Sources of nutrition in intertidal sea anemones from the south-western Cape, South Africa

Lisa M. Kruger and Charles L. Griffiths*
Zoology Department, University of Cape Town, Rondebosch 7700, South Africa
email: clgriff@ucthpx.uct.ac.za

Received 6 March 1996; accepted 23 May 1996

Respiration rates of seven species of intertidal sea anemones from the south-western Cape, South Africa were measured with and without illumination to determine whether zooxanthellae contributed to their nutritional needs. Light had no significant effect on oxygen exchange in any of the species, suggesting that all are azooxanthellate. Diets of anemones from two sites, Wooley's Pool in False Bay and Blouberg on the Atlantic coast some 20 km north of Cape Town, were examined by gut content analysis. Seven species occurred at Wooley's Pool, but only one (*Bunodactis reynaudi*) at Blouberg. At Wooley's Pool 39.4% of anemones contained food, while at Blouberg only 7.4% did so. A wide spectrum of prey taxa were consumed by the various anemone species, although considerable dietary overlap occurred. Pelecypods, gastropods and isopods were ingested by all the species examined. Pelecypods dominated the diet of *B. reynaudi* at Blouberg (91% occurrence), but were recorded in only 42% of the same species at Wooley's Pool. The frequency of occurrence of pelecypods in the guts of the other species ranged from 9% (*Anthothoe stimpsoni*) to 28% (*Actinia equina*). Gastropods were the main prey items eaten by *Anthopleura michaelseni* (67% occurrence), *Pseudactinia flagellifera* (43%) and *Pseudactinia varia* (42%), while isopods were the most frequently occurring constituent in the diets of *A. stimpsoni* (62%) and *Bunodosoma capensis* (16%). *A. equina* was the only species for which insects were a regular part of the diet (26% occurrence). Platyhelminths were found only in the guts of *B. capensis* (11%); holothurians only in *B. reynaudi* at Wooley's Pool (2%), and crinoids only in *P. flagellifera* (2%). Large quantities of algal material and indigestible debris were also ingested, indicating that sea anemones are non-selective feeders. Cluster analysis and multi-dimensional scaling techniques revealed four distinct feeding groups among the anemone assemblages. These are characterized as microphagous (*A. stimpsoni*), generalist (*B. capensis* and *A. equina*), macrophagous (*B. reynaudi* at Wooley's Pool, *A. michaelseni*, *P. flagellifera* and *P. varia*) and specialist bivalve-feeder (*B. reynaudi* at Blouberg).

* To whom correspondence should be addressed

Sea anemones utilize various methods to meet their nutritional requirements. Many harbour endosymbiotic dinoflagellate algae (zooxanthellae) within their tissues (Kellogg & Patton 1983) from which they obtain a significant autotrophic input of energy (Tytler & Spencer Davies 1984). In nutrient-poor tropical environments these zooxanthellae often supply 100% or more of the host's daily metabolic carbon requirements (Tsuchida & Potts 1994). In temperate regions, however, anemones rely more on captured prey. Sea anemones have been described by Sebens (1982a) as intermediate between motile predators and sessile passive suspension feeders. Their motility is not used to chase or locate specific prey items. Rather, they employ a 'wait-and-hope' strategy depending, to a large extent, on ambient water movement to deliver prey to them.

Although sea anemones form an important component of intertidal and shallow subtidal ecosystems, especially in temperate zones (Harris 1991) relatively few studies have been done on their natural diets world-wide.

In South Africa sea anemones achieve their greatest densities in the western and south-western Cape (McQuaid & Branch 1984; Field & Griffiths 1991; Griffiths & Branch 1991). Seven species of sympatric actiniarian anemones occur on the False Bay coastline (Kruger 1995). Of these *Actinia equina, Anthopleura michaelseni, Bunodactis reynaudi, Bunodosoma capensis, Pseudactinia flagellifera* and *P. varia* are all members of the family Actiniidae, while *Anthothoe stimpsoni* belongs to the family Sagartiidae. Distinct vertical zonation of individual species on the shore is apparent, although considerable overlap occurs. By contrast a single species, *Bunodactis reynaudi,* dominates the shore in Table Bay, where it shows clear size-partitioning on the shore (Kruger 1995). Studies pertaining specifically to the diets of South African anemones are exceedingly scarce. Krijgsman & Talbot (1953) referred briefly to the gut contents of *Pseudactinia flagellifera* and *B. reynaudi* from the Cape Peninsula. However, besides the examination of the coelenteron contents of a very small sample of *A. equina* from the same region (Ayre 1984), no work has been done on the diets of any other South African species.

Quantitative information on the trophic ecology of sea anemone assemblages on rocky shores in the south-western Cape is essential to determine their importance as consumers in littoral ecosystems and to provide information on the partitioning of available resources. This paper forms part of such a study and aims to determine sources of nutrition utilized by the seven most common species of sea anemones in this area, by examining the coelenteron contents as well as by testing each species for signs of autotrophic nutrition.

Methods

Anemones were collected from two sites on opposite sides of the Cape Peninsula — Wooley's Pool in False Bay (34°12'S;

18°43'E) and Blouberg Strand in Table Bay (33°47'S; 18°29'E). Wooley's Pool is a fairly protected site where the force of the waves is broken by a gently sloping shore and offshore reefs and is colonized by seven species of sea anemones. Blouberg Strand is subjected to much more direct wave action, although it is sheltered to some extent by Table Bay and Robben Island. The force of the waves there results in large quantities of sand accumulating in the rocky intertidal. *Bunodactis reynaudi* is the only species of anemone at this site, and is found in dense beds in water channels, pools and crevices (Kruger 1995).

