

1976/20.

"Ecology of coastal reefs : The nurseries for juvenile
western rock lobsters"

Final Report to the Fishing Industry Research Committee.

Introduction

The proposal to study the nurseries for juvenile western rock lobsters (*Panulirus cygnus*) stemmed from broadly based research upon various stages of the life cycle. It was concluded that density-dependant pressures on mortality and growth operating upon juveniles during the 4-5 years spent on coastal nursery reefs were the main determinants for natural regulation of this population. These pressures apparently act through limitations of food and shelter with the interaction of predation. The project was designed to elucidate the main features of the diet of juvenile rock lobsters to provide the first step in understanding the relationships of prey, competitors and predators within the reef community.

Two localities were chosen for study, Cliff Head and Seven Mile Beach, near Dongara, W.A. Studies carried out at Seven Mile Beach since 1970 have shown it to be an area of high density of rock lobsters with high mortality rates (Chittleborough and Phillips 1975) and reduced annual growth (Chittleborough 1976). Moulting increments at Seven Mile Beach were found to be significantly less than those of animals raised under optimal, constant temperature (25°C) conditions in aquaria and were considered to be a major contributor to the reduced annual growth. Limited field work at Cliff Head, including the transplanting of lobsters from Seven Mile Beach, had shown it to be an area of high annual growth comparable with aquarium animals (Chittleborough 1976). Laboratory work on factors influencing the growth of rock lobsters by Chittleborough (1975) had shown that both moulting increment and moulting frequency were affected by a variety of environmental factors. However, of the factors examined, only extreme food shortage during the preceding intermoult period and shortage of oxygen at the time of the moult affected moulting increment. Oxygen levels measured in the field were found to be close to 100% saturation. The reduced moulting increments were considered by Chittleborough (1976) to indicate that food was probably

in short supply at Seven Mile Beach while the more limited studies at Cliff Head indicated that this was an area of high food availability.

Methods

Sampling commenced in April 1977 and was carried out at approximately 3- monthly intervals until October 1978. As rock lobsters are nocturnal foragers (Fielder 1965, Morgan 1978) the time of sampling was adjusted with seasonal changes in the time of sunrise and was restricted to a one hour period between two hours and one hour before sunrise. The rock lobsters were caught by hand by SCUBA diving and the stomachs removed and fixed in buffered 10% formol sea-water within two hours of capture. The stomachs were subsequently transferred to 70% alcohol. In the laboratory the volume of the contents of the foregut of each individual was determined to the nearest 0.05 cc by displacement in a volumetric cylinder. The contents of the stomach were sorted under a binocular microscope to the lowest taxonomic category possible and the contribution (percentage) of each item to the total amount of food present estimated by eye. Density and mortality data were collected for Seven Mile Beach using the techniques described by Chittleborough and Phillips (1975) as part of a continuing monitoring at this site. In 1978 an attempt was made to also collect these data for Cliff Head. Annual growth and moult increment data were obtained from both sites by tagging.

Gastric evacuation times were measured in the aquarium at 25°C. Four foods were used - the foliose coralline algae *Corallina cuvieri* and *Metagoniolithon stelligera*, the littorinid gastropod *Littorina unifasciata* and foot muscle of the abalone *Haliotis roei*. Rock lobsters were held individually and starved for 24 hrs prior to the experiment. They were presented with a weighed quantity of one of the four foods and allowed to eat for 2 hrs. Experimental animals were then killed at 0, 2, 4 and 6 hrs after the termination of the feeding period and the weight of

Food in the stomach determined.

A limited number of determinations of the uptake of organic matter from *C. cuvieri* and *M. stelligera* were also made. Samples of these algae and material from the hindguts of animals which had fed on them were ashed in a muffle furnace at 500°C for 4 hrs. Organic uptake was calculated using the ash ratio method of Conover (1966).

The possibility of uptake of calcium by rock lobsters from coralline algae was examined by feeding Ca₄₅ labelled *C. cuvieri* to rock lobsters in aquaria. A control group of animals was maintained in seawater "spiked" with Ca₄₅. One group of animals was killed the following day and various tissues removed for analysis. Another group was killed after being maintained unfed for three days in flowing seawater and the same tissue types removed for analysis.

Results

i) Food: A total of 779 rock lobsters were collected and examined, 393 from Seven Mile Beach and 386 from Cliff Head. Some had empty or only partially filled stomachs and animals with amounts of food less than 10% of the maximum stomach capacity (Maller et al. in prep.) were eliminated from the data set. The diets for each sample date (Tables 1, 2 and 3) show that, at least for most months, marked differences occurred between the two sites.

At Seven Mile Beach rock lobsters ate considerable quantities of plant material. Coralline algae accounted for the greater part of this plant matter, showing values ranging from 28.8% (by volume) of the diet in November 1977 to 55.8% in April 1977 (Table 1). Species eaten were the foliose corallines *Corallina cuvieri* and *Metagoniolithon stelligera* with occasional pieces of *Jania* spp. Non-coralline algal species ranged from 2.0% to

21.1% of the diet in April 1977 and October 1978 respectively. They were represented by an assorted mixture of browns, reds and greens but were dominated by the fleshy green alga *Caulerpa cactoides*. Seagrasses were also a large proportion of the diet, ranging from 6.7% in May 1978 to 21.9% in February 1978. The fragments of seagrass could not be consistently identified to specific or generic level but fragments of all four genera (*Amphibolus*, *Halophila*, *Syringodium* and *Heterozostera*) present in the Seven Mile Beach area were recognized.

The dominant invertebrates in the diet were molluscs and crustacea, with polychaetes being somewhat less important. While several mollusc groups (the Solemyidae and Lucinidae amongst the bivalves and *Bittium* sp. amongst the gastropods) stand out as being somewhat more important than others (Table 2), the variety of species consumed is also impressive. Most of the molluscs consumed were small (< 5 mm maximum dimension) while some (*Diala* spp., *Mitrella* sp., *Eatoniella* sp.) were sufficiently small to be eaten whole. Many of the species ingested are common components of the epifauna of the seagrasses, particularly *Amphibolus* spp. They also occur commonly amongst the corallines *C. cuvieri* and *M. stelligera* which are epiphytic on *Amphibolus* spp. The two dominant bivalve families, Lucinidae and Solemyidae, however, occur as infauna in the sediments of seagrass beds.

The diversity of crustacean species consumed appears lower than that of molluscs but this is partly a result of the difficulty in identifying the fragmented remains of many of the crustaceans. Amphipods and isopods were usually very fragmented and it was not possible to identify these at lower taxonomic levels. Crabs of the genus *Hallicarcinus* contributed between 0.1 and 1.0% of the diet whilst other crabs comprised only between 0.06 and 0.48% (Table 2). Fragments of *Panulirus* exoskeleton occurred in all samples except that from August 1977. The fragments were predominantly

antennae and antennules, the tips of the pereopods and portions of the carapace. The percentage was highest in November 1977 and this corresponded with the high moulting activity occurring at that time. Indeed all the *Panulirus* fragments appeared to be from moults as no attached tissue was apparent. The particular portions of the exoskeleton eaten also correspond with those portions of moults eaten by animals in aquaria. The correspondence between the percentage consumed and general moulting activity, the particular appendages eaten and their lack of visible tissue all point to the ingestion of moults rather than cannibalism.

Polychaetes contributed only a small proportion of the total diet and were represented mostly by jaws and setae, although they were sometimes encountered in a semi-digested state. The more rapid digestion of the soft bodies of these animals undoubtedly causes their contribution on a volume basis in the stomach to be smaller than in the ingested food. On a frequency of occurrence basis polychaetes occurred in between 25.5 and 89.6% of stomachs (Table 3). The dominant polychaete families were Nereidae, Eunicidae and Aphroditidae.

The category entitled "other" comprises a hotch-potch of organisms and inanimate material such as sand and siliceous and calcareous spicules. Sand is the dominant item of the category and it is likely that this is ingested accidentally in the consumption of other items of the diet. The digested material was a flocculant "goo" which contributed between 16 and 22% of the volume of the food. It was not possible to distinguish which components of the stomach contents contributed to this category but it was presumably the more digestible items.

The diet of animals from Cliff Head showed marked differences in most months from the diet of animals at Seven Mile Beach. Animals at Cliff Head showed an overall mean percentage by volume of coralline algae of

18.3% compared with 41.2% for Seven Mile Beach (Table 1). Although *C. cuvieri* was still the dominant species of algae consumed, species of the genus *Jania* showed a greater contribution at Cliff Head (Table 2). The consumption of non-corallines was also less at Cliff Head with a mean 3.4% compared with 10.5% at Seven Mile Beach. This difference was largely due to a much smaller consumption of *C. cactoides* at Cliff Head. Seagrass consumption at Cliff Head was also smaller, than at Seven Mile Beach (5.8% compared with 12.8%). There were only small differences in the polychaete content of the diet at the two localities on either a percentage volume basis (0.63% at Cliff Head, 1.39% at Seven Mile Beach) or a percentage frequency of occurrence (43.5% at Cliff Head, 59.5% at Seven Mile Beach). Probably the most important difference between the two sites was the mollusc component which showed a mean of 24.9% (by volume) of the diet at Cliff Head compared with only 7.3% at Seven Mile Beach. In February 1978 molluscs comprised 43.5% of the diet (by volume) compared with a maximum of 12.8% at Seven Mile Beach. The molluscan portion of the diet was dominated by a single species of trochid gastropod, *Prothalotia lepidus*, with mytilid bivalves (primarily *Brachydontes* sp.) making a significant contribution in some samples. The mean crustacean component of the diet showed little difference between the two sites (2.9% at Cliff Head compared with 2.1% at Seven Mile Beach). The greater proportion of *Panulirus* exoskeleton at Cliff Head (12.2%) compared with that at Seven Mile Beach (2.6%) may reflect a higher moulting frequency at Cliff Head or it may be coincidental. A number of environmental factors, especially temperature, (Chittleborough 1975) affect moulting frequency and it may be that samples at Cliff Head coincided with moulting periods more frequently than at Seven Mile Beach. A further possibility is that animals at Cliff Head consume greater quantities of moulted

exoskeletons to satisfy some nutritional requirement.

There was a somewhat larger contribution by the "other" category at Cliff Head, (7.5% compared with 3.7%) due primarily to a greater consumption of echinoids, ascidians and unidentified tissue. The overall mean of the percentage of digested material was also slightly higher (24.4% compared with 18.4%).

ii) Growth and Density. Annual growth and moult increments at the two sites were monitored during 1978 to provide growth data in the same time period as the food sampling was conducted. The annual growth in 1978 (Fig. 1) at the two sites was significantly different ($P < 0.001$). However annual growth at each site was not significantly different ($P > 0.05$) to that recorded by Chittleborough (1976) for previous years.

Single moult increments (Table 4) also showed significant differences ($P < 0.05$) between the two sites for animals of equivalent ages in 1978. Single moult increments for animals at Cliff Head did not differ significantly ($P > 0.05$) from those of aquarium reared animals (Chittleborough (1976)).

Densities and mortalities were recorded at Seven Mile Beach in both 1977 and 1978 as part of a continuing programme at that site while special measurements of these data were carried out at Cliff Head only in 1978 (Table 5). Total densities at Seven Mile Beach were considerably higher at Seven Mile Beach in both years than at Cliff Head in 1978. The mortality rates at Seven Mile Beach varied widely between the two years considered, that in 1978 being the second highest on record. It was not possible to determine the mortality coefficient for Cliff Head in 1978 as the density of animals was greater in August than in January. Water temperatures in the density test area were extremely high in January (28-29°C) and it appeared that animals moved out of the test area and re-invaded it when the temperatures improved.

iii) Gastric evacuation. Differences in the rate of gastric evacuation may lead to errors in volumetric analysis of stomach contents as slowly evacuating foods remain in the stomach for longer periods of time than the more rapidly evacuating foods. Of the four foods examined the time for complete, or almost complete, gastric evacuation was 4 to 6 hrs at 25°C (Fig. 2), although there was considerable individual variation. Animal foods (*L. unifasciata* and abalone foot muscle) were evacuated somewhat more rapidly than the two coralline species but the differences between them were relatively small. In the *Littorina* diet it was observed that the tissue was evacuated more rapidly than the shell and operculae. While only four species were examined they represent a fairly diverse range of food types and it would seem reasonable to generalize from the results that extremely wide differences in evacuation rate, such as reported by Hill (1976) for *Scylla serrata*, are unlikely. Consequently large biases in the gut content analysis due to differences in evacuation rate are also unlikely. Foods with a high proportion of tissue to hard parts (e.g. polychaetes) are, however, probably somewhat underestimated.

iv) Nutritive value of corallines. The presence of large quantities of coralline algae in the diet of animals from Seven Mile Beach raises questions about its nutritive value. Uptake of organic material from both *C. cuvieri* and *M. stelligera* was found, although the efficiency of absorption measured by the ash ratio method varied from 0% to 40.3%. A basic assumption of the ash ratio technique is that the mineral (ash) component passes through the animal unabsorbed. However one of the nutritive values of consuming coralline algae may be the calcium contained in the skeleton of the algae. Uptake of calcium would cause the organic absorptions measured by the ash ratio technique to be underestimated. Using Ca_45 labelled *C. cuvieri* fed to intermoult rock lobsters it was

found that calcium is indeed taken up from *C. cuvieri*. Immediately after the meal the calcium is fairly evenly distributed through the tissues of the animal but after 3 days is mostly localized in the exoskeleton.

