

**DIET OF THE WEST COAST ROCK LOBSTER *JASUS LALANDII*:
INFLUENCE OF LOBSTER SIZE, SEX, CAPTURE DEPTH, LATITUDE
AND MOULT STAGE**

S. MAYFIELD*‡, L. J. ATKINSON*, G. M. BRANCH* and A. C. COCKCROFT†

Diets of male and female West Coast rock lobster *Jasus lalandii* in South Africa were compared across a large size range of 10–85 mm carapace length (*CL*). The diets of male rock lobsters were compared between two different depths, different seasons, across the moult cycle, and among eight sites along the South-Western Cape coast. There was no significant difference in diet between male and female rock lobsters for any of the size-classes examined. Male rock lobsters showed large differences in diet between small and large size-classes. The diet of small lobsters (<75mm *CL*) consisted of a wide range of species, which included, in order of importance, coralline algae, barnacles *Notomegabalanus algicola*, sponges and ribbed mussels *Aulacomya ater*. However, prey items rich in inorganic material were not dominant in their diet, as had been predicted. By contrast, large rock lobsters (>80mm *CL*) fed on few species, and fish and ribbed mussels were their most abundant prey items. There were some dietary differences between individuals captured at 20 m and those collected at 50 m, but these differences were less marked than between the two sampling sites (the Knol and Olifantsbos). There was seasonal variation in diet at the Dassen Island and Olifantsbos sites. Cannibalism was highest during the moulting periods. Gut fullness varied seasonally at Dassen Island, and was consistently high at Olifantsbos. However, the proportion of the population feeding showed marked seasonal trends at both sites, tracking the commercial catch per unit effort of rock lobster. Ribbed mussels were a ubiquitous and dominant component of the diet at the eight sites sampled. However, south of Dassen Island, black mussels *Choromytilus meridionalis* were scarce in the diet of rock lobster and sponges predominated. Gut fullness was lowest at the northernmost sites.

Studies on the diet of various lobster species have shown differences with lobster size, depth of capture and moult cycle. Ontogenetic changes in diet have been observed in *Homarus americanus* (Lawton and Lavalli 1995), as well as for *Panulirus homarus* (Berry 1971), *Polycheles typhlops* and *Stereomastis sculpta* (Cartes and Abelló 1992). Seasonal variation in diet was demonstrated for *H. americanus* (Ennis 1973), whereas depth-related dietary changes have been observed in *Polycheles typhlops* and *Stereomastis sculpta*, with diet altering as prey species abundance changed (Cartes and Abelló 1992). The diets of immature *Panulirus cygnus* (Joll and Phillips 1984, Jernakoff *et al.* 1993) and *H. americanus* (Carter and Steele 1982, Lawton and Lavalli 1995) differ from those of adults.

The West Coast rock lobster *Jasus lalandii*, a panulirid spiny lobster, is found in commercially exploitable densities from 25°S off Namibia to Cape Point (34°22'S) on the south coast of South Africa (Pollock 1986). It is a voracious predator, strongly influencing the abundance and population structure of its prey (Barkai *et al.* 1996), even to the extent of creating alternate stable states on two nearby islands (Barkai and McQuaid 1988).

Several assessments of diet of *J. lalandii* have been

made over a wide geographical range (Barkai *et al.* 1996), as well as detailed studies at more localized areas (Newman and Pollock 1974, Pollock 1979, Barkai and Branch 1988) and in the laboratory (Griffiths and Seiderer 1980, Zoutendyk 1988 a, b, Van Zyl *et al.* 1998). However, with the exception of Barkai and Branch (1988), none of these studies considered the diet of juvenile lobsters (<65 mm carapace length, *CL*), variation in their diet with size or sex, or the influence of moult stage and depth of capture.

In this paper, the influence of all these factors on rock lobster diet is investigated. Based on past studies, it was predicted that:

- (i) the diet of juvenile lobsters will be different from that of mature conspecifics. More specifically, smaller rock lobsters will have higher levels of gut fullness (i.e. a larger daily ration), a higher prey diversity, less cannibalism and a higher intake of calcium (and other inorganic material) in their diet relative to body mass. These predictions follow from the facts that small rock lobsters moult frequently and can feed on a diverse array of small prey;
- (ii) the diet of mature female rock lobsters will differ

* Marine Biology Research Institute, Zoology Department, University of Cape Town, Rondebosch 7701, South Africa;

† Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa

‡ Now Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa. E-mail: mayfield@sfri.wcape.gov.za

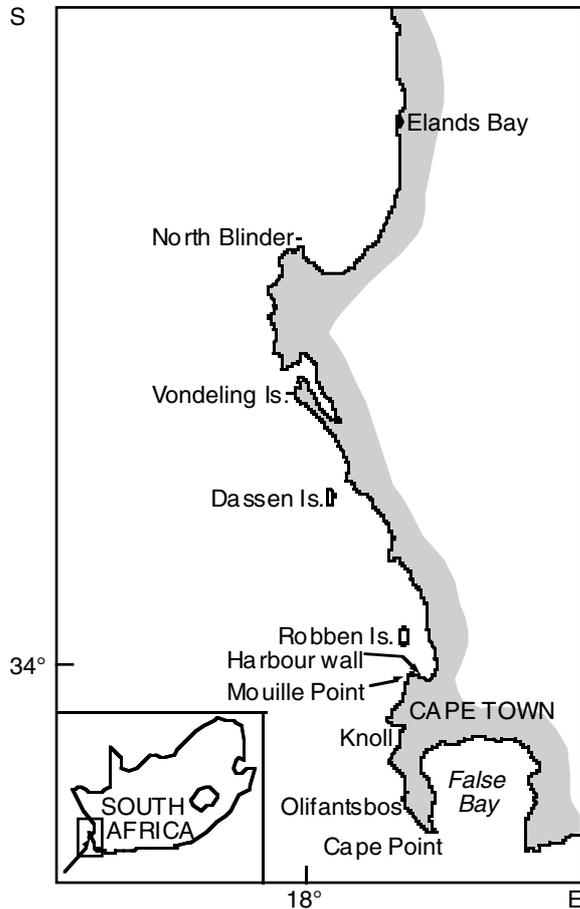


Fig. 1: Map of the study area showing the locations of the study sites

- from that of similarly sized males, because egg production is energetically more expensive than sperm production;
- (iii) diet will vary through the moult cycle, showing reduced consumption during the “hard old” (early pre-moult) and “hard new” (early intermoult) shell states, being dominated by prey species high in inorganic material during the early intermoult period when the new exoskeleton is laid down;
 - (iv) diet will vary bathymetrically, with low diversity in deeper water where prey is more scarce and less diverse;
 - (v) diet will not differ geographically within the same biogeographic province, because prey species availability should be similar.

MATERIAL AND METHODS

Logistics precluded the possibility of sampling all combinations of dates, sizes, depths and areas simultaneously, so each of these factors was investigated in isolation, holding the other variables constant. Stages in the moult cycle were assigned on the basis of shell state criteria (Heydorn 1969, Cockcroft 1997).

