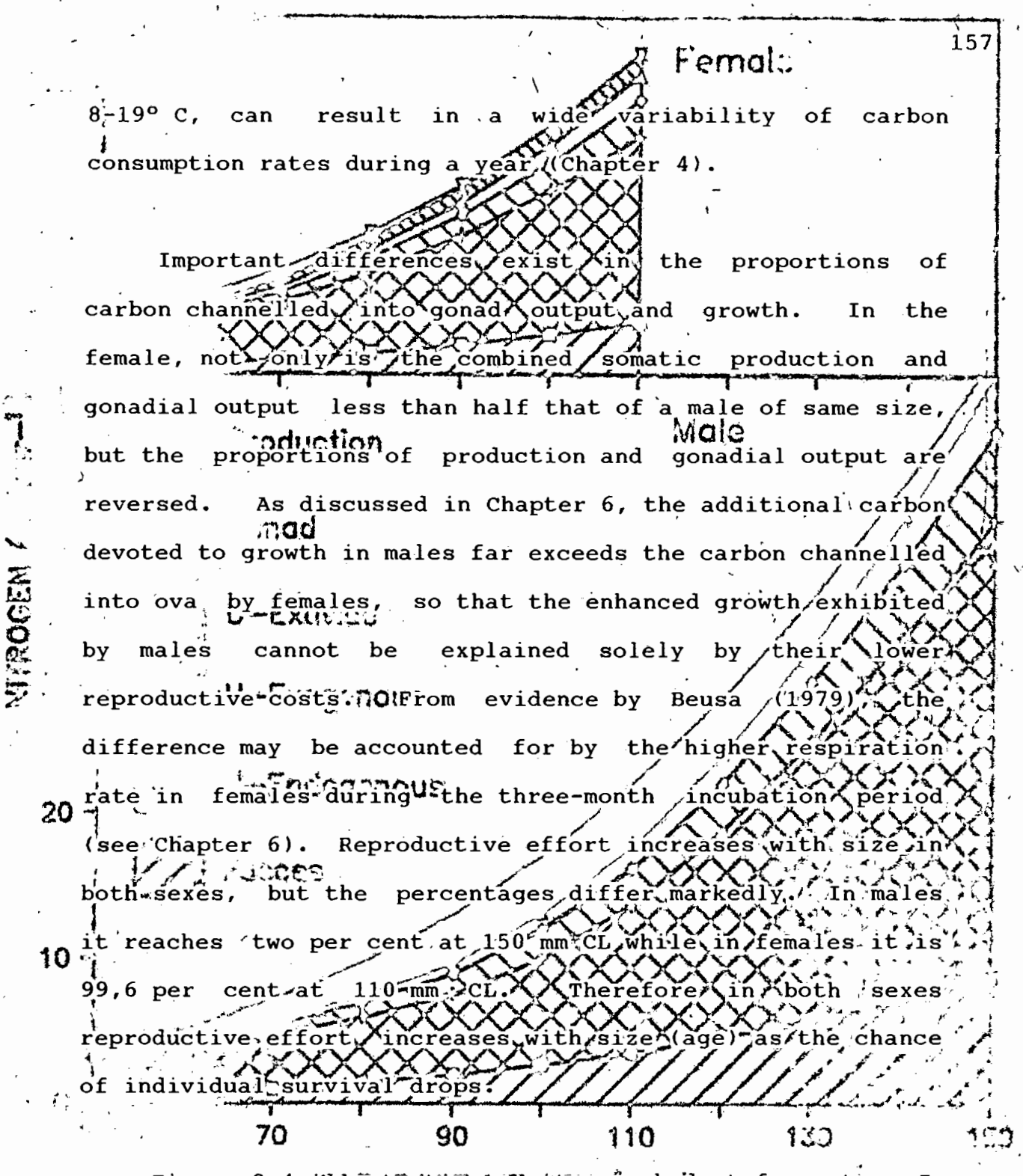

Figure 9.4 illustrating a nitrogen budget for mature *J. lalandii* appears to mirror Figure 9.3 for carbon. However, several important differences exist. Firstly nitrogen

9.4. A nitrogen budget for mature male and female *J. lalandii* ($gN.yr^{-1}$)

values are approximately one quarter those of carbon which is reflected from the C:N ratio of the consumed ration