Discussion

The dietary data showed major differences in the diet between the two localities in most seasons. At Cliff Head the diet had a much greater proportion of invertebrate animal material, predominantly molluscs, than at Seven Mile Beach. The diet at Cliff Head was correlated with annual growth and moult increments comparable with that of animals reared in the aquarium under constant temperature conditions on a diet of mussels and abalone to excess. The diet of animals at Seven Mile Beach was characterized by a large proportion of plant matter, notably a variety of seagrasses, two species of coralline algae and a fleshy green alga (*C. cactoides*). The role of the seagrasses and *C. cactoides* in the diet are unknown. The seagrasses appeared more or less intact throughout the digestive tract and it may be that they are consumed accidentally in the consumption of other organisms and do not contribute directly to the animals' nutrition. *C. cactoides*, on the other hand, was usually encountered in a very broken up condition and in fact this plant proved one of the most difficult items to identify because of its state in the stomach. Its role in overall nutrition is also unclear but its degree of digestion suggests that it may be of direct nutritive value. The two species of coralline algae were shown to be a source of some organic nutrition as well as a source of calcium for the exoskeleton.

Newman and Pollock (1974) reported a similar situation with male South African rock lobsters (*Jasus lalandii*) at Dassen I. Rock lobsters in areas of high food availability showed significantly higher moult increments

than those from areas of low food availability. The principal food for *J. lalandii* was the mussel *Aulocomya magellanica* but there was no evidence that animals in the low food availability areas turned to plant material as an alternative food. The presence of large amounts of plant material in the diet of *P. cygnus* at Seven Mile Beach is, however, not without parallels in the diets of other Palinurids. Heydorn (1969) reported that the diet of *J. tristani* from Gough I. and Tristan da Cunha was almost entirely vegetarian, consisting predominantly of fragments of both red and green algae. Juveniles of *P. argus* from Brazil were reported by Fernandes (1971) to have a mixed diet of plant and animal material, with plant material in 25% of the stomachs examined. This consisted of both seagrass (*Diplanthera* sp.) and algae, with the coralline alga *Jania* being the commonest alga. Winget (1968) reported that the diet of the Californian spiny lobster *P. interruptus* was also a mixture of plant and animal material. Algae, both corallines and brown algae, and the surf grass *Phyllospadix* constituted between 0.2 and 34% of the diet by dry weight and between 10 and 78% on a frequency of occurrence basis, depending on locality and season.

Despite the presence of plant material in the diet of many palinurids both this work and that of Newman and Pollock (1974) indicate that a certain proportion of animal material is required in the diet to achieve full growth potential. Why then are rock lobsters at Seven Mile Beach unable to attain the required intake of animal matter? The very high densities of juvenile rock lobsters at Seven Mile Beach means that the available food supply at this site is divided up amongst more animals. The role of competitors at both sites is unknown but it would appear that the number of rock lobsters at Seven Mile Beach exceeds the carrying capacity of the sea bed. Chittleborough and Phillips (1975) suggested that the

high, density-dependant wastage of young juveniles could be avoided without affecting the level of subsequent recruitment to the fishery by cropping off the excess animals. These excess animals could then be used to stock underpopulated reefs or reared in captivity. Experiments are planned for 1981 to examine the effect on growth, survival and nutritional condition of artificially reduced densities. Concurrent programmes are examining other components of the fauna to identify possible competitors and predators.

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Table 1

Mean percentage by volume of major food categories in the
stomach contents of juvenile rock lobsters

a) Seven Mile Beach

	Coralline Algae	Non- Coralline Algae	Seagrass	Poly- chaetes	Molluscs	Crust- acea	Panulirus	Other	Digested Material
April 1977 N=63	55.76	2.03	12.98	1.41	4.37	3.10	1.06	2.71	16.56
Aug. 1977 N=8	44.31	11.27	9.33	1.06	9.42	2.15	0	4.13	18.33
Nov. 1977 N=67	28.78	14.58	11.04	1.19	11.45	3.30	6.12	2.06	21.48
Feb. 1978 N=65	41.03	4.62	21.92	0.92	12.83	1.18	2.55	0.95	13.98
May 1978 N=46	49.80	8.91	6.72	3.83	2.50	0.89	3.80	3.35	20.20
Aug. 1978 N=45	36.20	13.22	9.47	1.56	3.87	1.98	0.93	10.29	22.49
Oct. 1978 N=51	33.84	21.08	14.63	0.22	3.94	1.76	2.65	4.90	16.98
Overall Total N=385	41.25	10.46	12.76	1.39	7.32	2.12	2.58	3.37	18.38

b) Cliff Head

April 1977 N=13	6.19	2.98	2.56	0.26	34.60	1.39	17.46	11.93	22.63
Aug. 1977 N=16	55.06	3.12	14.44	0.25	1.12	0	1.0	12.25	16.75
Nov. 1977 N=66	13.15	2.68	7.74	0.50	20.26	3.55	25.42	7.98	18.71
Feb. 1978 N=23	3.52	3.22	1.13	0.17	43.52	8.30	2.78	7.22	30.13
May 1978 N=43	20.19	1.30	6.42	1.77	31.77	3.60	4.47	3.95	26.53
Aug. 1978 N=11	33.55	3.64	6.64	1.27	14.36	3.18	6.09	3.91	27.36
Nov. 1978 N=37	28.05	7.84	6.08	0.22	15.76	0.24	3.81	4.89	33.11
Overall N=239	18.29	3.41	5.81	0.63	24.90	2.86	12.17	7.51	24.42

Table 2. Mean percentage by volume of stomach
contents of juvenile rock lobsters

Table 2a Seven Mile Beach

Date	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
Food type	N=63	N=48	N=67	N=65	N=46	N=45	N=51	N=385
1. Corallina cuvieri	32.90	19.02	8.31	19.97	33.11	19.82	15.75	20.93
2. Metagoniolithon stelligera	22.84	25.21	18.75	20.83	16.69	16.36	17.65	19.90
3. Jania spp.	0.02	0.08	1.72	0.23	-	0.02	0.45	0.41
4. Other corallines	-	-	-	-	-	-	-	-
5. Other reds	0.62	0.17	0.51	0.31	0.46	0.13	0.18	0.36
6. Caulerpa cactoides	0.97	11.06	13.57	4.09	4.82	12.36	19.86	9.24
7. Other greens	0.32	-	0.22	0.20	3.37	0.56	0.84	0.71
8. Browns	0.11	0.02	0.03	0.02	0.24	0.18	0.16	0.10
9. Blue-greens	0.02	-	-	-	-	-	-	-
10. Ui/d algae	-	0.02	0.25	-	0.02	-	0.04	0.05
11. Seagrasses	12.98	9.33	11.04	21.92	6.72	9.47	14.63	12.76
12. Nereidae	0.13	0.69	0.45	0.05	0.72	0.13	0.06	0.30
13. Eunicidae	0.11	0.21	0.37	0.03	2.20	0.71	-	0.46
14. Aphroditidae	0.62	0.02	0.09	-	0.17	0.09	-	0.15
15. Pectinariidae	-	0.02	0.21	-	-	0.02	0.10	0.05
16. Other polychaetes	-	0.02	0.01	0.02	0.04	0.20	-	0.04
17. Ui/d polychaetes	0.03	0.04	-	0.05	0.56	0.29	-	0.12

Da	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
18. Sipunculoidea	0.32	-	0.03	-	0.11	-	-	0.07
19. Ui/d "worms"	0.21	0.06	0.03	0.78	0.02	0.11	0.06	0.20
20. Solemyidae	0.65	2.92	2.13	1.25	0.02	0.22	0.04	1.09
21. Lucidinidae	0.51	2.44	2.09	7.89	0.11	0.38	0.22	2.17
22. Mytilidae	0.84	0.15	0.15	0.43	0.28	0.16	0.20	0.33
Other bivalves	0.05	0.04	-	-	-	-	0.08	0.02
24. Ui/d bivalves	0.02	0.37	0.72	0.45	0.24	0.56	0.94	0.47
25. Gastropod egg capsules	0.02	-	0.84	0.28	0.43	0.11	0.02	0.26
26. Amphineura	0.16	0.23	0.18	0.01	-	-	-	0.09
27. "Limpets"	-	0.17	0.04	-	-	-	-	0.03
28. Prothalotia lepidus	0.11	0.06	0.04	0.16	0.06	0.07	0.14	0.09
Prothalotia spp.	0.03	-	0.66	0.17	0.06	-	0.16	0.18
30. Komaitrochus pulcher	0.27	0.23	0.10	0.09	0.19	0.09	0.16	0.16
31. Other Trochidae	0.08	0.02	0.09	0.06	-	-	0.08	0.05
32. Tricolia spp.	0.16	-	0.28	0.09	-	0.02	0.02	0.10
33. Phasianella spp.	0.38	0.50	0.18	0.19	0.04	0.16	0.02	0.21
34. Other Turbinidae	0.05	0.02	-	0.03	-	-	-	0.01
35. Bittium sp.	0.90	1.00	2.70	0.63	0.24	0.71	1.00	1.10

Date	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
36. <i>Diala</i> spp.	-	-	0.48	-	0.02	0.04	0.04	0.10
37. Other Cerithiidae	-	-	0.27	-	0.02	0.04	0.10	0.07
38. <i>Pyrene</i> sp.	0.06	0.37	0.01	0.58	0.26	0.17	0.27	0.24
39. <i>Dentimitrella</i> sp.	0.03	0.04	0.09	0.09	-	0.04	-	0.05
40. <i>Mitrella</i> sp.	-	-	-	-	-	-	-	-
Other Columbelloidea	-	-	0.01	-	-	-	-	-
42. <i>Eatoniella</i> sp.	0.03	-	0.03	-	-	-	0.02	0.01
43. Other Rissoidea	-	-	0.01	0.05	0.02	0.18	0.29	0.07
44. <i>Chemnitzia</i> sp.	-	0.27	0.04	0.09	0.02	0.64	0.04	0.14
45. Other Pyramidelloidea	0.02	0.02	0.03	0.02	-	0.02	-	0.02
46. Nassariid sp.	-	0.02	0.03	0.08	0.06	0.07	0.06	0.04
47. Other Nassariidae	-	0.02	0.01	-	-	-	-	0.01
48. "Bubble shells"	-	-	0.03	0.02	0.02	-	0.02	0.01
49. U/d opisthobranchs	-	-	0.01	-	-	-	-	-
50. Other gastropods	-	-	0.01	0.02	-	-	0.04	0.01
51. U/d gastropods	-	0.15	0.09	0.02	-	0.16	-	0.05
52. Gastropod foot muscle	-	0.10	0.01	0.11	0.33	-	-	0.07
53. U/d mollusc tissue	-	0.27	0.03	0.02	0.04	0.02	-	0.05

Da	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
54. Other mollusc material	-	-	0.01	0.03	-	-	-	0.01
55. Isopoda	0.22	-	0.98	0.45	0.09	0.04	0.27	0.34
56. Amphipoda	0.38	0.08	0.88	0.12	0.30	0.73	0.29	0.41
57. Stomatopoda	-	-	-	-	-	-	-	-
58. Alpheidae	-	0.31	-	-	-	-	0.02	0.05
59. Other carids and penaeids	0.05	-	0.07	-	-	-	-	0.02
60. Halicarcinus spp.	1.02	0.71	0.10	0.27	0.30	0.13	0.10	0.38
61. Hermit crabs	0.63	-	-	-	-	-	-	0.10
62. Other crabs	0.24	0.48	0.43	0.02	0.06	0.27	0.14	0.23
63. Panulirus (exoskeleton)	1.06	-	6.12	2.55	3.80	0.93	2.65	2.58
64. Other macrurans	0.02	-	-	-	-	-	-	-
65. Other crustacea	0.30	0.10	-	0.02	-	-	-	0.06
66. Ui/d crustacea	0.24	0.46	0.82	0.33	0.13	0.80	0.84	0.52
67. Discorbis sp.	0.14	0.04	-	0.03	0.28	0.22	0.14	0.11
68. Marginopara sp.	0.02	0.08	0.13	0.02	0.02	0.31	0.18	0.10
69. Elphidium spp.	-	-	-	-	-	0.07	-	0.01
70. Other foraminifera	-	-	0.01	-	-	0.09	-	0.01
71. Ui/d foraminifera	-	-	-	-	-	-	-	-
72. Echinoidea	0.02	-	0.18	-	0.02	-	-	0.04