Rock lobster collection

Effect of moult stage on diet was investigated using samples collected each month between February 1994 and July 1995 from two localities (Fig. 1), Olifantsbos (where rock lobsters grow slowly) and Dassen Island (where rock lobsters grow fast – Goosen and Cockcroft 1995), between 15 and 25 m water depth. In some months, inclement weather prevented diving. At each site, 60 rock lobsters, standardized to include only males of 70–80 mm CL, were collected using bait-protected, longline lobster traps deployed at night at Olifantsbos, and by SCUBA divers operating shortly after dawn at Dassen Island. Lobsters were denied access to the bait by placing the bait inside a fine-meshed bag. Differences in dietary composition between diver- and trap-caught specimens were negligible, providing that account was taken of species that fell prey to lobsters only when lured into bait-protected traps. This applied particularly to the isopods *Cirrolana hirtipes*, *C. cranchii* and *C. imposita*, which are attracted to and consumed in traps by rock lobster (Griffiths *et al.* 2000). Consequently, isopods were excluded from any dietary analyses in the present study. Remnants of rock lobster exoskeletons found in the gut contents were considered to indicate cannibalism, because they were hard, pigmented and had distinct microstructures, unlike the pale and soft nature of exuviae.

Effect of size on diet was investigated in summer 1994 using 60 male rock lobsters from each of five size-classes (60–64, 65–70, 75–79, 80–85 and >85 mm CL) collected from Olifantsbos at a depth of 20 m, using bait-protected longline lobster traps. Sampling was repeated in summer 1998 for the size classes 10–35, 40–59 and 70–85 mm CL, which included sampling of sub-adult rock lobsters at Mouille Point, the Cape Town Harbour wall and Olifantsbos. Although not all sites sampled yielded sufficient animals in each size-class for rigorous analysis, the data yield new information on the diet of small rock lobsters between 10 and 35 mm CL.

Effect of sex on diet was examined in summer 1998 using male and female rock lobsters from three size-classes (10–35, 40–59 and 70–85 mm CL) collected by means of SCUBA diving at 15 m at five sites (Dassen

Island, Mouille Point, Olifantsbos, the Harbour wall and Robben Island).

Effects of water depth on diet was examined using male rock lobsters (70–80 mm *CL*) collected at night on a once-off basis during December 1995 from Cape Point and Olifantsbos at a shallow (20 m) and a deep (50 m) site, using bait-protected, longline lobster traps.

Effect of geographic location was examined using 60 rock lobsters (70–80 mm *CL*) collected at depths between 15 and 20 m from each of eight sites: Cape Point, Robben Island, Dassen Island, Vondeling Island, Elands Bay, Olifantsbos, the Knoll and North Blinder (Fig. 1), in summer 1994/5 (during their intermoult period, Cockcroft 1997). Most rock lobsters were caught at night using bait-protected longline commercial traps. The exception was at Dassen Island, where rock lobsters were collected at dawn by means of SCUBA.

Stomach content analysis

Upon collection, rock lobsters were anaesthetized by immersion in a water-ice slush and their gastric-mill stomachs (referred hereafter as stomachs) removed. The first 30 full stomach samples were frozen at -20°C for further analysis. Full stomachs were defined as those with a bolus of at least 1 cm^3 (adults, *CL* > 70 mm) or 0.5 cm^3 (small rock lobsters, *CL* < 70 mm).

When analysed, all stomachs were defrosted, blotted dry and then weighed to the nearest 0.001 g. Stomach contents were then flushed into a Petri dish and the gut membrane re-weighed as above. The gut fullness index was calculated as:

$$\frac{\text{Total stomach mass (g)} - \text{stomach membrane mass (g)}}{\text{Total stomach mass (g)}} \times 100 .$$

Prey species were identified from diagnostic fragments in the stomach contents viewed under a binocular microscope at $8\times$ magnification. The percentage contribution of each prey species to the total stomach volume was estimated visually (after Hyslop 1980, Williams 1981). For analysis of diet, the frequency of occurrence of each prey species in the stomachs was expressed as a percentage of the total number of stomachs. The proportion of the population that was feeding was calculated as the number of rock lobsters with full stomachs expressed as a percentage of the number of stomachs examined.

Statistical analyses

The *a priori* hypotheses that (1) diet would differ

with size and sex of rock lobster and (2) that diet would differ bathymetrically were tested using Analysis of Similarity (ANOSIM). The Shannon-Wiener diversity (*H*) and Margalef's species richness (*D*) indices were calculated for prey species composition (data for all individuals of each size-class pooled), after Clarke and Warwick (1994):

$$H = \sum P_i (\log_e P_i)$$

and

$$D = S - 1 / (\log_e N) ,$$

where P_i is the proportion of the biomass attributed to the i^{th} prey species, *S* is the total number of species and *N* is the number of individuals. The "diet at depth" data were further analysed using Bray-Curtis similarity and a Multidimensional Scaling Plot (MDS, which places similar samples together in 2-D space, Primer v4.0, Plymouth Marine Laboratory).

The contribution of inorganic material by the prey items to each bolus in the five size-classes sampled during summer 1994 was estimated by multiplying the bolus mass by the proportion of the bolus volume comprising that species. These masses were then converted to dry mass and finally to an inorganic material mass (based on ash-free dry mass) using the conversions of Field *et al.* (1980). The mass of inorganic material per gramme of bolus was then calculated. These values, the gut fullness levels and the absolute bolus masses between the five size-classes were compared using a Kruskal-Wallis ANOVA by ranks (Zar 1984), followed, where appropriate, with a Newman-Keuls multiple range test ($\alpha = 0.05$) using Statistica v5. No comparisons were made with the size-range samples collected during summer 1998, because of the temporal separation between the two sampling events. The diets of male and female rock lobsters were compared within each size-class using ANOSIM ($\alpha = 0.01$ to avoid Type I statistical errors).

RESULTS

Effects of moult stage

Less seasonal variation in rock lobster diet was observed at Dassen Island than at Olifantsbos (Figs 2, 3). At Dassen Island, cannibalism was more prevalent during winter (June), spring (August) and, to a lesser extent, early summer (October–November). The most frequently eaten prey items at Dassen Island were ribbed mussels *Aulacomya ater* and barnacles *Notomegalanus algicola*. At Olifantsbos, ribbed mussels were more abundant in the diet of rock lobsters during summer (November–March), and barnacles constituted