Table 9.2. Summary of mass conversions, energy content and elemental analyses for mussel and lobster tissues

TISSUE	WM	DM	AFDM	O.C%	I.C%	N%	H%	kJg-1	C:N
C. MERIDIONALIS Flesh		1		38,73		10,24	5,98	18,86	3,78
A. ATER Flesh		1		40,64		10,93	6,67	19,12	3,72
J. LALANDII Exoskeleton	1,49	1	0,46	12,41	10,65	3,88	3,45	6,05	3,19
Exuviae	3,6	1	0,33	9,35	9,25	2,95	2,21	4,56	3,17
Faeces (rectal)	2,13	1	0,22	10,61	8,52	2,45	1,65	4,00	4,33
Muscle	4,05	1	0,92	42,83	2,89	15,13	7,51	20,90	2,83
Ova	4,83	1	0,91	41,72	10,71	11,20	8,35	20,36	3,73
Seminal fluid	5,25	1	0,83	39,82	0,21	10,70	6,43	19,43	3,72
Whole *Jasus*	3,10	1	0,74	29,92	7,60	9,90	6,35	14,60	3,02

Legend: WM = Wet Mass; DM = Dry Mass; AFDM = Ash-free Dry Mass; O.C = Organic carbon; I.C = Inorganic carbon; N = Nitrogen; H = Hydrogen

(Table 9.2). But the proportions of the components of the energy flow equation differ due to carbon and nitrogen being absorbed, utilized or excreted differentially.

The largest component of the nitrogen budget is that of endogenous nitrogen which is excreted (U_{DN}). It is seen from Chapter 5 that after the excretion of the large pulse of exogenous nitrogen following feeding, nitrogen continues to be excreted at a steady low rate. It appears quantitatively equivalent to the respiratory component in the carbon budget (Figure 9.3). Although nitrogen is not respired *per se*, a portion of the nitrogen released is due to respiration as a result of protein being catabolized (Gnaiger 1983, In Gnaiger and Forstner 1983).

The proportions of nitrogen devoted to growth (P) and reproduction (G) follow the pattern already described for carbon.

Population level - Figure 9.5 shows a carbon budget for an unexploited population of *J. lalandii* in the rock-lobster sanctuary off Robben Island 10 km NW of Cape Town. The bulk of the flow takes place through animals of 65-95 mm CL reflected in the size composition of the population and in the higher P/B ratio of animals in this group (Chapter 6). Respiration (calculated for a mean annual temperature of 13° C) accounts for the largest mass of carbon in the

budget. As the rates of biochemical reactions are controlled by temperature, so will the rate of oxygen consumption vary with changes in environmental temperature and, thus, have a large influence on the total carbon budget.

The hatched line records the observed annual consumption of carbon by captive lobsters (Chapter 3). As is seen it slightly underestimates the sum of the components P+R+G+U+F, by *c.* 10-20 per cent. The temperature at which the consumption experiment was conducted was 12° C, one degree lower than the temperature at which the budget for Robben Island has been calculated and probably accounts for much of the difference. With a Q_{10} of 2,5 for metabolism over the range of 8-19° C, a 1° C elevation of temperature will increase metabolic costs by about 15 per cent. This alone could account for the discrepancy.

Ecosystem level - Newell *et al.* (1982) and later Branch and Griffiths (1988) combined available energy budgets of the kelp-bed primary producers and fauna to model energy flow for an idealized kelp bed which formed part of the nearshore Benguela system. Primary producers were responsible for 1304 $gC.m^{-2}.yr^{-1}$. The standing stock of fauna equalled 151 $gC.m^{-2}$ of which lobsters made up 17 per cent (26,17 $gC.m^{-2}$). Figure 9.6 shows the interactions - in terms of carbon ($gC.m^{-2}.yr^{-1}$) - between a population of *J.*