Date	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
73. Ophiuroidea	-	-	-	-	-	-	0.82	0.11
74. Sand	1.59	2.23	1.03	0.36	1.48	8.60	2.51	2.30
75. Fish:scales/bones/ tissue	0.17	0.21	0.16	0.03	0.35	0.07	0.20	0.16
76. Siliceous and calcareous spicules	-	-	0.07	-	0.20	0.44	0.20	0.11
77. Sponge tissue	0.08	0.75	0.03	0.08	0.20	-	0.16	0.17
88. Ascidian	-	-	-	0.16	-	-	0.22	0.05
79. U/d tissue	0.29	0.42	0.28	-	0.02	0.44	0.25	0.24
80. Pycnogonida	-	-	0.09	0.12	0.02	-	0.20	0.06
81. Hydrozca	0.05	0.06	0.05	0.08	0.02	-	0.04	0.04
82. Bryozoa	-	-	-	-	0.04	-	-	-
83. Unidentifiable	0.36	0.33	0.01	0.09	0.70	0.04	-	0.21
84. Cow hide and hair	-	-	-	-	-	-	-	-
85. Digested material	16.56	18.33	21.48	13.98	20.20	22.49	16.98	18.38

Table 2b Cliff Head

Date		Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
Food type		N=43	N=16	N=66	N=23	N=43	N=11	N=37	N=239
1.	Corallina cuvieri	1.07	44.62	6.68	0.91	14.49	33.54	22.84	12.80
2.	Metagoniolithon stelligera	1.00	7.69	1.70	1.91	3.53	-	2.81	2.42
3.	Jania spp.	4.11	2.75	4.77	0.70	0.37	-	2.40	2.75
4.	Other corallines	-	-	-	-	1.79	-	-	0.32
5.	Other reds	1.21	2.25	0.09	0.04	0.39	1.18	0.05	0.53
6.	Caulerpa cactoides	-	0.62	1.38	-	0.19	2.27	3.27	1.07
7.	Other greens	0.84	0.25	1.20	0.04	0.33	0.09	4.24	1.22
8.	Browns	0.88	-	0.01	0.74	0.33	0.09	0.27	0.34
9.	Blue-greens	-	-	-	-	-	-	-	-
10.	Ui/d algae	0.05	-	-	2.39	0.07	-	-	0.25
11.	Seagrasses	2.56	10.44	7.74	1.13	6.42	6.64	6.08	5.81
12.	Nereidae	0.02	-	0.06	-	0.14	0.27	-	0.06
13.	Eunicidae	0.07	-	0.11	0.13	0.46	0.36	0.08	0.17
14.	Aphroditidae	-	-	0.06	-	0.05	-	-	0.02
15.	Pectinariidae	-	-	-	-	0.05	0.45	-	0.03
16.	Other polychaetes	0.05	-	0.05	-	0.19	0.18	-	0.06
17.	Ui/d polychaetes	-	-	0.06	0.04	0.65	-	0.08	0.15

Date	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
36. <i>Diala</i> spp.	0.16	-	-	0.91	0.07	-	-	0.13
37. Other Cerithiidae	-	-	0.01	-	-	-	-	-
38. <i>Pyrene</i> sp.	0.16	-	-	-	0.21	-	0.03	0.07
39. <i>Dentimitrella</i> sp.	0.16	-	-	-	-	-	-	0.03
40. <i>Mitrella</i> sp.	0.46	-	0.14	0.65	1.42	-	0.05	0.44
41. Other Columbellidae	-	-	-	-	-	-	-	-
42. <i>Eatoniella</i> sp.	0.02	-	0.03	-	-	-	-	0.01
43. Other Rissoidae	0.02	-	0.03	-	-	-	0.08	0.02
44. <i>Chemnitzia</i> sp.	0.02	-	0.07	-	-	-	0.11	0.04
45. Other Pyramidellidae	0.05	-	0.07	-	-	-	-	0.03
46. Nassariid sp.	0.63	-	0.26	0.17	0.39	-	0.08	0.29
47. Other Nassariidae	-	-	0.03	-	-	-	-	0.01
48. "Bubble shells"	-	-	0.11	0.30	-	-	-	0.06
49. <i>U/d</i> opisthobranchs	-	-	0.03	-	-	-	-	0.01
50. Other gastropods	-	-	-	0.04	-	-	-	-
51. <i>U/d</i> gastropods	-	0.06	0.04	-	0.07	-	0.05	0.04
52. Gastropod foot muscle	-	-	0.08	0.78	0.07	-	-	0.11
53. <i>U/d</i> mollusc tissue	-	-	0.15	-	0.26	0.45	0.05	0.12

Date	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct.	Overall
54. Other mollusc material	0.09	0.06	-	-	-	-	-	0.02
55. Isopoda	0.49	-	0.56	5.39	0.77	-	0.08	0.91
56. Amphipoda	0.02	-	0.35	0.70	0.07	-	0.13	0.20
57. Stomatopoda	-	-	-	-	1.46	-	-	0.27
58. Alpheidae	-	-	-	-	-	-	-	-
59. Other carids and penaeids	-	-	-	-	0.02	-	-	-
60. Halicarcinus spp.	0.39	-	0.65	0.48	0.16	-	-	0.33
61. Hermit crabs	-	-	-	-	-	-	-	-
62. Other crabs	0.02	-	0.11	-	0.46	-	0.03	0.12
63. Panulirus (exoskeleton)	17.46	1.00	25.42	2.78	4.46	6.09	3.81	12.17
64. Other macrurans	-	-	-	-	-	-	-	-
65. Other crustacea	-	-	-	-	-	-	-	-
66. Ui/d crustacea	0.46	-	1.88	1.74	0.65	3.18	-	1.03
67. Discorbis sp.	-	-	0.03	-	-	-	0.11	0.02
68. Marginopara sp.	-	-	0.17	0.04	-	-	0.03	0.05
69. Elphidium spp.	-	-	0.14	-	-	-	0.03	0.04
70. Other foraminifera	-	-	-	-	-	-	-	-
71. Ui/d foraminifera	-	-	0.01	0.04	-	-	-	0.01
72. Echinoidea	-	-	5.36	-	0.35	-	-	1.54

Date	Apr. 77	May 77	Nov. 77	Feb. 78	May 78	Aug. 78	Oct. 78	Overall
73. Ophiuroidea	-	-	0.01	-	-	-	-	-
74. Sand	1.00	0.12	0.77	1.61	0.30	3.82	1.03	0.95
75. Fish:scales/bones/ tissue	0.12	-	0.61	-	0.09	-	1.46	0.43
76. Siliceous and calcareous spicules	0.02	-	0.06	-	-	-	0.08	0.03
77. Sponge tissue	0.30	-	0.09	0.22	-	-	-	0.10
78. Ascidian	2.79	0.12	0.29	2.26	2.72	-	1.08	1.46
79. U/i/d tissue	7.33	1.37	0.04	1.78	0.37	-	-	1.66
80. Pycnogonida	-	-	-	-	-	-	0.03	-
81. Hydrozoa	0.37	0.31	0.11	0.04	-	-	-	0.12
82. Bryozoa	-	-	0.01	0.56	-	-	-	0.06
83. Unidentifiable	-	-	0.27	0.65	0.11	0.09	1.05	0.33
84. Cow hide and hair	-	10.31	-	-	-	-	-	0.70
85. Digested material	22.63	16.75	18.71	30.13	26.53	27.36	33.11	24.42

Table 3

Percentage frequency of occurrence of major categories in the stomach contents
of juvenile P. cygnus

a) Seven Mile Beach

		Coralline Algae	Non- Coralline Algae	Seagrass	Poly- chaetes	Molluscs	Crust- acea	Panulirus	Other	Digested Material
	N	%	%	%	%	%	%	%	%	%
April 77	63	98.4	66.7	98.4	54.0	100.0	60.3	6.3	92.1	100.0
Aug. 77	48	100.0	91.7	100.0	89.6	100.0	64.6	4.2	93.7	100.0
Nov. 77	67	97.0	91.0	97.0	85.1	98.5	79.1	35.8	85.1	100.0
Dec. 77	65	96.9	76.9	98.5	36.9	100.0	52.3	21.5	87.7	100.0
May 78	46	97.8	87.0	100.0	58.7	82.6	43.5	30.4	87.0	100.0
Aug. 78	45	97.8	86.7	97.8	68.9	95.5	44.4	31.1	97.8	100.0
Oct. 78	51	98.0	98.0	98.0	25.5	90.2	47.1	39.2	86.3	100.0
Overall	385	97.9	84.7	98.4	59.5	95.8	57.1	23.9	89.6	100.0

b) Cliff Head

		Coralline Algae	Non- Coralline Algae	Seagrass	Poly- chaetes	Molluscs	Crust- acea	Panulirus	Other	Digested Material
	N	%	%	%	%	%	%	%	%	%
April 77	43	76.7	86.0	93.0	39.5	100.0	60.5	48.8	90.7	100.0
Aug. 77	16	93.7	93.7	100.0	18.7	50.0	12.5	12.5	93.7	100.0
Nov. 77	66	89.4	77.3	93.9	53.0	92.4	53.0	69.7	12.1	100.0
Feb. 78	23	47.8	87.0	43.5	26.1	100.0	87.0	13.0	78.3	100.0
May 78	43	76.7	72.1	76.7	53.5	100.0	60.5	25.6	62.8	100.0
Aug. 78	11	90.9	72.7	72.7	54.5	90.9	36.4	9.1	63.6	100.0
Oct. 78	37	94.6	73.0	97.3	37.8	94.6	16.2	45.9	81.1	100.0
Overall	239	82.0	79.1	85.8	43.5	93.3	49.8	42.3	60.2	100.0

Table 4Single Moulth Increments of Western Rock Lobsters

(Aquarium data from Chittleborough (1976); Field data
is from 1978 only)

Males

Females

1. Aquarium

(food to excess, 25°C)

<u>Age</u>	<u>Mean</u>	<u>se</u>	<u>n</u>	<u>Mean</u>	<u>se</u>	<u>n</u>
2+	5.0	0.2	15	5.6	0.2	14
3+	5.1	0.5	11	4.3	0.4	12
4+	3.5	0.5	11	4.0	0.3	10
5+	2.5	0.4	5	2.0	0.3	8
6+	1.4	0.3	5	0.8	0.1	9

2. Seven Mile Beach

<u>Age</u>	<u>Mean</u>	<u>se</u>	<u>n</u>	<u>Mean</u>	<u>se</u>	<u>n</u>
2+	2.6	0.5	8	3.2	0.4	11
3+	2.6	0.3	11	3.2	0.4	6
4++	3.0	0.4	16	2.4	0.3	10

3. Cliff Head

<u>Age</u>	<u>Mean</u>	<u>se</u>	<u>n</u>	<u>Mean</u>	<u>se</u>	<u>n</u>
2+	5.7	0.1	41	5.5	0.1	22
3+	5.2	0.9	3	5.0	-	2

Table 5

Total density (No. per ha.) and annual mortality coefficients
(of animals > 3 yrs) at Seven Mile Beach and Cliff Head

	Total Density in January (\pm SD)	Total Density in in August (\pm SD)	Annual Mortality coeff. (> 3 yrs)
<u>Seven Mile Beach</u>			
1977	12728 (\pm 468)	7269 (\pm 420)	0.657
1978	14452 (\pm 727)	7682 (\pm 322)	1.879
<u>Cliff Head</u>			
1978	3151 (\pm 501)	5905 (\pm 272)	-

Fig. 1. Annual growth of tagged juvenile rock lobsters at Seven Mile Beach and Cliff Head in 1978. Broken line shows the annual growth of rock lobsters in aquaria under near-optimal conditions.