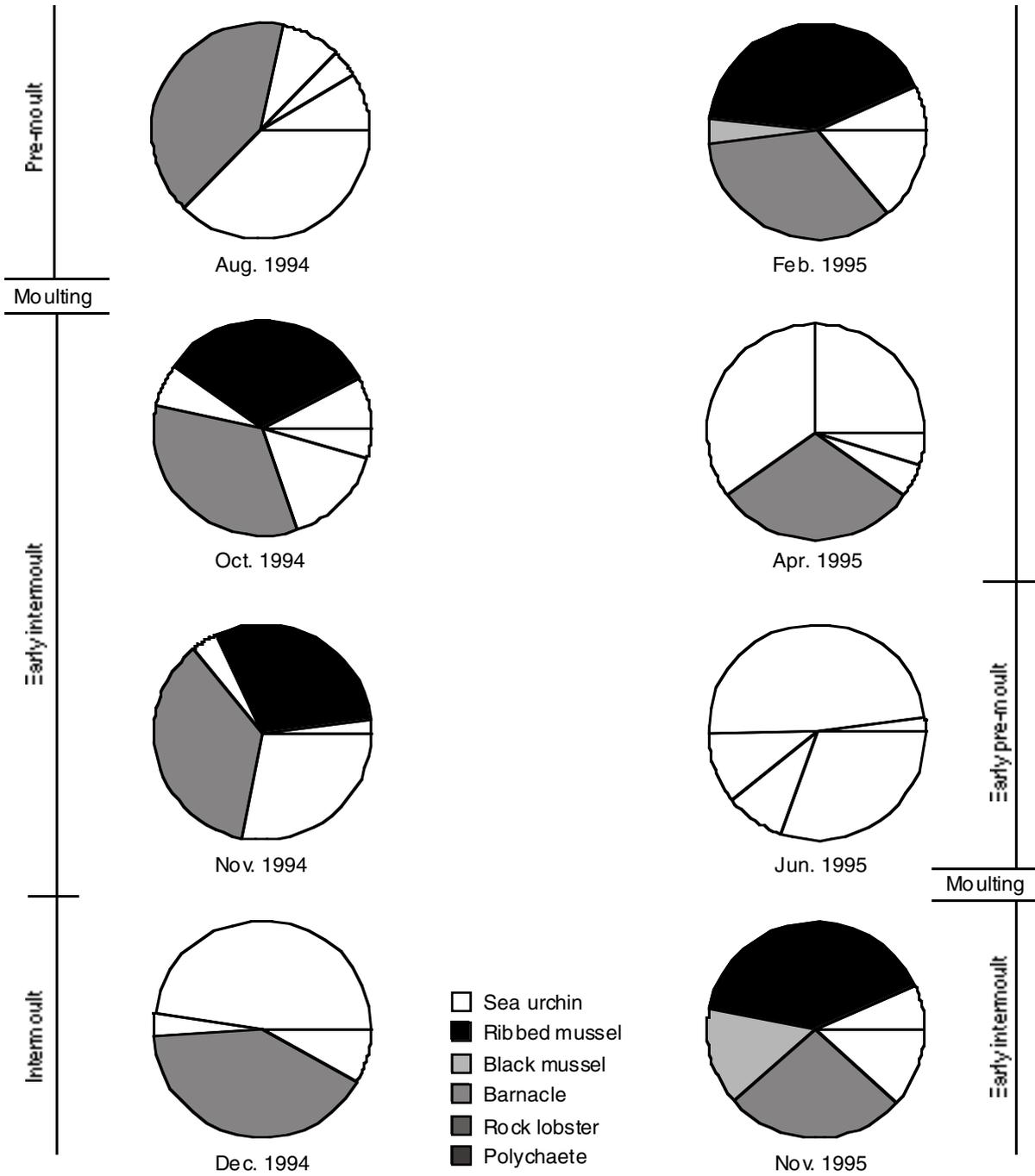


Fig. 2: Diet (expressed as a percentage of the frequency of occurrence) of male rock lobsters (70–80 mm CL) sampled from Dassen Island between August 1994 and November 1995

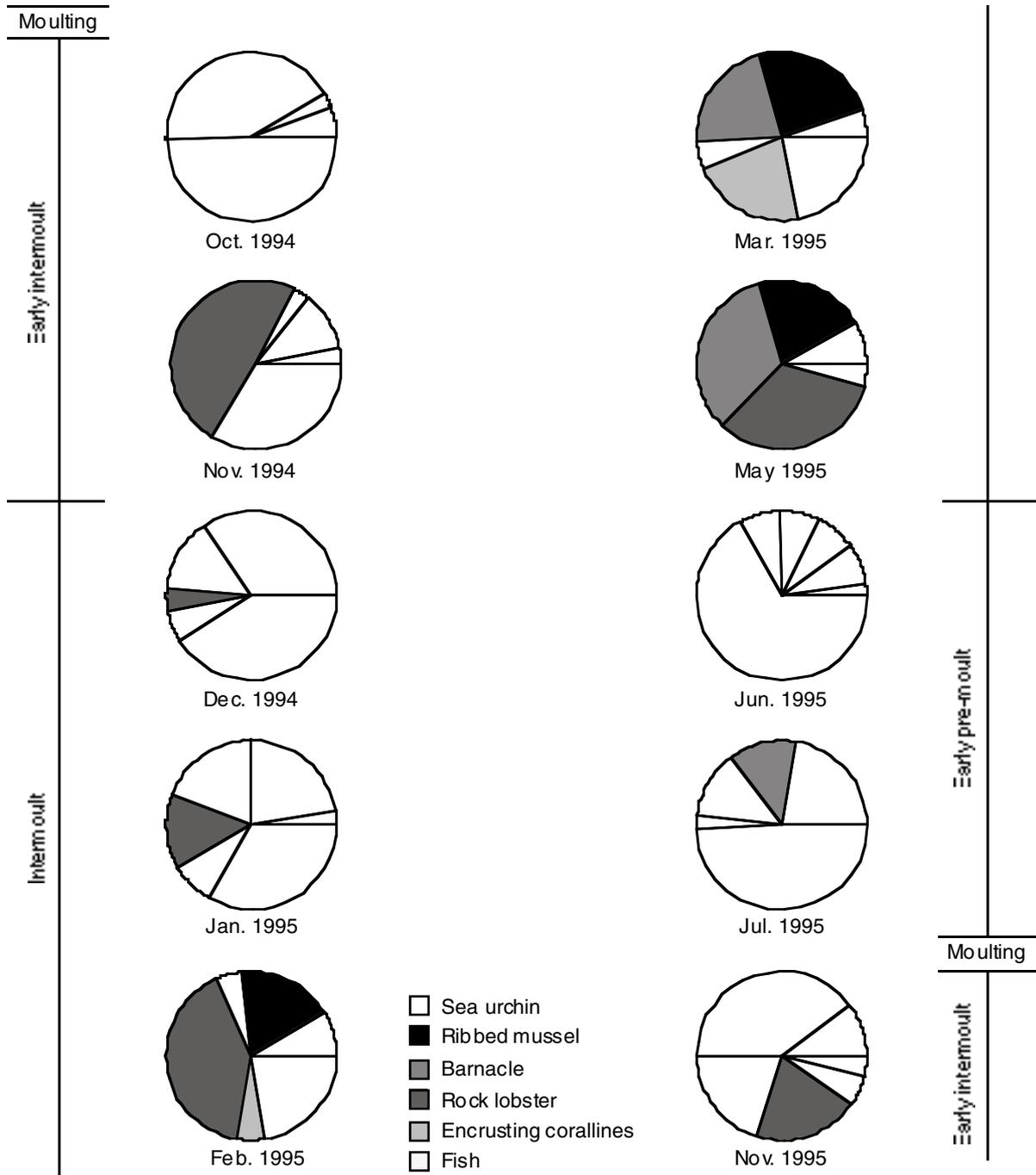


Fig. 3: Diet (expressed as a percentage of the frequency of occurrence) of male rock lobsters (70–80 mm CL) sampled from Olifantsbos between October 1994 and November 1995

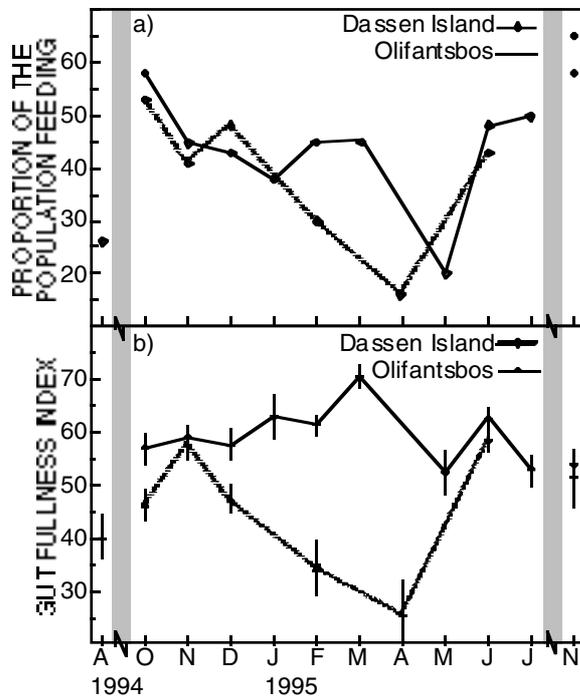


Fig. 4: (a) Proportion of the rock lobster population feeding and (b) gut fullness indices (mean \pm standard error) of lobsters caught at Dassen Island and Olifantsbos. The shaded area shows the male rock lobster moult period

a large component of the diet during the pre-moult and early intermoult periods. Rock lobsters captured during winter (June–July) and late spring (October) at Olifantsbos had a high occurrence of fish in the diet, and cannibalism, although encountered in samples taken throughout the year, was most prevalent from late spring to early summer (October–November).