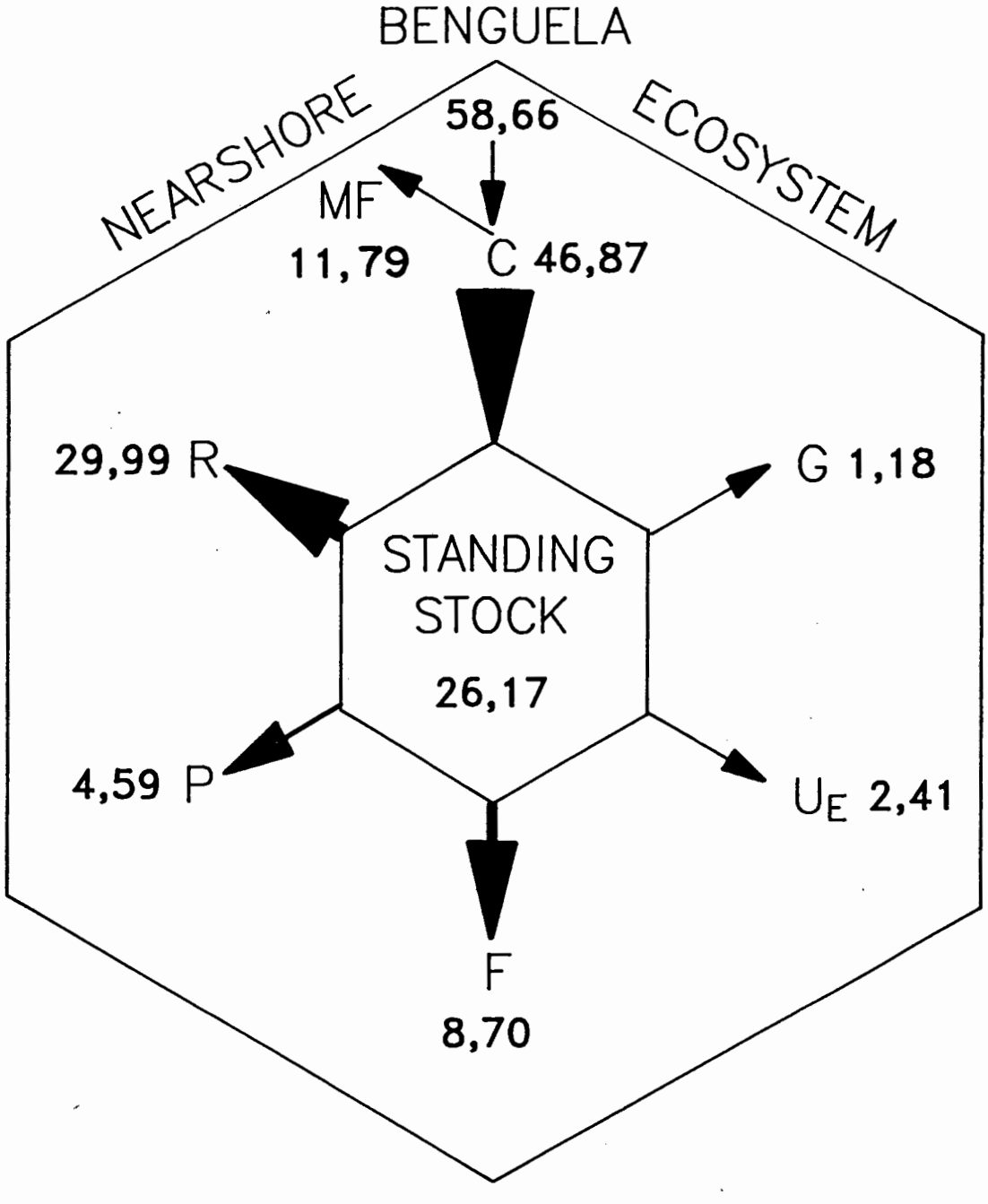

Figure 9.6. The rôle of *J. lalandii* in terms of carbon ($gC.m^{-2}.year^{-1}$) in the nearshore Benguela system using the population at Robben Island (chapter 2) as representative of the unexploited situation

Legend: C = consumption, F = faeces, G = gonad, MF = messy feeding, P = production, R = respiration, U_E = excretion (exuviae).

lalandii and this system. Feeding accounts for the mobilization of 58,66 gC, but because of the problems of ingestion in an aqueous medium, 11,79 g of this (20,1 per cent; Chapter 2) is lost to the environment due to messy feeding, resulting in a consumption (C) value of 46.87 gC. Taking into account the 20,1 per cent loss, Barkai and Branch (1988) calculated the energy requirements for a lobster population at Malgas Island 58 naut. miles NNW of Cape Town. Compared to the predicted consumption for a similar-sized population at Robben Island, the two estimates differ by only 12 per cent, which is considered to be in good agreement. In comparison, the carnivorous kelp-bed isopod *Cirolana imposita*, with a low biomass of 17,6 $gC.m^{-2}$, but with a high P/B ratio of 5.56, consumes 86.6 $gC.m^{-2}.yr^{-1}$ (Shafir and Field 1980).