X Male
 ● Female

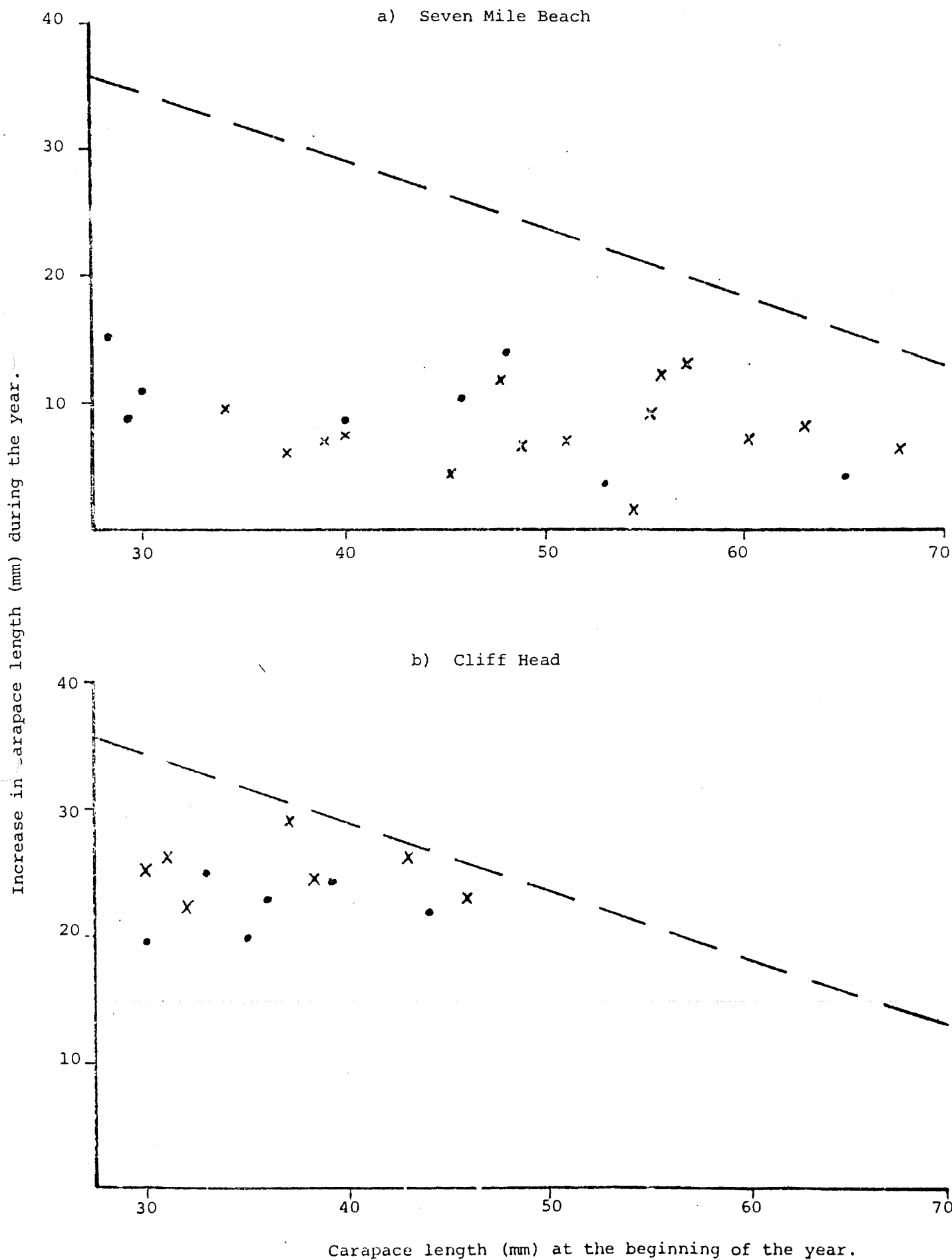
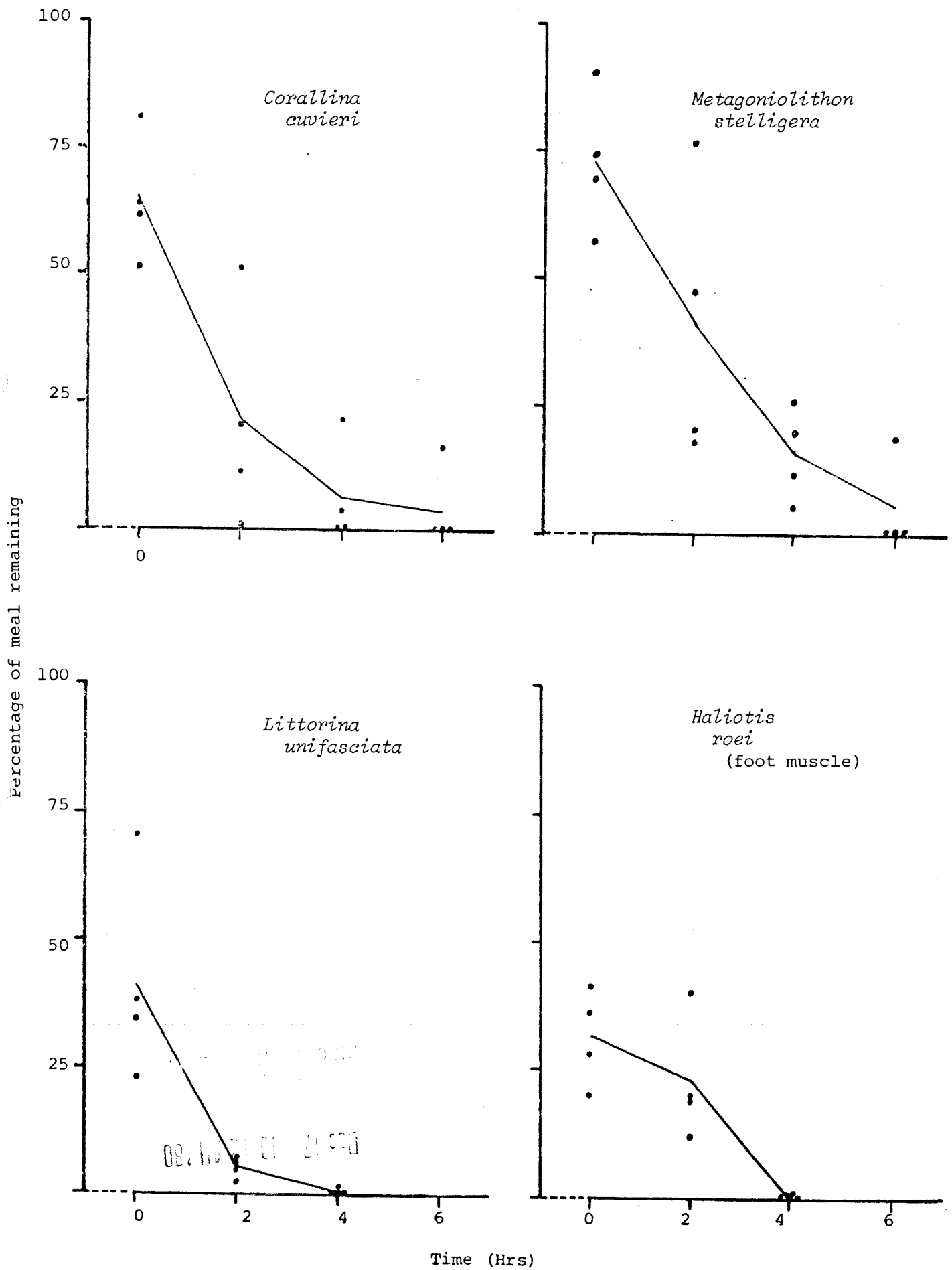


Fig. 2. Wet weight of food remaining in the stomach expressed as a percentage of the wet weight consumed. Points are individual animals; line connects the arithmetic mean for each time. Temp. 25°C.



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NATURAL DIET AND GROWTH OF JUVENILE WESTERN ROCK LOBSTERS *PANULIRUS CYGNUS*¹ George

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Abstract: The natural diet of juvenile western rock lobsters (*Panulirus cygnus* George) at two sites, one of high and one of low growth rate, was examined to determine if there was a relationship between natural diet and growth rate. The diet of *P. cygnus* at the high growth rate site (Cliff Head in Western Australia) encompassed a wide range of animal and plant material, but was dominated by molluscs. There were significant variations in both the proportions of the different dietary items and in the degree of foregut filling with time of year. At the low growth rate site (Seven Mile Beach) the diet covered a similar range of animal and plant material as at Cliff Head, but was dominated by two species of foliose coralline algae. There was little variation in the proportions of the various dietary items with time of year, but the degree of foregut filling showed significant seasonal variation.

The dietary data did not provide any evidence to support the hypothesis of Chittleborough that limited food supply is the cause of differences in growth between the sex/age-class groups, although there was an obvious association between the animal-rich diet at Cliff Head and the plant-rich diet at Seven Mile Beach and annual growth at the two sites. The nutritional role of the various dietary items, particularly the plant material, requires further evaluation. The allocation of nutritional resources to competitors also requires examination. The broad dietary spectrum of *P. cygnus* and their high densities in the coastal reef ecosystem suggest a significant role of grazing and predation by this species in the control of shallow reef communities of Western Australia.

INTRODUCTION

Juvenile western rock lobsters (*Panulirus cygnus* George) occur at high densities in the coastal limestone reef ecosystem of southern Western Australia (to depths of 10 m, with some larger juveniles to 20 m), the adult population occurring further offshore in 30-150 m depth (Chittleborough & Phillips, 1975). Their high densities (Morgan *et al.*, 1982) and limited home ranges (Chittleborough, 1974a) suggest that they may be important as regulators within this ecosystem, as has been observed with decapod crustaceans in other places (Virnstein, 1977; Young *et al.*, 1976; Nelson, 1981).

Studies of growth and mortality by Chittleborough (1970, 1975, 1976) and Chittleborough & Phillips (1975) and of the gastric fluid protein concentration (a measure of nutritional state) by Dall (1975) have suggested that at some sites populations of juvenile *P. cygnus* are food limited. Annual growth of juveniles at two of these sites (Garden Island and Seven Mile Beach) was less than that of aquarium-held animals reared under near-optimal conditions, but the reduction in annual growth was greater than would

¹ The western rock lobster is referred to as *Panulirus longipes* or *P. longipes cygnus* in some of the literature quoted; these are synonymous with *P. cygnus*.

have been expected on the basis of the sub-optimal temperatures at these sites. At a third site (Cliff Head) annual growth of juveniles was equal to that of aquarium-held animals, despite sub-optimal temperatures, as was the annual growth of juveniles transplanted from Seven Mile Beach to Cliff Head. Dall (1975) showed that mean gastric fluid protein concentration of *P. cygnus* at Seven Mile Beach was comparable with that of long-starved laboratory animals.

Reduced moult increments were an important component of the reduced annual growth rates at Seven Mile Beach and Garden Island. Of a number of environmental variables examined by Chittleborough (1975) for their effect on moult frequency and moult increment only a severe shortage of food during the preceding intermoult period and a mild deficiency of oxygen (60–70% saturation) at the time of the moult were found to cause reduced moult increments. Oxygen levels measured around the inshore reefs (during daylight), however, ranged from 76–115% saturation, suggesting that lowered oxygen levels were not the cause of the reduced single moult increments.

At Seven Mile Beach the reduced moult increments occurred throughout the population, but at Garden Island there were significant differences in moult increments between the sexes and age-classes. The pattern of differences in moult increments was interpreted by Chittleborough (1976) as indicating that the intensity of competition between sex/age-class groups was regulated by the food supply. He hypothesized that under conditions of abundant food, or in an extreme shortage, there would be no difference in growth rate between the sex/age class groups. In a situation of moderate food shortage competitive interactions would result in the growth of younger age groups being more retarded than that of older animals, while that of females would be more retarded than that of males.

This paper examines the diet of juvenile *P. cygnus* at two sites, one of high growth rate (Cliff Head) and one of low growth rate (Seven Mile Beach), and considers the nature of the diet and whether there are any relationships between the quality and quantity of the diet and growth rate at these sites. The presence of significant differences in moult increments between the age-classes at Seven Mile Beach during the period of the study permitted a consideration of the dietary data with regard to the competition hypothesis of Chittleborough (1976).

MATERIALS AND METHODS

NATURAL DIET

Sampling

Seven sets of samples were taken from Seven Mile Beach (29°08'S : 114°54'E) and Cliff Head (29°31'S : 114°59'E) in Western Australia at ≈3-monthly intervals from April 1977 to October 1978. Rock lobsters were caught by hand by SCUBA-diving in the early hours of the morning when they were completing their nightly foraging.