The proportion of rock lobsters feeding at both sites was low during the late intermoult period and peaked in the early intermoult stage (Fig. 4a). There was no seasonal variation in the gut fullness at Olifantsbos. However, gut fullness was lowest during summer at Dassen Island (Fig. 4b), where it tracked the proportion of rock lobsters feeding there.

Effects of size and sex

During summer 1994, male rock lobsters of different sizes (60–90 mm CL) had significantly (Global $R = 0.09$, $p < 0.05$) different proportions of prey items in their stomachs (Fig. 5). Ribbed mussels *Aulacomya ater* and fish dominated the diet of rock lobsters >80 mm CL. The diet of smaller individuals (60–70 mm CL) consisted of numerous species, but coralline algae, barnacles *Notomegabalanus algicola* and rock lobster remains were the dominant prey items in the stomachs. Rock lobsters between 75 and 79 mm CL had a diet spectrum intermediate between these two size-groups and the highest rate of cannibalism. Moreover, the Shannon-Wiener index and Margalef's species richness indices were higher for small rock lobsters (1.58 and 1.12 respectively) than for large individuals (1.00 and 0.46 respectively, Table I). There were no significant differences in gut fullness between the five size-groups ($H = 1.56$, $p > 0.05$), nor in the amounts of inorganic material (inorganic material (g)·bolus mass (g)⁻¹) in the stomachs ($H = 3.75$, $p > 0.05$, Table I). Large rock lobsters (>85 mm CL), however, had significantly larger bolus masses relative to the other size-classes ($H = 12.55$, $p < 0.05$), which did not differ significantly between each other (Table I).

The diet of juvenile (10–35 mm CL) rock lobsters (sampled in summer 1998) consisted of numerous prey items, but primarily mussels (both ribbed mussels and black mussels *Choromytilus meridionalis*) and barnacles. Larger (40–60 mm CL) rock lobsters consumed

Table I: Margalef's and Shannon-Wiener diversity indices, gut fullness index (%) and various parameters relating the relationship between gut contents and mass of different size-classes of rock lobsters

Parameter	Size-class (mm CL)				
	60–64	65–70	75–79	80–85	>85
Margalef's index	1.12	1.08	0.736	0.444	0.461
Shannon-Wiener index	1.58	1.67	1.11	0.93	1.00
Gut fullness index (%)	54.7	51.8	55.5	46.8	64.5
Bolus mass (g)	0.84	0.91	1.74	1.61	3.41
Bolus inorganic content (g)	0.24	0.14	0.17	0.59	0.63
Inorganic content (g)·bolus mass (g) ⁻¹	0.31	0.22	0.13	0.27	0.23
Bolus (mg)·body (g) ⁻¹	6.6	5.2	6.6	5.3	8
Inorganic (mg)·body mass (g) ⁻¹	1.9	0.8	0.7	1.9	1.7

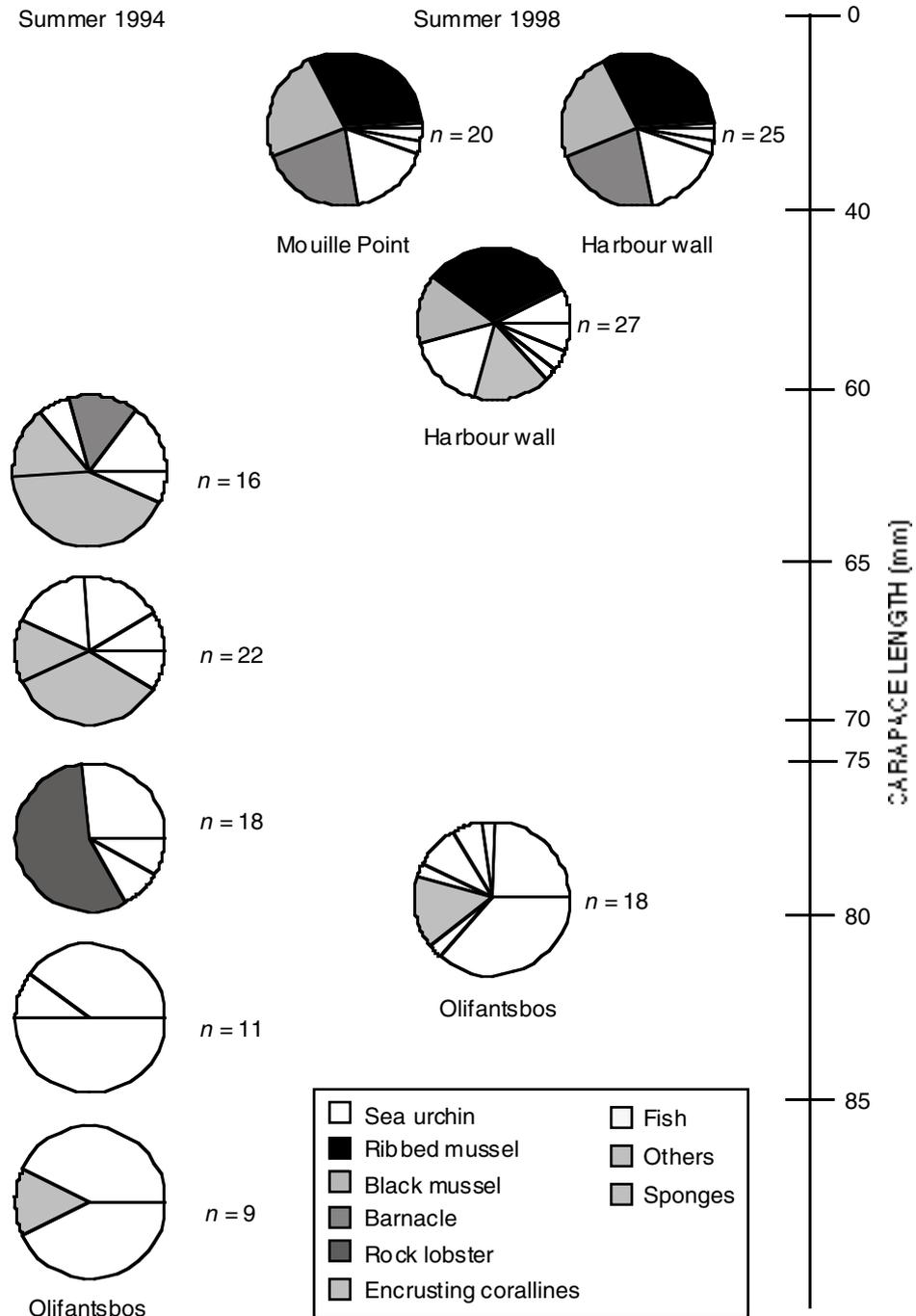


Fig. 5: Variation in the diet of rock lobsters (expressed as a percentage of the frequency of occurrence) with size at various sampling sites

Table II: Comparison of the diet of male and female rock lobsters of various size based on the null hypothesis (H_0) that the diet of male and female rock lobsters is the same

Site	Sex comparison	Global R	p	Reject H_0
Dassen Island	Small male v. small female	0.14	>0.01	No
Mouille Point	Small male v. small female	0.02	>0.01	No
Harbour wall	Small male v. small female	0.02	>0.01	No
Dassen Island	Medium male v. medium female	0.047	>0.01	No
Mouille Point	Medium male v. medium female	0.06	>0.01	No
Olifantsbos	Medium male v. medium female	0.026	>0.01	No
Harbour wall	Medium male v. medium female	0.003	>0.01	No
Robben Island	Medium male v. medium female	0.088	>0.01	No
Robben Island	Large male v. large female	0.052	>0.01	No

similar number of prey items. The diet of large rock lobsters at Olifantsbos in 1998 was similar to that observed in 1994, indicating temporal stability. Again, the Shannon-Wiener and gut fullness indices were highest for juvenile rock lobsters (2.71 and 46.29% respectively), declining for adults (70–85 mm CL , 0.11 and 33.53% respectively). Furthermore, large rock lobsters had significantly larger bolus masses ($H = 19.49$, $p < 0.01$).