Absorption efficiency (A/C=79,5 per cent) is high, with a corresponding loss of 8,70 gC as faeces. Apart from shell fragments, the faeces are fine and filamentous and provide a large surface area for bacterial activity. In this form it is also available to the many kelp-bed filter-feeders (Velimirov *et al.* 1977; Field *et al.* 1980a).

Moulting accounts for 2,41 gC. Part is lost to the ecosystem by fragmentation of the exuviae through wave action, followed by bacterial mineralization. However, a fraction may be retained within the system through ingestion

by lobsters (Chapter 7; Heydorn 1969; Pollock 1978; Barkai and Branch 1988a).

Growth efficiency (P/A) is *c.* 16 per cent. In a stable population this results in the production of 4,59 gC which become available to the nearshore system during natural mortality due to disease, predation or old age (Chapter 6).

Reproductive output (G) in terms of carbon (1,18 $g.m^{-2}.yr^{-1}$) plays a minimal rôle in the neashore system. *J. lalandii* larvae after hatching in spring become part of the plankton and are exported during upwelling.

Population respiration in the ribbed mussel *Aylacomya ater* utilizes 298 $gC.m^{-2}.yr^{-1}$ (Griffiths and King 1979), which is 42,7 per cent of the overall annual kelp-bed faunal figure (Newell *et al.* 1982). In the isopod *C. imposita*, respiration amounts to 13,6 $gC.m^{-2}.yr^{-1}$ (Shafir and Field 1980) and accounts for only 15,7 per cent of its annual consumption.

By comparison respiration accounts for the major utilization of carbon by *J. lalandii*, accounting for 64 per cent of its consumption. The annual respiratory requirement is 29,99 $gC.m^{-2}$ and results in the transfer of a similar mass of carbon as carbon dioxide to the environment. In the process energy which is transformed into heat is also lost

to the environment. Thus respiration results in an irreversible energy loss to the system (Chapter 4), although the carbon dioxide is available to the primary producers for the production of organic molecules during photosynthesis.

Therefore, within the nearshore system 97 per cent of the carbon mobilized by *J. lalandii* ($MF+P+U_E+F+R$) remains to be recycled, but of the energy only 47 per cent remains while 53 per cent (R+G) is lost.

Figure 9.7 comprises a nitrogen budget for *J. lalandii* in the nearshore Benguela system. The fate of nitrogen is broadly channelled three ways. Firstly, the nitrogen contained in larvae as a result of ova hatching is exported from the system and amounts to 0.32 g ($gN.m^{-2}.yr^{-1}$) or 2,1 per cent (Chapter 8). Then, nitrogen bound in organic compounds ($MF+F+P+U_E$) amounts to 6,32 g or 40.7 per cent and is ultimately remineralized by bacteria and returned to the system. But, by far the greatest mass (8.88 g) is excreted ($U_{XN}+U_{DN}$; Chapter 5) and forms 57.2 per cent of the total budget of 13,33 g ($gN.m^{-2}.yr^{-1}$). This, together with the remineralized nitrogen quantified above, is readily available to the primary producers and could provide as much as 14 per cent of the annual requirements of the kelp and kelp-bed phytoplankton.