Samples were taken within the new-moon period of the lunar cycle, while the time of sampling was adjusted with seasonal changes in the time of sunrise and was restricted to a 1-h period between 2 h and 1 h before sunrise.

Initially it was planned to take rock lobsters which were foraging out in the open, away from the reef ledges which are their normal daytime refuges. Although such animals (categorized as "open") were generally readily available at Seven Mile Beach this was not the case at Cliff Head. On most occasions, in order to take samples of reasonable size from Cliff Head, rock lobsters were also taken from their refuges under reef ledges (categorized as "ledge"). Rock lobsters were brought ashore and the digestive tract removed and fixed in buffered 10% formal-sea water within 2 h. The carapace length, sex and moult-condition of the exoskeleton were recorded and a uropod removed and preserved to allow detailed moult staging.

Laboratory treatment

In the laboratory the percent fullness of each foregut was estimated by eye before opening. The foregut was then opened, excess fluid blotted up and the volume of the contents determined to the nearest 0.05 ml in a small volumetric cylinder. Volume measurements of two samples (April and August 1977, Seven Mile Beach) were determined in a modified "Ussachev" apparatus (Beers, 1976) but this gave inaccurate results due to faulty seating of the stopper. Each individual was assigned to a moult stage after examination of the preserved uropod and consideration of the moult details recorded at the time of dissection. The criteria used were basically those of Dall & Barclay (1977) but it was not possible to separate the sub-stages of intermoult (C_1 - C_4).

The contents of each foregut were sorted under a stereo-microscope to the lowest taxonomic level possible. With some groups (e.g. molluscs, coralline algae) identification to generic or specific level was possible, while in other groups only higher order classifications could be achieved. Although over 80 taxa at various taxonomic levels were recognized, organisms were grouped for data representation under nine main headings - coralline algae, non-coralline algae, seagrass, "worms", molluscs, crustaceans, *Panulirus* (identifiable parts of *P. cygnus* exoskeleton), other organisms, and digested material.

A volumetric method of analysis was chosen as being most appropriate to the aims of the study and the nature of the material. Following Pillay (1952) and Larimore (1957) the volume of food present in the foregut was taken as unity and the percent contribution by volume of each taxon to the individual's foregut contents estimated by eye. Estimation of volume involves a degree of subjectivity in the allocation of percentages but the fragmented nature of the material precluded direct measurement of volumes of individual taxa. Items estimated to be < 1% of the food volume were recorded as a "trace", allowing frequency of occurrence (Windell, 1971) to be determined.

The method used gives small animals the same weight as large ones and partly filled foreguts the same weight as completely filled foreguts. While the former property was

considered an advantage, the latter may cause undesirable effects. Therefore all analyses were restricted to animals with foreguts $> 10\%$ full. Percent fullness of the foregut was determined objectively for most samples from the measured volume of food and an estimate of the maximum foregut volume, using the trimming method constants of Maller *et al.* (in press). This method assumes a normal distribution around the "maximum" foregut volume and, because of this, some foreguts contained greater volumes of food than the estimated maximum foregut volume. Such values were read as 100% full. For the April and August 1977 samples from Seven Mile Beach, for which the food volume data were inaccurate, the initial "by-eye" estimates of foregut fullness were used.

DIETARY COMPARISONS

Diets quantified by a volumetric analysis may vary in two primary areas. First, animals may consume the same total amount (volume) of food but with different proportions of the components. Secondly, animals may eat various foods in the same relative proportions but differ in the total amount consumed. The main comparisons were between the two sites (Seven Mile Beach and Cliff Head) over a number of seasons and between the sex/age-class groups within each location. Because of the nature of the material, however, the effect of moult-stage and position (open or ledge) also required consideration.

Variation in the proportions of food categories

Canonical variate analysis (Fisher, 1936) was selected for the analysis of variations in the proportions of food categories. The method is described fully in Rao (1952) and Campbell & Atchley (1981). Briefly, canonical variate analysis takes linear combinations of the original variables in such a way that the differences between a number of groups are maximized relative to the variation within the groups. Initially the group configuration may be displayed in a two-dimensional sub-space defined by the first two canonical vectors. The first canonical vector is given by the coefficients of the linear combination which maximizes the ratio of the between-groups to within-groups sum of squares for the resulting canonical variate. The ratio itself is the canonical root.

The degree to which the first two canonical vectors successfully represent the axes of greatest variability may be interpreted by examining the corresponding canonical roots. In general, for reasonable sample sizes, a canonical root of < 0.5 indicates that the particular canonical vector is not an important axis for separating variation (Campbell, pers. comm.). Pythagorean distance between the canonical variate means of the different groups is appropriate for interpreting scatter plots of the group means. The important variables effecting group separation can be determined from the canonical variate coefficients standardized to unit standard deviation within groups (standardized canonical vectors). Variables with the larger absolute values of the standardized canonical vectors are usually the more important ones. However, the data must be examined for variables which may be highly correlated.

To reduce the number of variables considered, and because some components of the diet showed skewed distributions, polychaetes, molluscs and crustacea were grouped under one heading – “animal”. Examination of frequency distributions of the data grouped under the reduced number of headings indicated no major departures from normality and the original, untransformed data were used. Inclusion of a robustness factor (Campbell & Reyment, 1980) provided for downweighting of disparate values.

In the initial stages of the proportion comparisons, data within each sample from each site were grouped by their attributes of sex, age-class, moult-stage and position. Groups having less than three individuals were deleted from the data sets as being too small to contribute realistic values to the means. This effectively excluded moult stage as a variable at Seven Mile Beach, while only premoult animals formed sufficient numbers in any of the Cliff Head samples to allow the influence of moult stage to be considered. One sampling date at Cliff Head was also excluded, as only one group contained three or more individuals.

Variation in the percent fullness of the foregut

Percent fullness of the foregut, determined from the measured volume of food and the estimate of maximum foregut volume (Maller *et al.*, in press), was analysed using a non-orthogonal five-factor analysis of variance, computation being done using the analysis of variance routine available on GLIM (Baker & Nelder, 1978). The factors considered were date, site, sex, age and position. Only first-order interactions were considered, higher orders being included with the residual. Non-intermoult animals were deleted from the data set, as their occurrence with date and site was very patchy, and the effect of moult stage was considered separately. Examination of the residuals using the original data indicated a reasonable fit to normality and the data were not transformed. The samples from Seven Mile Beach for April and August 1977 could not be included in the analysis of variance as the food volumes were inaccurate.

For graphical presentation of the mean percent fullness of the April and August 1977 samples from Seven Mile Beach, and comparison with the means of samples taken at Cliff Head on the same date (determined from the measured food volume), the “by-eye” estimates made prior to opening the foregut were used. Comparison of 50 “by-eye” estimates made on subsequent samples with values derived from the food volume and estimated maximum foregut volume showed that “by-eye” estimates significantly (*t*-test, $P < 0.05$) over-estimated the percent filling, due primarily to overestimation of individuals with foreguts < 70% full. Mean values of the “by-eye” estimates for the April and August 1977 samples were adjusted down by the ratio of the means for the 50 paired samples (0.91).

GROWTH, DENSITY AND MORTALITY RATE

Annual growth

Approximately 300 rock lobsters from test reefs at each location were measured and marked in January 1978 at Seven Mile Beach and in January and February 1978 at Cliff Head. Animals with carapace length (C.L.) ≥ 40 mm were tagged with individually numbered tags (Chittleborough, 1974b) while animals with C.L. < 40 mm were marked with a coded set of punch marks (Chittleborough, 1970, 1974b) in the uropods ("tail-punched") to indicate their C.L. at capture. Tail-punched animals were tagged with individually numbered tags if, on recapture, they had attained a C.L. ≥ 40 mm. Annual growth data were obtained from tagged individuals recaptured on the test reefs 12 months later.

Moult increments

Growth of tagged individuals recaptured within 3 months, or tail-punched individuals recaptured within 2 months, of a previous capture provided data on moult increments. Data were restricted to animals recaptured in the period January to May, as there was some evidence in the data that moult increments at both sites were significantly reduced in the period May to October. Animals which had lost more than three limbs were excluded from both the moult increment and annual growth data. Age classes were identified from length-frequency distributions as described by Chittleborough (1970) and Chittleborough & Phillips (1975).

Density and mortality rates

Estimates of the density and natural mortality coefficients of juveniles on test reefs have been made at Seven Mile Beach since 1970. These were continued during the period of the feeding study using the methods described by Chittleborough (1970) and Chittleborough & Phillips (1975). Density estimates were made at Cliff Head between September 1977 and January 1979.

RESULTS

NATURAL DIET

Intermoult animals

A total of 779 animals was sampled, most of them in intermoult condition (Table I). At both Cliff Head and Seven Mile Beach the diets of these animals covered a broad but similar range of organisms. They were, however, dominated by different groups of organisms. These differences are more apparent in the percentage by volume data (Table II) than in the percent frequency of occurrence (Table III) as the percentage by

volume figures are not influenced by the frequent occurrence of small quantities of particular foods.

The dominant dietary component at Seven Mile Beach was coralline algae. The corallines were all foliose forms, with two species (*Corallina cuvieri* Lamouroux and *Metagoniolithon stelliferum* (Lamark) W.v. Bosse) contributing 21.0% and 19.9% by

TABLE I

Numbers of *P. cygnus* sampled from Seven Mile Beach and Cliff Head with respect to moult stage and degree of foregut filling.

	Seven Mile Beach		Cliff Head	
	≤ 10% full	> 10% full	≤ 10% full	> 10% full
Postmoult	0	2	11	3
Intermoult	7	372	84	209
Premoult	1	11	52	27

TABLE II

Mean percentage by volume of the major food categories in the foregut contents of intermoult, juvenile, *P. cygnus* > 10% full.

	Sampling date							Overall
	April 1977	Aug. 1977	Nov. 1977	Feb. 1978	May 1978	Aug. 1978	Oct. 1978	
(a) Seven Mile Beach								
<i>N</i>	62	48	61	65	46	45	45	372
Coralline algae	55.5	44.3	29.1	41.0	49.8	36.2	31.8	41.3
Non-coralline algae	2.1	11.3	14.0	4.6	8.9	13.2	22.3	10.3
Seagrass	13.1	9.3	10.8	21.9	6.7	9.5	15.1	12.8
"Worms"	1.4	1.1	1.3	0.9	3.8	1.6	0.2	1.4
Molluscs	4.4	9.4	11.5	12.8	2.5	3.9	3.1	7.2
Crustacea	3.1	2.2	3.4	1.2	0.9	2.0	2.0	2.2
<i>Panulirus</i>	1.1	0	6.0	2.6	3.8	0.9	2.8	2.5
Other organisms	2.7	4.1	2.1	1.0	3.4	10.3	5.2	3.8
Digested material	16.5	18.3	21.8	14.0	20.2	22.5	17.4	18.5
(b) Cliff Head								
<i>N</i>	37	16	57	13	42	11	33	209
Coralline algae	5.4	55.1	11.3	1.9	19.5	33.6	29.3	18.7
Non-coralline algae	3.2	3.1	2.7	5.2	1.0	3.6	7.2	3.4
Seagrass	2.7	10.4	8.5	1.5	6.4	6.6	6.2	6.3
"Worms"	0.3	0.3	0.6	0.2	1.7	1.3	0.2	0.7
Molluscs	34.5	1.1	21.7	37.9	32.4	14.4	17.2	24.4
Crustacea	1.1	0	3.4	5.2	3.7	3.2	0.3	2.4
<i>Panulirus</i>	18.0	1.0	23.7	1.7	4.6	6.1	3.2	11.6
Other organisms	12.8	12.3	9.0	12.0	4.1	3.9	5.3	8.3
Digested material	22.1	16.8	19.1	34.4	26.7	27.4	31.0	24.3

volume respectively to the overall mean for coralline algae of 41.3%. *Jania* spp. and *Metagoniolithon* spp. made up the remainder. At Cliff Head coralline algae were more variable in their contribution and were often exceeded by the molluscan component. The same suite of coralline algal species was encountered but it was usually dominated by *Corallina cuvieri*.

TABLE III

Percent frequency of occurrence of the major food categories in the foregut contents of intermoult, juvenile, *P. cygnus* > 10% full.