The diets of male and female rock lobsters did not differ within each size-class (small, medium and large) for sites that had sufficient data for rigorous analyses (Table II). For all comparisons, Global R ranged between 0.003 and 0.14, dictating acceptance of the null hypothesis of no difference in diet between male and female rock lobsters, $\alpha = 1\%$). Because of the significant differences in diet with lobster size (see above), the diets of small, medium and large rock lobsters of both sexes were statistically separable.

Effect of depth

Ribbed mussels and coralline algae were the most common prey items of rock lobsters collected in the shallows off Cape Point, but fish were the most commonly consumed prey in deeper water there. At Olifantsbos, the number of prey items in the diet at the shallow station was double that at the deep station, although fish dominated the diet at both depths. At both sites, the species richness and prey diversity indices

were lowest for the deep station, although the difference was only marginal in some cases (Table III). There were differences between the diet of rock lobsters caught at different depths in both Cape Point and Olifantsbos (Global $R = 0.019$, $p > 0.05$). Bray-Curtis similarity and the associated MDS plots showed that there were larger differences in diet between the two sites than between the two sampling depths.

Effects of geographic location

Gut fullness increased from north to south, the lowest being at Elands Bay and the highest at Robben Island (Fig. 6). Examination of the components of the diet reveals geographic differences (Fig. 5), the most marked being the disappearance of black mussels from the stomachs of rock lobster caught south of Dassen Island, where they were replaced by sponges. The ribbed mussel was a ubiquitous and dominant dietary item. Cape urchins *Parechinus angulosus* and rock lobster remains were recorded in the stomachs from all of the study sites.

DISCUSSION

Possible trap effects on diet

Many rock lobsters collected at Olifantsbos had fish remains in their stomachs. It is believed that this is not an artefact of capturing the rock lobsters in fish-baited traps, because the bait used was Cape horse mackerel *Trachurus trachurus capensis* and remains of that species were not found in the stomachs examined. A concurrent study by Griffiths *et al.* (2000) also showed high levels of non-bait fish remains in the diet of rock lobsters caught in baited traps. The fish eaten by rock lobster in that study were probably small clinids (S. J. Lamberth, Marine & Coastal Management, pers. comm.). Small fish are consumed by captive

Table III: Margalef's and Shannon-Wiener indices for the diet of rock lobsters collected from shallow and deep stations at Olifantsbos and Cape Point

Parameter	Cape Point		Olifantsbos	
	Shallow	Deep	Shallow	Deep
Margalef's index	1.152	1.124	0.681	0.266
Shannon-Wiener index	0.854	0.818	0.557	0.365

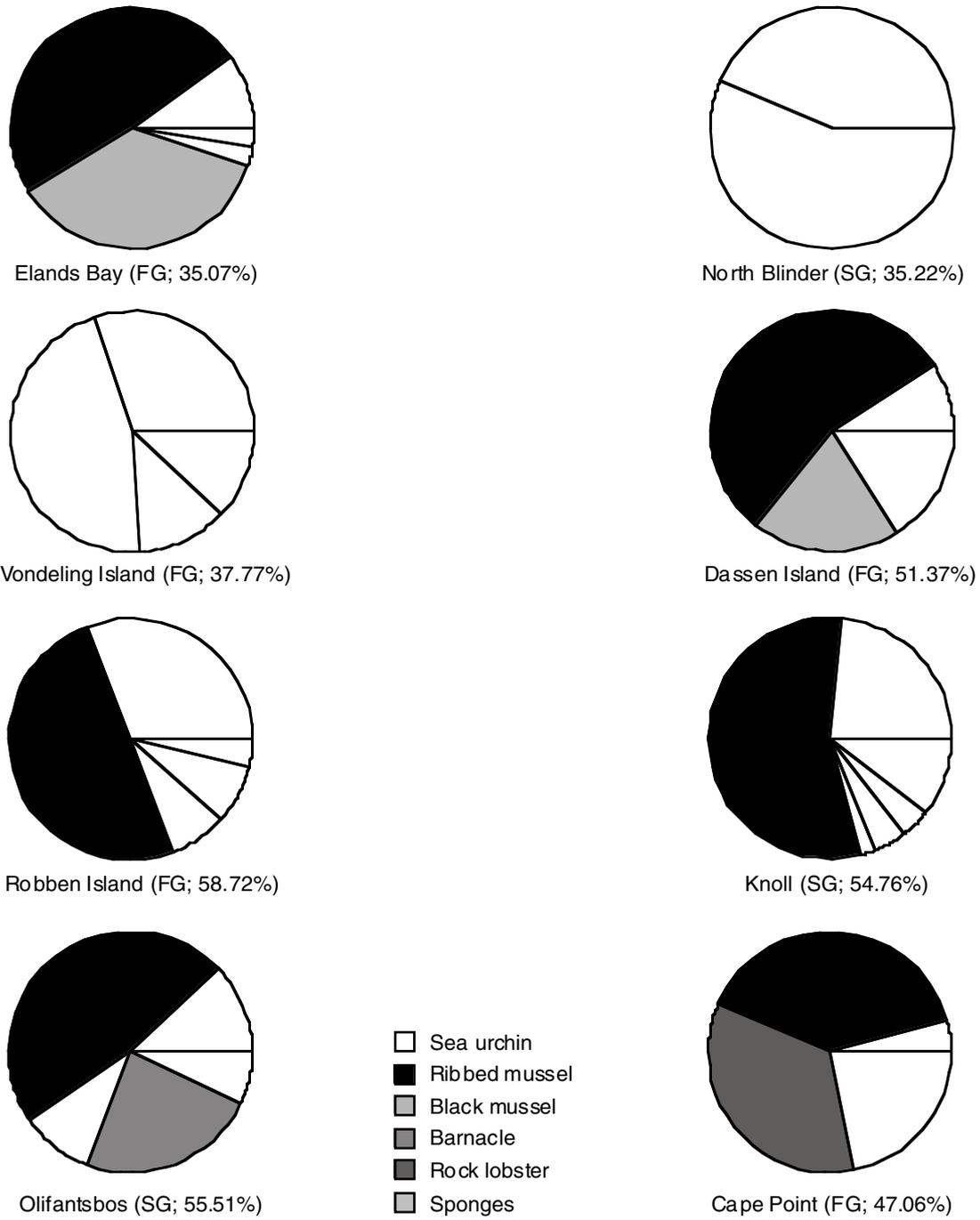


Fig. 6: Diet (expressed as a percentage of the frequency of occurrence) of male rock lobsters (70–80 mm CL) sampled from eight sites ranging between Elands Bay and Cape Point (see Fig. 1). Percentages in brackets refer to the average gut fullness. FG and SG donate fast and slow growth areas respectively

J. lalandii (SM, pers. obs.), and they have been observed in the wild holding small fish. Capture of live fish has been reported for *H. americanus* (Lawton and Lavalli 1995) and for some deep-water clawed lobsters, e.g. *Metanephrops* spp. (Wassenberg and Hill 1989). It is considered that the fish found in the stomachs of the rock lobsters in this study reflected their natural diet.