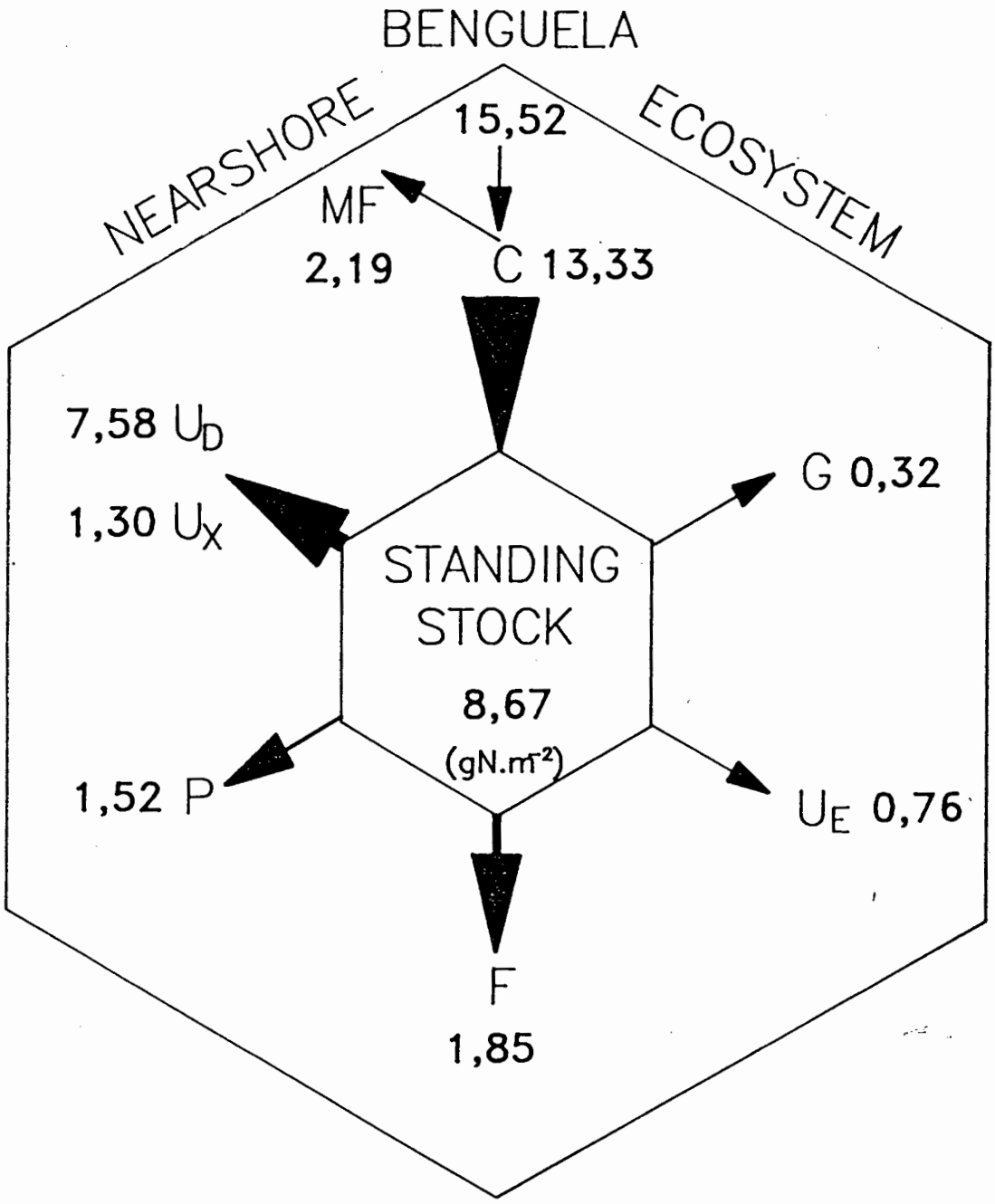

Figure 9.7. The rôle of *J. lalandii* in the nearshore Benguela system in terms of nitrogen (gN.m^{-2}.yr^{-1}). Nitrogen values have been calculated from the carbon values in Table 9.6 using C:N ratios from Table 9.2 and percentages from Table 5.2

Legend: C = consumption, F = faeces, G = gonad, MF = messy feeding, P = production, U_D = excretion (endogenous), U_E = excretion (exuviae), U_X = excretion (exogenous)

Such provision of nitrogen could be of particular significance to the primary producers during static conditions or weak downwelling when availability of new nitrogen is limited.

Therefore, *Jasus lalandii* is, on balance, an exporter of energy from the nearshore Benguela system, but of the nitrogen it mobilizes, 97,9 per cent remains, which may be a significant supplement to the primary producers during static conditions or weak downwelling.

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