	Sampling date							Overall
	April 1977	Aug. 1977	Nov. 1977	Feb. 1978	May 1978	Aug. 1978	Oct. 1978	
(a) Seven Mile Beach								
<i>N</i>	62	48	61	65	46	45	45	372
Coralline algae	98.4	100	96.7	96.9	97.8	97.8	97.8	97.8
Non-coralline algae	67.7	91.7	90.2	76.9	87.0	86.7	97.8	84.4
Seagrass	98.4	100	96.7	98.5	100	97.8	100	98.7
"Worms"	54.8	89.6	83.6	36.9	58.7	68.9	26.7	59.7
Molluscs	100	100	100	100	82.6	95.5	91.1	96.2
Crustacea	59.7	64.6	80.3	52.3	43.5	44.4	46.7	57.0
<i>Panulirus</i>	6.5	4.2	34.4	21.5	30.4	31.1	40.0	23.4
Other organisms	91.9	93.7	83.6	87.7	87.0	97.8	84.4	89.2
Digested material	100	100	100	100	100	100	100	100
(b) Cliff Head								
<i>N</i>	37	16	57	13	42	11	33	209
Coralline algae	73.0	93.7	89.5	53.8	76.2	90.9	93.9	82.8
Non-coralline algae	86.5	93.7	75.4	92.3	71.4	72.7	69.7	78.0
Seagrass	94.6	100	94.7	53.8	76.2	72.7	97.0	88.0
"Worms"	45.9	18.7	52.6	30.8	54.8	54.5	39.4	45.9
Molluscs	100	50.0	96.5	100	100	90.9	93.9	93.8
Crustacea	56.8	12.5	59.6	92.3	61.9	36.4	18.2	50.2
<i>Panulirus</i>	51.4	12.5	66.7	15.4	26.2	9.1	42.4	41.6
Other organisms	94.6	93.7	87.7	84.6	64.3	63.6	78.8	81.8
Digested material	100	100	100	100	100	100	100	100

The non-coralline algal component at Seven Mile Beach was dominated by the fleshy green alga *Caulerpa cactoides* (Turner) J. Agardh., which contributed 9.1% to the overall mean of 10.3%. The balance of the material was a variety of small, primarily epiphytic, red and green algae. At Cliff Head there was no dominant non-coralline alga, this component being composed of a general suite of primarily epiphytic red and green algae. Seagrass fragments could not be consistently separated into species but recognizable fragments of *Amphibolis* spp., *Halophila ovalis* (R.Br.) Hook, *Heterozostera tasmanica* (Mortens ex Aschers) and *Syringodium isoetifolium* (Aschers) were present in samples from both areas. The condition of the seagrasses indicated that some, if not most, were ingested live.

"Worms" formed a relatively minor group in terms of percentage by volume at both localities although the frequency of occurrence data indicate that they are a common dietary component. Recognition was limited by the generally advanced stage of digestion of this group. Nereid and eunicid polychaetes (recognized by their jaws) and sipunculids were the main identifiable groups at both localities.

The molluscan component of the diet was an area of marked contrast between the diets. The frequency of occurrence data indicate that most animals at both sites include molluscs in their diet. The contribution by volume, however, showed wide differences between the sites. There were also large differences across time in the percentage by volume of molluscs at Cliff Head. The variety of taxa also showed considerable variation between the two sites. The molluscan component at Seven Mile Beach was consistently based on a wide range of taxa while the Cliff Head material was usually dominated by one or two species. Taxa commonly recognized in the Seven Mile Beach material included bivalves of the families Lucinidae, Solemyidae and Mytilidae (mostly *Musculus* spp.) and the gastropods *Prothalotia lepidus* Philippi, *Komaitrochus pulcher* Kuroda & Taki (Trochidae), *Tricolia* spp., *Phasianella* spp. (Phasianellidae), *Bittium* sp., *Diala* spp. (Cerithiidae), *Pyrene scripta* Lamark, *Dentimitrella* sp. (Columbellidae), *Nassarius fufula* Kiener (Nassariidae) and *Eatoniella* sp. (Rissoidae). A similar suite of molluscs was encountered at Cliff Head on an overall basis but their occurrence in the diet was considerably more patchy. The important molluscan taxa at Cliff Head were the trochid *Prothalotia lepidus* and the mytilid *Brachydontes ustulatus* (Lamark). At Cliff Head these species individually contributed up to 30% by volume in some samples whereas individual taxa never exceeded 3% by volume at Seven Mile Beach.

At both sites the crustacean component of the diet was composed of isopods, amphipods and a variety of small crabs, particularly the genus *Halicarcinus*. Exoskeletal fragments of *P. cygnus* varied considerably in both percent frequency of occurrence and percentage by volume at both sites. This variability appeared to be related to moulting activity in the population, with larger quantities of exoskeleton appearing in the diet at times of greater moulting activity. A number of points indicate that the exoskeletal material was derived from the ingestion of exuvia rather than cannibalism of newly moulted individuals. First, the exoskeletal fragments were hard and devoid of any associated tissue. Secondly, the parts most often consumed were the antennae, antennules and pereopods, the parts most often eaten from exuvia in the aquarium (unpubl. obs.). Thirdly, parts of the carapace often had the spirorbid polychaete *Eulaeospira convexis* (Wisely) attached to them, indicating an exoskeleton exposed to environmental conditions for some time.

A wide variety of items, present in foreguts from both localities, were included under the category "other organisms". They included Foraminifera, echinoderm (mostly echinoid) fragments, scales, bones and tissue of fish, tissue and spicules of sponges, ascidians, pycnogonids, hydrozoans, sand and unidentifiable material. At Cliff Head only sand and echinoid material contributed >1% to the overall mean percentage by volume (1.0% and 1.8% respectively) while at Seven Mile Beach sand (2.3%) was the

TABLE IV

Mean percentage by volume of the major food categories in the foregut contents of premoult and postmoult juvenile *P. cygnus* > 10% full.

	Seven Mile Beach				Cliff Head					
	Premoult		Postmoult		Premoult			Postmoult		
	Sampling date									
	April 1977	Nov. 1977	Oct. 1978	Oct. 1978	April 1977	Nov. 1977	Feb. 1978	May 1978	Oct. 1978	Nov. 1977
<i>N</i>	1	6	4	2	6	6	10	1	4	3
Coralline algae	73	25.3	39.2	69.0	11.3	16.2	5.6	50	17.5	42.7
Non-coralline algae	0	20.5	12.3	11.0	1.5	2.5	0.7	10	13.5	2.0
Seagrass	5	13.7	12.5	7.5	1.8	1.8	0.6	15	4.8	4.7
"Worms"	0	0.7	0	0	0	0.2	0.1	0	0	0
Molluscs	0	11.0	14.5	1.0	35.5	16.5	50.9	5	3.7	0.7
Crustacea	1	2.3	0	0	3.0	6.7	12.3	0	0	0
<i>Panulirus</i>	0	6.8	2.0	0	14.5	40.0	4.2	0	9.0	29.0
Other organisms	1	2.0	1.0	6.5	6.7	1.3	1.0	0	1.3	2.3
Digested material	20	17.7	18.5	5.0	25.7	14.7	24.6	20	50.2	18.7
% similarity with intermoult animals	79.1	90.6	80.3	61.6	87.6	75.0	73.7	51.9	63.8	63.4
Mean % fullness	95	75.0	52.5	65.2	33.3	46.6	20.5	36.7	26.8	25.9

only item in this category which exceeded the 1% level. The digested material was a flocculant "soup" of finely divided particles and presumably represented the partly digested products of the items present in the foregut.

Diets of other moult stages

Percent similarity (Whittaker, 1967) of the diets of premoult and postmoult animals > 10% full with intermoult animals from the same sample ranged from 51.9 to 90.6% (Table IV). Many premoult and some postmoult stage animals were eliminated from the analysis because their foreguts were $\leq 10\%$ full (Table I), although for most of these the foregut was completely empty. Premoult animals up to and including stage D₂ contained food. Postmoult animals collected in the field are difficult to moult stage accurately. Amongst the soft and "paper-shelled" (late B to very early C stages) animals sampled, however, only those with hardened mandibles contained food.

DIETARY COMPARISONS

Variations in the proportions of food categories

Unpooled data. Two-dimensional scatter plots of the canonical variate means for the first two canonical vectors showed a wide degree of variation in most samples between groups of individuals defined by their sex, age, moult-stage and position. Although some significant separations (defined as > 2 SD) were apparent there were no systematic groupings indicative of any sex or age effects consistent with the hypothesis of Chittleborough (1976).

The data on moult-stage and position were rather sparse, due to the restriction of the analysis to groups with a minimum of three individuals. Two premoult groups were present in the February 1978 sample but were not significantly separated from some groups of intermoult animals. Position was a factor in three samples at Cliff Head and one at Seven Mile Beach. In the May and October 1978 samples at Cliff Head open and ledge animals showed separations > 2 SD.

The rather chaotic pattern of groupings and separations observed in the unpooled data may be partly the result of the small size of groups (mean size of groups: Seven Mile Beach 9.2; Cliff Head 7.0). In view of the lack of systematic influences of sex, age, moult-stage and position in the unpooled data the data for each sampling date were pooled for the consideration of seasonal and location effects. Non-intermoult animals, however, were excluded from the pooled data set to maintain a core data set relating to intermoult animals.

Pooled data. A two-dimensional scatter plot of the canonical variate means for each sample at each location (Fig. 1) showed all the Seven Mile Beach samples to be tightly clustered along the axis of the first canonical vector (CVI), with a total spread of 1.0 SD.

Although there was a broad spread of the Seven Mile Beach samples along CVII the canonical roots indicate that CVI is the axis of primary importance (canonical roots CVI: 1.403, CVII: 0.337). The Cliff Head samples, on the other hand, were widely scattered on CVI and generally clearly separated from the Seven Mile Beach samples. The standardized canonical vectors indicated that separation along CVI derived principally from differences in the proportions of coralline algae, and "animal", (polychaetes, molluscs and crustaceans), with some further influence by *Panulirus* and seagrass.

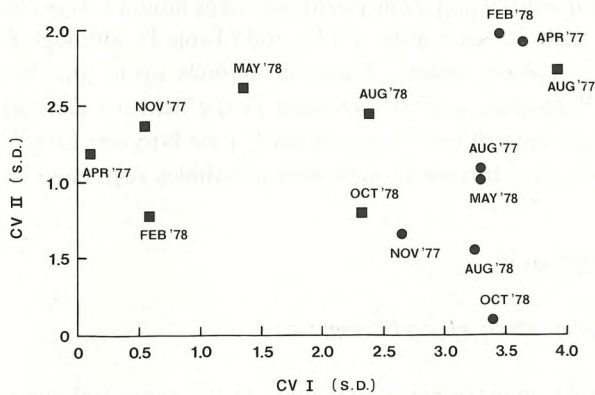


Fig. 1. Two-dimensional scattergram of the canonical variate means for the diets of intermoult *P. cygnus* > 10% full: ■, Cliff Head; ●, Seven Mile Beach.

Within the Cliff Head samples two zones were distinguishable: (1) more separated from Seven Mile Beach (April and November 1977, February and May 1978); (2) less separated from Seven Mile Beach (August and October 1978 and August 1977).

Examination of the group means* indicated that samples in Zone 1 were characterized by high "animal" (> 29%), low coralline algae (< 20%) and low seagrass (< 6%). Within the Zone 1 samples April and November 1977 were high in *Panulirus* (> 19%) while February and May 1978 were low in *Panulirus* (< 3%). Samples in Zone 2 were characterized by high coralline algae (> 30%), moderate amounts of seagrass (> 6%) and low *Panulirus* (< 3%). August 1977 was very low in "animal" (1.5%) while August and October 1978 showed higher levels of this component (21.5% and 18.3% respectively).

The data indicate that variations with time are an important factor at Cliff Head and that the degree of difference between the two sites in the nature of the diet is dependent on the time of year. Within the period studied, variations with time at Cliff Head showed a degree of seasonality with summer and autumn samples (February, April and May) falling into Zone 1 and winter samples (August) into Zone 2. Spring samples (November and October), however, occurred in both groups.

* Group means will not correspond exactly with the sample means in Table I because of the influence of the robustness factor.

Because of the temporal homogeneity of the data from Seven Mile Beach, a further pooling over samples from different dates was carried out to examine again, with the benefit of larger sample sizes, the influence of sex and age on diet at this site. In all cases, for groups characterized by age and sex, the canonical root for the first canonical vector was small (< 0.1), indicating no significant differences in the nature of the diet between the age groups or the sexes.

Variations in the percent fullness of the foregut

The percent fullness of the foregut of intermoult animals $> 10\%$ full differed significantly ($P < 0.001$) with date, location and position (Table V). The latter two variables were, however, largely confounded but their effects could be separated by changing their order of fitting in the analysis of variance (ANOVA). By separating their effects in this way (Table Vb) the only significant variable was found to be location. Sex and age did not significantly ($P > 0.05$) influence the percent filling of the foregut at either locality.