Ontogenetic changes and sex-related differences in diet

In summer 1994, the diet of small rock lobster (<70 mm *CL*) was dominated by coralline algae, with barnacles and sponges being other important prey items. By contrast, large rock lobsters (>80 mm *CL*) consumed mostly ribbed mussel and fish. Repeat studies in May 1998 also showed barnacles and sponges to be important dietary components for individuals <60 mm *CL* (even in those as small as 10 mm), although in that study the importance of coralline algae was less noticeable.

Coralline algae and barnacles are rich in inorganic material, whereas mussels and fish tend to be richer in protein (Field *et al.* 1980). The rock lobsters under study consumed the same mass of inorganic material per unit mass of bolus and per unit body mass (Table I). Therefore, the prediction that small individuals would have a diet with a higher inorganic content than large ones was not upheld by the present data. Furthermore, because small rock lobsters moult more frequently than adults (Pollock 1979, Griffiths and Seiderer 1980, Lawton and Lavalli 1995), it was predicted that they would have a relatively higher gut fullness. This prediction was also not borne out in the present data.

It was also predicted that the diets of small rock lobsters would be highly diverse (i.e. high species richness). There are two possible reasons for this. First, there is a greater range of species in the smaller size-spectrum of prey than among large prey. Second, if access to preferred prey is limited or reduced by competition with large rock lobsters, then small individuals may have to diversify to meet their energy needs – which are likely to be higher per unit mass because of their fast growth and frequent moulting (Beyers *et al.* 1994). For large rock lobsters, competition should be less and they may concentrate on preferred prey, resulting in lower prey diversity indices. Griffiths and Seiderer (1980) showed evidence that the preferred size range of mussels available to small rock lobsters is often depleted as a result of predation. Small rock lobsters had a much higher number of prey species in their stomachs in both the summer 1994 and 1998 samples (up to six in one lobster). By contrast, the gut contents of larger lobsters tended to

be dominated by one prey item.

Cannibalism has been shown to be prevalent in adult *H. americanus* (Elner and Campbell 1987, Lawton and Lavalli 1995), but (exuviae excluded) almost absent in small lobsters (Carter and Steele 1982). Cannibalism was low in the small rock lobsters in this study, and was most prevalent in the medium-sized rock lobsters (>50% of the stomachs) rather than in large individuals (5% of the stomachs). Previous studies have generally recorded high levels of cannibalism in *J. lalandii* (Pollock 1979, Barkai and Branch 1988, Barkai *et al.* 1996). The low level of cannibalism found in this study may be a reflection of less competition for food.

Variation in diet with predator size is a common feature in decapods. Ontogenetic changes in diet have been shown for *J. lalandii* at Marcus and Malgas islands (Barkai and Branch 1988), as evident in the present study. Similar dietary changes have been described for the South African East Coast rock lobster *Panulirus homarus*, and elsewhere for other lobster species such as *Polycheles typhlops*, *Stereomastis sculpta* and *H. americanus* (Cartes and Abelló 1992, Lawton and Lavalli 1995). In general, fish and mussels are more important in the diet of large lobsters than in than small individuals. Ontogenetic dietary shifts have been also shown in prawns (O'Brien 1994) and crabs (Cerdeira and Wolff 1993).

A reason for ontogenetic changes in the diet of *J. lalandii* could be that small individuals, because of their shorter intermoult period, require a diet rich in inorganic material to facilitate frequent exoskeleton replacement. Dietary intake of prey items high in minerals is highest in pre- and post-moult specimens of *H. americanus* (Ennis 1973, Leavitt *et al.* 1979). Also, Barkai and Branch (1988) found that post-moult *J. lalandii* fed predominantly on barnacles and small non-bivalve molluscs. This suggests that food high in calcareous material is important as a preparation for moulting. The proportion of inorganic components of barnacles, ribbed mussels, rock lobsters and fish are reported to be 82, 88, 38 and 18% of dry mass respectively (Field *et al.* 1980), and 70% of dry mass for coralline algae (Manneveltdt 1995). Although juvenile rock lobsters fed predominantly on these mineral-rich prey at the study sites, the intake of inorganic material per unit body mass did not differ with size of lobster. This finding does not support the above hypothesis.

The finding of no significant differences in diet between male and female rock lobsters was unexpected, given that the energetic demands of sexually mature females were likely to exceed those of males of similar size. In reality, the energetic requirements of males and females may be equal, because females curtail their growth once they start producing energy-demanding eggs (Beyers and Goosen 1987).

Variation in diet with depth

As predicted, the diets of male rock lobster did not differ with depth. At the shallow station at Cape Point, the diet was diverse, but consisted principally of ribbed mussels and coralline algae. At 50 m in the same area, fish remains were found in more than 45% of stomachs, although ribbed mussels and coralline algae were still eaten there. For both depths, the species richness and diversity indices were similar, but slightly depressed for the deeper station (Table III). By contrast, the diet of rock lobsters at the shallow station at Olifantsbos showed twice the prey richness when compared to the deep station, although fish were the dominant prey item at both depths. This was confirmed by the Margalef's and Shannon-Wiener indices for Olifantsbos, both of which were about 50% less at the shallow station. The regular consumption of fish is a finding of great interest in its own right.

Thus, there were differences in the relative contributions of individual species in the diets of shallow versus deep rock lobsters. However, when the diets were considered as a whole and the data subjected to an analysis of similarity (ANOSIM), the result was not significant (Global $R = 0.019$, $p > 0.05$), indicating little overall dependence of diet on capture depth. Analyses using Bray-Curtis similarity and MDS plots suggested that the reason for this non-significant result was because much larger differences were observed between the diets of individual rock lobsters caught at the two sites (Cape Point and Olifantsbos), than between the two depths at each site.

Limited information is available on bathymetric differences in the diet of rock lobster elsewhere, primarily because of the difficulties in sampling lobsters below 100 m depth. Cartes and Abelló (1992) observed that the diet of the polychelid lobster *Polycheloides typhlops* differed between 550 and 1 200 m, and suggested that this reflected changes in prey availability. Similar trends have been observed in the deep-sea Mediterranean crab *Geryon longipes* (Cartes 1993a), in pandalid (Cartes 1993b) and in aristeid shrimps (Cartes 1994). However, for *J. lalandii*, although some depth-related differences were observed (notably a shift to increased consumption of fish at greater depth), these were less marked than the inter-site differences between the two localities sampled.

Variation in diet with moult stage

Rock lobster diet varied seasonally at both Dassen Island and Olifantsbos. At Dassen Island, barnacles and ribbed mussels were the dominant prey items virtually throughout the sampling period (Fig. 2). Cannibalism

was more prevalent during winter (June) and spring (August), coinciding with the female and male moulting periods respectively (Heydorn 1969, Newman and Pollock 1974). In 1994, most male rock lobsters moulted in September (Cockcroft 1997), so the high cannibalism observed around that period may be a result of the consumption of early and late moulters. Male rock lobsters show great synchrony during moulting, ostensibly to prevent high mortalities attributable to cannibalism.