Comparison of the means for each locality within dates (or the adjusted means in the case of the April and August 1977 samples from Seven Mile Beach) (Fig. 2) showed that for five of the seven pairs of samples the mean percent fullness of animals at Seven Mile Beach was significantly greater than at Cliff Head (t -test, $P < 0.001$ – using the residual mean square from the ANOVA as the estimate of variance (Snedecor & Cochran, 1978)). In November 1977, however, Cliff Head showed a significantly ($P < 0.05$) greater percentage fill than Seven Mile Beach, while there were no significant ($P > 0.05$) differences between the sites in October 1978.

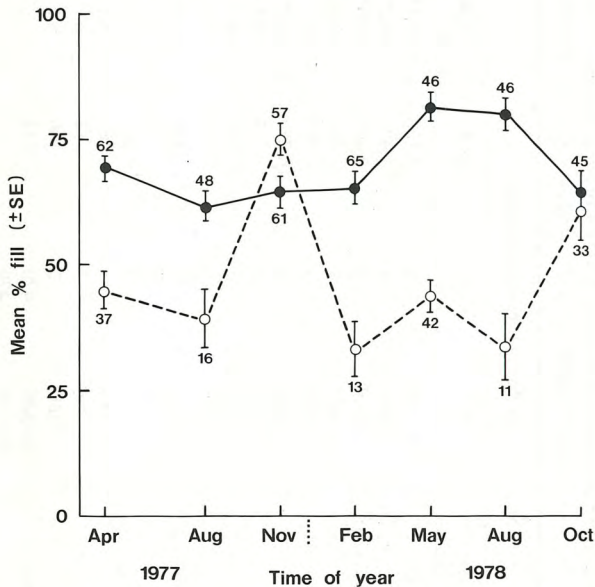


Fig. 2. Mean (\pm SE) percent fullness of intermoult *P. cygnus* $> 10\%$ full: values for April and August 1977 at Seven Mile Beach are adjusted from the "by-eye" data; ○, Cliff Head; ●, Seven Mile Beach.

TABLE V

Analysis of variance table for five-way ANOVA of percent fullness of the foregut of juvenile *P. cygnus*: ***, $P < 0.001$, all other values of variance ratio (V.R.) are not significant at $P > 0.05$; in part (b) of the table all values other than those marked are the same as in part (a).

(a) Position before location					(b) Location before position				
Factor	S.S.	d.f.	M.S.	V.R.	Factor	S.S.	d.f.	M.S.	V.R.
Date (D)	30,900	6	5,150	9.7***					
Position (P)	5,400	1	5,400	10.2***	Location	15,400	1	15,400	28.9***
Location (L)	10,400	1	10,400	19.5***	Position	400	1	400	0.8
Sex (S)	400	1	400	0.8					
Age (A)	800	3	267	0.5					
D.L.	41,000	4	10,250	19.3***					
D.S.	2,300	6	383	0.7					
D.P.	1,500	3	500	0.9					
D.A.	10,900	15	727	1.4					
L.S.	1,200	1	1,200	1.2					
L.P.	0 ^a	0	0	0					
L.A.	3,500	3	1,167	2.2					
S.P.	600	1	600	1.1					
S.A.	200	3	67	0.1					
P.A.	1,000	2	500	0.9					
Residual	223,600	420	532						
Total	333,700	470							

^a Within the accuracy of the calculations.

Variations in the proportion of the population which is feeding is also an important measure of the level of feeding activity. At Seven Mile Beach the proportion of animals feeding (taken as the proportion $> 10\%$ full) was relatively constant (Table VI). At Cliff Head, however, there were significant variations with time (χ^2 , $P < 0.001$) in the proportion of animals $> 10\%$ full.

TABLE VI

Numbers of intermoult *P. cygnus* in the samples with percent fills above and below 10%.

Date	Seven Mile Beach		Cliff Head	
	$\leq 10\%$	$> 10\%$	$\leq 10\%$	$> 10\%$
April 1977	0	62	5	37
August 1977	0	48	7	16
November 1977	2	61	2	57
February 1978	2	65	23	13
May 1978	2	46	5	42
August 1978	0	45	38	11
October 1978	1	45	4	33

The data on moult stage (Table IV) were very limited, particularly at Seven Mile Beach where the sampling of predominantly "open" animals reduced the number of non-intermoult animals encountered. At Cliff Head the mean percent fullness of premoult animals $> 10\%$ full was less than that of intermoult animals in the same sample (sign test, $P < 0.05$). Also significantly more (χ^2 , $P < 0.001$) premoult animals at that site had foreguts $\leq 10\%$ full (Table 1).

Variations in the absolute amounts of food

Diets at the two sites differed in both the nature of the diet and the percent fullness at the time of sampling. However, the differences between the diets at the two sites in the proportions of the various food categories may not reflect any differences in absolute amounts because of the difference in percent fullness. Absolute amounts of various food categories were compared for animals of equal size by multiplying the mean percent fullness for each sample by a common foregut volume to give the mean absolute volume of food in the foregut. Multiplication of this mean food volume by the mean percentage by volume represented by the particular food category in the sample gives the mean absolute volume of that food category. Ratios of the two sites for data derived in this way are independent of the foregut volume used.

As differences between the two sites in the canonical variate analysis were effected primarily by differences in the amount of "animal" and coralline algae, a comparison of the ratios of the mean absolute amounts of these two categories was made (Table VII). This showed that, in absolute terms, the foreguts of juvenile *P. cygnus* at Cliff Head in

most of the samples had between 1.5 and 3 times the amount of "animal" material found in the foreguts of animals of the same size at Seven Mile Beach. The relative amounts of coralline algae showed much wider fluctuations, with Seven Mile Beach animals

TABLE VII

Ratios of the absolute amounts of "animal" and coralline algae in the foreguts of juvenile *P. cygnus* of the same size from Seven Mile Beach and Cliff Head, derived as described in the text.

Sampling date	"Animal" ^a	Coralline algae ^b
April 1977	2.6	15.8
August 1977	0.1	1.3
November 1977	1.9	2.2
February 1978	1.5	42.3
May 1978	2.9	4.7
August 1978	1.1	2.5
October 1978	3.2	1.2

^a Ratio is Cliff Head: Seven Mile Beach.

^b Ratio is Seven Mile Beach: Cliff Head.

having up to 42 times the amount of coralline algae found in the foreguts of Cliff Head animals.

GROWTH, DENSITY AND MORTALITY RATES

Growth

Annual. Annual growth at both sites in 1978 of animals recaptured on the test reefs 12 months later (Fig. 3) showed no significant regressions ($P > 0.05$) on C.L. over the size range considered. Because of the lack of any relationship of annual growth with initial size, comparisons between sites were made by a *t*-test of mean annual growth. This showed that annual growth at Cliff Head was significantly greater ($P < 0.001$) than at Seven Mile Beach. Comparison of annual growth at the field sites with that of aquarium-reared animals is complicated by a significant regression of annual growth on C.L. for aquarium animals (Chittleborough, 1976). However, comparison of the mean annual growth at Cliff Head with the annual growth of a restricted size range of Chittleborough's aquarium-reared animals (<47.1 mm initial length; mean annual increment (\pm SE) = 28.4 (\pm 2.2) mm ($n = 6$), from Chittleborough's original data), for which there was no significant regression of annual growth on C.L., showed no significant differences (*t*-test, $P > 0.05$).

Although animals up to 74 mm C.L. were tagged at Cliff Head, annual growth data were obtained only from animals with an initial C.L. \leq 46 mm, while data from Seven Mile Beach were obtained from a wider range of initial carapace lengths. The lack of returns from animals of initial C.L. $>$ 46 mm was, presumably, largely the result of

emigration of such animals from the Cliff Head test reef. Chittleborough's (1976) annual growth data for this site were obtained from animals of initial C.L. > 49 mm, all of which were caught by professional fishermen at points 1–25 km away from the test reef.

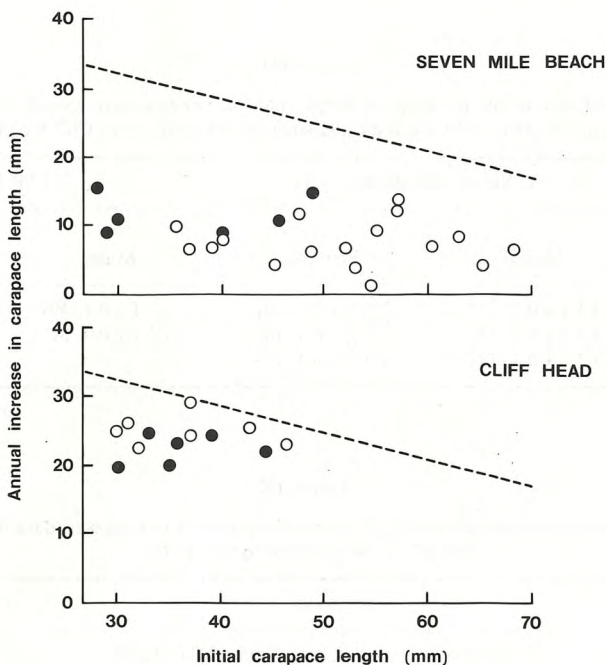


Fig. 3. Annual growth of tagged *P. cygnus* at Seven Mile Beach and Cliff Head in 1978: ○, male; ●, female; ---, annual growth in aquaria under near-optimal conditions from Chittleborough (1976).

Twelve other animals from the present study (initial C.L. 44–68 mm) were returned by commercial fishermen operating well offshore from the test reef area at Cliff Head.

Moult increments. Moult increments at Cliff Head (Table VIII) were not significantly different (two-way ANOVA, $P > 0.05$) between the sexes or age-classes. At Seven Mile Beach, however, there were significant differences (two-way ANOVA, $P < 0.001$) in moult increment between animals of different ages, but no significant differences ($P > 0.05$) between the sexes or any interactive effects. The significant difference between the age-classes arose from significantly higher moult increments by 2-yr-olds compared with 3-yr-olds ($P < 0.001$) and 4-yr-olds ($P < 0.05$) (*t*-tests, residual mean square used as the estimate of variance).

There were no significant differences (*t*-test, $P > 0.05$) between moult increments of animals at Cliff Head in the period January to May and those of animals of the same sex/age-class group reared under near-optimal conditions in aquaria (Chittleborough, 1976), with the exception of 2-yr-old males which showed a significantly higher incre-

ment (t -test, $P < 0.01$) at Cliff Head. Moulting increments of the various sex/age-class group from Seven Mile Beach, however, cannot be compared directly with those of aquarium-reared or Cliff Head animals as animals of the same age from both these sources are considerably larger. When compared to animals of equivalent carapace

TABLE VIII

Mean (\pm SE, n) moulting increments in carapace length (mm) of sex/age-class groups of juvenile *P. cygnus*, January–May 1978: no data available for 4-yr-olds from Cliff Head.

Age class (yr)	Seven Mile Beach		Cliff Head	
	Males	Females	Males	Females
2	3.3 (\pm 0.2, 21)	3.5 (\pm 0.1, 30)	5.7 (\pm 0.1, 40)	5.3 (\pm 0.1, 24)
3	2.2 (\pm 0.3, 14)	2.7 (\pm 0.4, 10)	5.2 (\pm 0.9, 3)	5.0 (\pm 1.0, 2)
4	3.2 (\pm 0.4, 11)	2.3 (\pm 0.3, 11)	–	–

TABLE IX

Mean (\pm SE, n) moulting increments of juvenile *P. cygnus* of equivalent size classes: data for aquarium-reared animals from Chittleborough (1976).

Size class (mm C.L.)	Location		
	Cliff Head (Jan.–May 78)	Seven Mile Beach (Jan.–May 78)	Aquarium-reared
30.1–50.0	5.42 (\pm 0.10, 59)	3.25 (\pm 0.13, 61)	5.06 (\pm 0.22, 13)
50.1–70.0	5.88 (\pm 0.41, 10)	2.67 (\pm 0.21, 32)	5.28 (\pm 0.24, 23)

length (Table IX), the moulting increments of Seven Mile Beach animals in both size classes (30–50 and 50–70 mm) were significantly less (t -test, $P < 0.001$) than those of both aquarium-reared and Cliff Head animals.