Considerably more seasonal variation in diet was observed at Olifantsbos (Fig. 3). Fish were frequent in the diet throughout the year (except in May and November 1995). Ribbed mussels and sea urchins were also common in the diet. Although barnacle and rock lobster remains were observed in nearly all stomachs examined, barnacle remains were more frequent during the reserve accumulation phase of the intermoult period (December–May 1995, Cockcroft 1997). Cannibalism peaked during late spring (October and November 1994) and again in winter (May 1995), a trend also found at Dassen Island.

Seasonal variation in diet has previously been reported for *J. lalandii* (Barkai and Branch 1988), with cannibalism highest during summer. At Malgas Island, peak consumption of ribbed mussels was in winter, and barnacle ingestion was highest during late spring/summer (Barkai and Branch 1988). A similar feeding behaviour was observed in the present study, suggesting the need to increase ingestion of calcium rich material to allow for exoskeleton deposition after moulting (Scarratt 1980, cited by Lawton and Lavalli 1995). *H. americanus* shift to a more calcium-rich diet during the moulting season in late summer (Ennis 1973, Carter and Steele 1982, Elner and Campbell 1987, Lawton and Lavalli 1995). It has been suggested that this dietary pattern follows the physiological requirements of moulting, rather than simply reflecting prey availability (Leavitt *et al.* 1979), involving active selectivity of prey (Lawton and Lavalli 1995). In contrast, no seasonal variation in diet was noted in *P. cygnus* (Joll and Phillips 1984).

The rock lobsters of this study showed marked seasonality in their feeding intensity, food intake being low during winter (late intermoult) and high immediately prior to moulting and so throughout the post-moult period (Fig. 4a). Previous studies on *J. lalandii* reported cessation of feeding of up to six weeks prior to and for five weeks following moulting (Heydorn 1969, Zoutendyk 1988a, Beyers *et al.* 1994), but it is the current belief that feeding stops for a maximum of 21 days (ACC unpublished data). Because male rock lobsters moulted during September 1994 (Cockcroft 1997), cessation of feeding should have

taken place between August and October. The present data do not show this. At Dassen Island, gut fullness was lower during that period than during the early intermoult period (Fig. 4b), but the present data show no suppression of feeding around the moult period. However, as the sampling resolution was coarse, it is likely that the moulting window (immediate pre- and post-moult) was missed. Therefore, while not completely supporting the original hypothesis, some depression in feeding was observed during the time surrounding moulting. The depression of feeding by males in winter may be because reproduction is taking place then, i.e. while the females are soft-shelled. The proportion of rock lobsters feeding tracked the commercial catch per unit effort (*cpue*) for both Olifantsbos and Dassen Island. Such feeding patterns may partially explain seasonal variations in *cpue*. Studies on *H. americanus* (Ennis 1973, Carter and Steele 1982, Elner and Campbell 1987) and *P. cygnus* (Joll and Phillips 1984) suggest seasonal patterns in their gut fullness. Such variations are most likely related to the difficulty of feeding when the lobsters' shells are soft (pre- and post-moult).

Effect of geographic distribution

The general diet of crustaceans, molluscs and echinoderms shown here for *J. lalandii* is similar to that reported for most other lobsters worldwide. (Ennis 1973, Elner and Campbell 1987, Lawton and Lavalli 1995). Only Norway lobsters *Nephrops norvegicus* seem to differ in that polychaetes dominate their diet (Baden *et al.* 1990).

Some spatial trends were observed in the diet of *J. lalandii*. The dietary switch from black mussels to sponges observed in rock lobster south of Dassen Island concurs with the findings of Barkai *et al.* (1996) and is likely a reflection of food availability: the abundance of subtidal sponges being highest in the south (Field *et al.* 1980). Furthermore, cannibalism was greater south of North Blinder, and the amount of food consumed (gut fullness) was also higher at the four southernmost study sites.

The dietary patterns of the rock lobster under study did not differ markedly from those of previous investigations (e.g. Heydorn 1969, Newman and Pollock 1974, Pollock 1979, Barkai and Branch 1988, Barkai *et al.* 1996). The exception was the frequent occurrence of barnacles in the diet, which were not found in studies on *J. lalandii* prior to 1988 (Heydorn 1969, Newman and Pollock 1974, Pollock 1979, Pollock *et al.* 1982). Thereafter, barnacles became an important prey item for *J. lalandii* (Barkai and Branch 1988, Barkai *et al.* 1996), as well as for the alien European

shore crab *Carcinus maenas* (Le Roux *et al.* 1990). Barnacles are also of dietary importance to the East Coast rock lobster *Palinurus delagoae* (Berry 1971). Unlike for the present study, Cape sea urchins were reported to be infrequent prey items (e.g. Heydorn 1969, Pollock 1979, Barkai and Branch 1988) or absent (Pollock *et al.* 1982) in the stomachs of rock lobster. The apparent increase in the quantity of barnacles and urchins consumed may reflect a reduction in the availability of mussels, which are generally considered to be the preferred food source of *J. lalandii* (Pollock 1979, Griffiths and Seiderer 1980, Pollock *et al.* 1982). The notable occurrence of sea urchins in the diet may have serious implications for abalone *Haliotis midae*. Juvenile abalone live almost exclusively beneath sea urchins, from which they derive not only protection but also food (Tarr *et al.* 1996, Day and Branch 2000). Predation by rock lobsters on sea urchins and the possible implications for abalone recruitment have been examined by Mayfield (1998). From an economic standpoint, the finding that recruitment of juvenile abalone has collapsed in certain areas, coincident with the near disappearance of sea urchins (Tarr *et al.* 1996), and the probable role of rock lobsters in this process (Mayfield 1998) remain of critical importance.

LITERATURE CITED

- BADEN, S. P., PIHL, L. and R. ROSENBERG 1990 — Effects of oxygen depletion on the ecology, blood physiology and fishery of the Norway lobster *Nephrops norvegicus*. *Mar. Ecol. Prog. Ser.* **67**: 141–155.
- BARKAI, A. and G. M. BRANCH 1988 — Energy requirements for a dense population of rock lobsters *Jasus lalandii*: novel importance of unorthodox food sources. *Mar. Ecol. Prog. Ser.* **50**: 83–96.
- BARKAI, A., DAVIS, C. L. and S. TUGWELL 1996 — Prey selection by the South African Cape rock lobster *Jasus lalandii*: ecological and physiological approaches. *Bull. mar. Sci.* **58**: 1–8.
- BARKAI, A. and C. McQUAID 1996 — Predator-prey role reversal in a marine benthic ecosystem. *Science* **242**: 62–64.
- BERRY, P. F. 1971 — The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of southern Africa. Unpublished Report, Oceanographic Research Institute, South Africa. **28**: 30 pp.
- BEYERS, C. J. DE B. and P. C. GOOSEN 1987 — Variations in fecundity and size at sexual maturity of female rock lobster *Jasus lalandii* in the southern Benguela ecosystem. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 513–521.
- BEYERS, C. J. DE B., WILKE, C. G. and P. C. GOOSEN 1994 — The effects of oxygen deficiency on growth, intermoult period, mortality and ingestion rates of aquarium-held juvenile rock lobster *Jasus lalandii*. *S. Afr. J. mar. Sci.* **14**: 79–87.
- CARTER, J. A. and D. H. STEELE 1982 — Stomach contents of