Density and mortality rates

Total densities of catchable animals on test reefs at the two sites were markedly different in January 1978 and January 1979 (Table X). The January density in both years at Seven Mile Beach was similar to that recorded in previous years (Chittleborough & Phillips, 1975; Chittleborough, unpubl. data) but the annual mortality coefficients for those ≥ 3 yr in 1978 and 1979 were the second and third highest respectively since rates have been studied. The mortality coefficient in 1977 was,

however, one of the lowest recorded. The increase in density between January and August 1978 at Cliff Head indicates that the population was not closed to immigration during the period and, consequently, a mortality rate could not be determined.

TABLE X

Density (no./hectare \pm SD) of juvenile *P. cygnus* on test reefs at Seven Mile Beach and Cliff Head in 1977–1979 and annual mortality coefficient for those \geq 3 yr.

	Density in January	Density in August	Annual mortality coefficient (\geq 3 yr)
1977 Seven Mile Beach	12,728 (\pm 468)	7,269 (\pm 420)	0.657
Cliff Head	— ^a	7,150 (\pm 846) ^b	—
1978 Seven Mile Beach	15,310 (\pm 668)	7,682 (\pm 322)	1.879
Cliff Head	3,151 (\pm 501)	5,904 (\pm 272)	?
1979 Seven Mile Beach	14,452 (\pm 727)	6,734 (\pm 490)	1.780
Cliff Head	1,625 (\pm 426)	— ^a	—

^a No data available. ^b Density value is for September. ? Mortality coefficient not determinable.

DISCUSSION

The variety of different classes of food items and the large number of organisms in the diet of *P. cygnus* indicate that it would be appropriately classified as a generalist feeder (Alcock, 1975). Observations of the feeding behaviour of *P. cygnus* during the sampling indicate that they would also be classified as “searchers” (Hughes, 1980). “Searchers” are typically opportunistic, have wide diets and feed predominantly on small prey.

The diet of juvenile *P. cygnus* shows similarities to the diets of several other palinurid species. The diet at Cliff Head, with its high molluscan component in some samples, is comparable to that of *Jasus lalandii* (Heydorn, 1969; Pollock, 1978) *Panulirus homarus* (Berry, 1971) and *Jasus novaehollandiae* (Fielder, 1965), which consume predominantly molluscan prey. The diet of *Panulirus cygnus* at Seven Mile Beach, and in some samples from Cliff Head, is similar to that of *P. argus* (Fernandes, 1971; Andree, 1981) and *P. interruptus* (Lindberg, 1955; Engle, 1979) in which the consumption of considerable quantities of coralline and non-coralline algae has been recorded.

Although the nature of the diet at Cliff Head showed variations with time of year the association between the high invertebrate (and predominantly molluscan) component in the Cliff Head diet and the high growth rate at that site is quite clear. The parallels between the high invertebrate diet at Cliff Head and the diet of animal matter fed to the aquarium-held rock lobsters by Chittleborough (1976) are also obvious. However, the relationship between mortality rate and diet was not clear. Mortality rates for Cliff Head could not be determined but the variation in mortality rates at Seven Mile Beach between 1977 and 1978 was not reflected in any of the dietary comparisons.

Moult increments for the period January to May at Cliff Head equalled, and in the

case of 2-yr-old males exceeded, those of aquarium animals held under near-optimal conditions. The maintenance by Cliff Head animals of an annual growth increment equivalent to that of aquarium animals corroborates the earlier finding of Chittleborough (1976). The ability of animals to achieve this rate of growth, despite sub-optimal temperatures and indications of reduced moult increments in winter (May to October), is not fully understood.

The maintenance of large moult increments and high rates of annual growth indicate that the diet of animals at Cliff Head is at least the nutritional equivalent of the animal matter diet offered to aquarium-reared animals by Chittleborough (1975, 1976). The nutritional role of the various dietary constituents, however, and particularly the plant material, requires further evaluation. Studies of other decapod crustaceans have suggested that plant material may play an important nutritional role. In high protein diets the inclusion of cellulose fibre can stimulate growth and assimilation of nitrogen beyond "normal" levels (Venkataramiah *et al.*, 1975; Fair *et al.*, 1980). In low protein diets plant material may act as an "extender", making low protein diets adequate for normal growth and survival (Syslo & Hughes, 1981).

The mechanisms by which plant material in the diet of some crustaceans may increase growth or nitrogen assimilation or reduce the requirement for high levels of dietary nitrogen is not clear. Fair *et al.* (1980) suggested two possible alternatives: (1) stimulation of microbial gut flora at high fibre concentration, resulting in preferential protein utilization and the formation of microbial by-products that may be utilized by the animal; (2) physiological factors (such as increased gut retention times) resulting in increased nitrogen assimilation. Neither of these suggestions appears to be appropriate for *Panulirus cygnus*. Evacuation of both animal and plant material from the foregut by *P. cygnus* is rapid, with evacuation almost complete by 4–6 h after feeding at 25 °C (Joll, 1982). Such rapid evacuation times would not be compatible with microbial digestion and gut retention times do not appear to be markedly increased in the presence of plant matter.

Corallina cuvieri can be digested by *Panulirus cygnus*, absorption efficiencies of up to 35% having been recorded (Joll & Crossland, 1983). Although these absorption efficiency values may be depressed by the simultaneous uptake of calcium, they indicate an ability of coralline algae to contribute to the nutrition of *P. cygnus*. The nature of the nutrients contributed by *Corallina cuvieri* to the metabolism of *Panulirus cygnus* was, however, not determined and it is not clear whether coralline algae can contribute nitrogen in its own right or whether it provides non-nitrogenous energy, allowing maximum utilization of dietary nitrogen for growth.

The possibility that some of the plant material is ingested incidentally and has no nutritional significance, must also be considered. Foliose coralline algae often contain a considerable infaunal community (Hicks, 1980) and it may be that some of the coralline algae is ingested incidentally by animals feeding on its associated invertebrates. The epiphytic red and green algae and some of the seagrass material may be similarly ingested by *P. cygnus* foraging for invertebrates on the stems and leaves of seagrasses.

P. cygnus also dig in the substratum of seagrass beds for infauna (e.g. lucinid bivalves) and may ingest seagrass rhizomes in the process.

Coralline algae appear to have additional dietary properties beyond their contribution to organic nutrition. Joll & Crossland (1983) have shown that dietary *Corallina cuvieri* contributes calcium to the exoskeleton of early intermoult *Panulirus cygnus*. It is not clear, however, whether the continued ingestion of high levels of coralline algae as well as shell material and exuviae indicates a high calcium requirement throughout intermoult or is simply a by-product of normal feeding. Weiss (1970), Ennis (1973) and Leavitt *et al.* (1979) have shown that there are shifts in the mineral composition of the diet of *Homarus americanus* through the moult cycle. There was no clear evidence of major differences in the nature of the diet of *Panulirus cygnus* between the various moult stages, although the guts of pre- and post-moult animals were often empty. The proportion of exoskeletal material in the diet of intermoult animals increased at times of high moulting activity but the evidence indicated that the material was derived from exuviae rather than cannibalism. Other investigators (Fernandes, 1971; Pollock, 1978) attributed, with some reason, at least some of the exoskeletal material in the diet of palinurids to cannibalism.

The effect of differential rates of evacuation on the composition of gut contents, and by inference the diet, has been pointed out by many authors (e.g. Hess & Rainwater, 1939; Peterson & Bradley, 1978; Hyslop, 1980). Wide differences in the rate of foregut clearance (evacuation) of organic tissue, shell and bone by *Scylla serrata* were reported by Hill (1976), with 50% of the animals retaining bone and shell for 2–3 and 5–6 days respectively. Carter & Steele (1982) found that in *Homarus americanus* hard parts were retained in the foregut for up to 180 days. The similar evacuation times of a variety of food organisms (coralline algae (two species)), abalone foot muscle and whole gastropods (*Littorina*) by *Panulirus cygnus* recorded by Joll (1982) indicates that the foregut contents should not be greatly distorted by differential rates of evacuation. The relatively small amounts of animal tissue in the *Littorina* diet were, however, evacuated more rapidly than the shell and opercula. The tissue component in the “animal” fractions of the diet is probably, therefore, underestimated.

Dall (1975) showed that gastric fluid protein concentration (GFPC) may be used as a reliable index of nutritional state for laboratory animals. His comparisons of GFPC at Cliff Head and Seven Mile Beach showed that overall there were no significant differences in GFPC between the two localities but that there were significant differences within each locality for samples taken at different times of the year. In several samples at both localities, as well as overall, there were also significant differences between animals of different sizes. The presence of time of year effects in the GFPC data corresponds with the presence of such effects in the dietary proportions at Cliff Head and the percent fill data at both localities. The presence of size effects in the GFPC at both locations, and the lack of location effects, does not agree with the dietary analysis.

In the September 1973 sample from Cliff Head Dall (1975) noted that all animals were in a uniformly high state of nutrition. Yet the gut samples from Cliff Head in August

1977 and 1978 were identified in the canonical variate analysis as being not greatly different from Seven Mile Beach and contained high proportions of coralline algae and very low to intermediate levels of molluscs. It may be that there was some major difference between the food in 1973 and 1977 and 1978, or that the diet changes greatly between August and September at Cliff Head. In the absence of paired data it is difficult to reconcile the differences between Dall's GFPC data and the dietary analysis. Dall (1975) commented that GFPC may show only short-term effects rather than those associated with annual growth.

The time of sampling used in this study corresponds with the period of peak foregut fullness (unpubl. obs.). Despite this the percent filling values for most samples at Cliff Head were significantly lower than at Seven Mile Beach. The mean percent fill showed the widest fluctuations at Cliff Head but there were no correlations with cyclical seasonal factors (e.g. temperature) at either site. The cause of the large increase in percent filling in the November 1977 and October 1978 samples at Cliff Head is not clear. These samples coincided with a time of high moulting activity in the population and it may be that many of the intermolt animals sampled were early intermolt and had relatively high food requirements (Chittleborough, 1975).

A minimum level of > 10% full was selected as the criterion for dietary analysis. This was an arbitrary criterion based on the need to examine the data for evidence of competition between the sex/age-class groups. Williams (1982) considered that individuals with a minimum of 50% filling were required to provide an adequate description of the diet of the crab *Portunus pelagicus* since animals with guts < 50% full contained fewer prey types. Examination of a random sub-sample of *P. cygnus* from Seven Mile Beach showed that the mean number (\pm SE) of major category items in the foregut contents of animals < 50% full (5.4 ± 0.22 , $n = 30$) was significantly less (t -test, $P < 0.001$) than for animals $\geq 50\%$ full (6.1 ± 0.18 , $n = 30$). Because of the standardization of the sampling time with respect to the nocturnal feeding pattern of *P. cygnus*, however, it was considered that low percent fill animals may reflect animals with low feeding rates rather than individuals in an advanced stage of digestion. At Cliff Head the mean percent fill (Fig. 2) was < 50% for most samples.

Chittleborough's (1976) hypothesis indicates that where differences in moult increment arise as a result of (presumed) competition for food among sex/age-class groups, then the effect of that competition should be such that the youngest age-classes should be the ones with the most depressed growth (moult increments). Such a result was not evident in the moult increment data for Seven Mile Beach in 1978 and, in fact, the reverse occurred, the youngest age-class showing the largest moult increment. There was, however, no reflection of this growth pattern in any of the dietary analyses. The cause of the differences in moult increments between age-classes at Seven Mile Beach is not clear, but the data indicate that it is not associated with diet. The differences in moult increments and annual growth between the two localities are, however, clearly associated with dietary differences.

Pollock & Beyers (1981) showed that, in general, single moult increments of *Jasus*

lalandii tended to be higher in areas where mussels (the principal food) had their highest biomass. They did not, however, quantify the densities or biomass of rock lobsters relative to the mussel biomass. The density data on *P. cygnus* (Table X) do not allow strict comparisons of the densities at Seven Mile Beach and Cliff Head, as densities at Cliff Head apparently fluctuated during the year. Overall, the impression was that the density at Cliff Head was generally lower than at Seven Mile Beach. It is not clear, however, whether the availability of an adequate supply of "quality" food at Cliff Head was merely the result of a similar food supply being distributed amongst fewer individuals or whether Cliff Head was an area of higher productivity than Seven Mile Beach. The occurrence and abundance of competitors at each of the two localities would also affect the quantity of food available to the rock lobster population.

Decapod crustaceans appear to be important regulators of macrobenthos in seagrass ecosystems (Young *et al.* 1976; Virnstein, 1977; Nelson, 1981). The broad dietary spectrum of juvenile *P. cygnus*, and their high densities in the coastal reef ecosystem, point to a significant role of grazing and predation by this species in the control of shallow reef communities of Western Australia.

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