- immature lobsters (*Homarus americanus*) from Placentia Bay, Newfoundland. *Can. J. Zool.* **60**: 337–347.
- CARTES, J. E. 1993a — Diets of deep-sea brachyuran crabs in the western Mediterranean Sea. *Mar. Biol.* **117**(3): 449–457.
- CARTES, J. E. 1993b — Diets of deep-water pandalid shrimps on the Western Mediterranean slope. *Mar. Ecol. Prog. Ser.* **96**: 49–61.
- CARTES, J. E. 1994 — Influence of depth and season on the diet of the deep-water aristeid *Aristeus antennatus* along the continental slope (400 to 2 300 m) in the Catalan Sea (western Mediterranean). *Mar. Biol.* **120**: 639–648.
- CARTES, J. E. and P. ABELLÓ 1992 — Comparative feeding habits of polychelid lobsters in the Western Mediterranean deep-sea communities. *Mar. Ecol. Prog. Ser.* **84**: 139–150.
- CERDA, G. and M. WOLFF 1993 — Feeding ecology of the crab *Cancer polyodon* in La Herradura Bay, northern Chile. 2. Food spectrum and prey consumption. *Mar. Ecol. Prog. Ser.* **100**: 119–125.
- CLARKE, K. R. and R. M. WARWICK 1994 — *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory, UK; Natural Environment Research Council: 160 pp.
- COCKCROFT, A. C. 1997 — Biochemical composition as a growth predictor in male west-coast rock lobster (*Jasus lalandii*). *Mar. Freshwat. Res.* **48**: 845–856.
- DAY, E. G. and G. M. BRANCH 2000 — Evidence for a positive relationship between juvenile abalone *Haliotis midae* and the sea urchin *Parechinus angulosus* in the South-Western Cape, South Africa. *S. Afr. J. mar. Sci.* **22**: 145–156.
- ELNER, R. W. and A. CAMPBELL 1987 — Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* **37**: 131–140.
- ENNIS, G. P. 1973 — Food, feeding and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. *J. Fish. Res. Bd Can.* **30**: 1905–1909.
- FIELD, J. G., GRIFFITHS, C. L., GRIFFITHS, R. J., JARMAN, N. [G.], ZOUTENDYK, P., VELIMIROV, B. and A. BOWES 1980 — Variation in structure and biomass of kelp communities along the southwest Cape coast. *Trans. R. Soc. Afr.* **44**(2): 145–203.
- GOOSEN, P. C. and A. C. COCKCROFT 1995 — Mean annual growth increments for male West Coast rock lobster *Jasus lalandii*, 1969–1993. *S. Afr. J. mar. Sci.* **16**: 377–386.
- GRIFFITHS, C. L. and J. L. SEIDERER 1980 — Rocklobsters and mussels – limitations and preferences in a predator-prey interaction. *J. expl mar. Biol. Ecol.* **44**(1): 95–109.
- GRIFFITHS, M. K. P., MAYFIELD, S. and G. M. BRANCH 2000 — A note on a possible influence of traps on assessment of the diet of *Jasus lalandii* (H. Milne-Edwards). *J. exp. Mar. Biol. Ecol.* **247**: 223–232.
- HEYDORN, A. E. F. 1969 — The rock lobster of the South African west coast *Jasus lalandii* (H. Milne-Edwards). 2. Population studies, behaviour, reproduction, moulting, growth and migration. *Investl Rep. Div. Sea Fish. S. Afr.* **71**: 52 pp.
- HYSLOP, E. J. 1980 — Stomach contents analysis – a review of methods and their application. *J. Fish Biol.* **17**(4): 411–429.
- JERNAKOFF, P., PHILLIPS, B. F. and J. J. FITZPATRICK 1993 — The diet of post-plerulus western rock lobster, *Panulirus cygnus* George, at Seven Mile Beach, Western Australia. *Aus. J. mar. Freshwat. Res.* **44**: 649–655.
- JOLL, L. M. and B. F. PHILLIPS 1984 — Natural diet and growth of juvenile western rock lobsters *Panulirus cygnus* George. *J. expl mar. Biol. Ecol.* **75**: 145–169.
- LAWTON, P. and K. L. LAVALLI 1995 — Postlarval, juvenile, adolescent and adult ecology. In *Biology of the Lobster Homarus americanus*. Factor, J. R. (Ed). New York; Academic Press: 47–88.
- LEAVITT, D. F., BAYER, R. C., GALLAGHER, M. L. and J. H. RITTENBURG 1979 — Dietary intake and nutritional characteristics in wild American lobsters (*Homarus americanus*). *J. Fish. Res. Bd Can.* **36**: 965–969.
- LE ROUX, P. J., BRANCH, G. M. and M. A. P. JOSKA 1990 — On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African coast. *S. Afr. J. mar. Sci.* **9**: 85–93.
- MANNEVELDT, G. W. 1995 — Geographical studies on the interaction between the pear limpet, *Patella cochlear*, and the encrusting coralline *Spongites yendoii*. M.Sc. thesis, University of the Western Cape: 197 pp.
- MAYFIELD, S. 1998 — Assessment of predation by the West Coast rock lobster (*Jasus lalandii*): relationships among growth rate, diet and benthic community composition, with implications for the survival of juvenile abalone (*Haliotis midae*). Ph.D. thesis, University of Cape Town: 213 pp.
- NEWMAN, G. G. and D. E. POLLOCK 1974 — Growth of the rock lobster *Jasus lalandii* and its relationship to benthos. *Mar. Biol.* **24**(4): 339–346.
- O'BRIEN, C. J. 1994 — Ontogenetic changes in the diet of juvenile brown tiger prawns *Penaeus esculentus*. *Mar. Ecol. Prog. Ser.* **112**: 195–200.
- POLLOCK, D. E. 1979 — Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape west coast of Africa. *Mar. Biol.* **52**(4): 347–356.
- POLLOCK, D. E. 1986 — Review of the fishery for and biology of the Cape rock lobster *Jasus lalandii* with notes on larval recruitment. *Can. J. Fish. aquat. Sci.* **43**(11): 2107–2117.
- POLLOCK, D. E., AUGUSTYN, C. J. and P. C. GOOSEN 1982 — The rock lobster *Jasus lalandii* and its environmental biology on the Saldanha–Columbine fishing ground off the Cape west coast, 1978–1981. *Investl Rep. Sea Fish. Inst. S. Afr.* **125**: 30 pp.
- TARR, R. J. Q., WILLIAMS, P. V. G. and A. J. MACKENZIE 1996 — Abalone, sea urchins and rock lobster: a possible ecological shift that may affect traditional fisheries. *S. Afr. J. mar. Sci.* **17**: 319–323.
- VAN ZYL, R. F., MAYFIELD, S., PULFRICH, A. and C. L. GRIFFITHS 1998 — Predation by West Coast rock lobsters (*Jasus lalandii*) on two species of wrinkle (*Oxysteles sinensis* and *Turbo cidaris*). *S. Afr. J. Zool.* **33**(4): 203–209.
- WASSENBERG, T. J. and B. J. HILL 1989 — Diets of four decapod crustaceans (*Linuparus trigonus*, *Metanephrops andamanicus*, *M. australiensis* and *M. boschmai*) from the continental shelf around Australia. *Mar. Biol.* **103**: 61–167.
- WILLIAMS, M. J. 1981 — Methods for the analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *J. expl mar. Biol. Ecol.* **52**: 103–113.
- ZAR, J. H. 1984 — *Biostatistical Analysis*, 2nd ed. Englewood Cliffs, New Jersey; Prentice-Hall: xiv + 718 pp.
- ZOUTENDYK, P. 1988a — Feeding, defaecation and absorption efficiency in the Cape rock lobster *Jasus lalandii*. *S. Afr. J. mar. Sci.* **6**: 59–65.
- ZOUTENDYK, P. 1988b — Consumption rates of captive Cape rock lobster *Jasus lalandii*. *S. Afr. J. mar. Sci.* **6**: 267–271.