Tests for autotrophic nutrition via light and dark respiration rates

Samples of each of the seven species of anemones were collected from Wooley's Pool during January and February 1995, together with rocks to which they were attached wherever possible, and transferred to the laboratory, where they were maintained in a through-flow sea water system at 19°C (the temperature at the collection site).

Measurements of oxygen consumption were made using a closed-system respirometer. Anemones were cleaned of all attached debris using forceps and placed on plastic platforms in closed perspex chambers. Small species such as *Anthothoe stimpsoni* and *Actinia equina* were placed in 0.25-ℓ chambers, while larger species occupied 1-ℓ chambers. Only expanded anemones were used. An empty control chamber was included in each run, simultaneously with the three experimental chambers, to control for the biological oxygen demand of the sea water. The water in each chamber was stirred continuously with a magnetic spin bar placed beneath the platform. A Yellow Springs Instrument Co. (YSI) oxygen electrode was inserted into the top of each chamber and routed via a switch gear to a Beckman multichannel DC potentiometric chart recorder. Respiration chambers were immersed in a constant-temperature (19°C) water bath. Light was provided by a Thorn 500W quartz halogen lamp, positioned above the respirometer so as to give a light intensity of 1160 $\mu E\ m^{-2}\ s^{-1}$ at the oral disc of the anemones. In each run a series of respiration measurements were made, each of 10 to 15 min duration, alternately in the light and dark. Each series was preceded by a 15 min acclimation period.

Coelenteron contents

The coelenteron contents of at least 50 individuals of each anemone species were examined to determine the composition of the diet of the different species. Anemones were collected at regular intervals from March 1992 to December 1993 in order to spread the analysis over a variety of weather and sea conditions.

Animals were carefully prized off the rocks during low spring tides. Any items attached to the column were removed and individual anemones were placed into collecting jars, filled with sea water. A 10% $MgCl_2$ solution was mixed 1:1 with the sea water in the collecting jar to narcotize and relax the freshly collected anemones. These were subsequently frozen at –4°C. Frozen samples were treated with 7% formalin poured onto the frozen sea water and mixed thoroughly when defrosted. Fixed anemones were then stored until ready for dissection, whereupon the liquid from each collecting jar was poured through a 15 μm mesh to retrieve any organisms egested during transportation or preservation. Preserved anemones, and items retrieved from the collecting jar were examined under a dissecting microscope using 35 × magnification. Anemones were then cut longitudinally to open the coelenteron. Large food items were removed, identified and wet weighed. Weights of hard-shelled prey included the shells. Mesenterial filaments were then separated and scraped, or sprayed with water, to free small prey items held there. Mucus aggregations containing fine sand grains were also carefully examined for microscopic prey items. Recognizable prey were counted and identified to the lowest possible taxonomic group.

Inedible items such as empty shells, fragments of crustacean exoskeletons and other debris were not included as food sources, as it was impossible to determine whether such items represented the remains of digested prey that had yet to be voided, or were simply ingested as debris (Dayton 1973). Unidentifiable detritus was also separated and excluded from further analysis.

The wet mass (to the nearest 0.01 g) of the individual prey items, together with the wet mass, column height and basal diameter — taken as the mean of the smallest and largest diameters, as suggested by Sebens (1982b) — of each anemone, were recorded. The overall mass of each food type was expressed as a percentage of the total mass of prey consumed by each sea anemone species. The percentage frequency of occurrence of each different prey category was also determined for each anemone species.

An 'index of relative importance' (IRI), a mathematical combination of both the percentage mass and percentage occurrence, was calculated following the method of Pinkas *et al.* (1971) as given in Berg (1979), to provide a more balanced picture of the dietary importance of each food item:

$$IRI = (\%N + \%M)*\%F \quad (1)$$

where

%N = average numerical percentage occurrence of each item in the diet;

%M = average percentage by mass of the food item in all the guts examined;

%F = frequency of occurrence of the food item.

Sample sizes for each species reflect only the number of guts examined that actually contained food. Occurrence is, therefore, expressed as the percentage of those guts containing food in which each particular food category was found.

In order to compare the diets of the various species, untransformed data (IRI) for each species were analysed using a cluster analysis technique. This was complemented with non-parametric multi-dimensional scaling techniques (MDS-ordination) (Field, Clarke & Warwick 1982).

Results

Tests for autotrophy

Rates of oxygen consumption recorded for all seven species of anemones at 19°C, under both light and dark conditions, are given in Table 1.

To test for differences in oxygen consumption by the different anemone species, during light and dark conditions, a

Table 1 Mean rate of oxygen consumption in each of seven species of intertidal sea anemones from the south-western Cape, measured in light and dark conditions at 19°C. Light intensity, measured at the upper surface of the anemones, was 1160 µE m^{-2} s^{-1}. The weight-specific respiration rate is expressed per unit wet weight. Each reading is the mean ± *SD* of nine 15 min periods for each of nine individuals

Anemone species	Respiration rate in dark ($mg\ O_2.g^{-1}.h^{-1}$)	Respiration rate in light ($mg\ O_2.g^{-1}.h^{-1}$)
Actinia equina	0.02 ± 0.32	0.02 ± 0.32
Anthothoe stimpsoni	0.02 ± 0.09	0.01 ± 0.10
Anthopleura michaelseni	0.03 ± 0.35	0.04 ± 0.48
Bunodosoma capensis	0.05 ± 0.39	0.05 ± 0.36
Pseudactinia flagellifera	0.07 ± 0.55	0.08 ± 0.73
Pseudactinia varia	0.07 ± 0.53	0.09 ± 0.74
Bunodactis reynaudi	0.03 ± 0.14	0.06 ± 0.25

nonparametric Mann-Whitney *U* test was performed (Zar 1984). The only species to show a significant difference in respiration rate under the different light conditions was *Bunodactis reynaudi* ($p < 0.05$; Z = 2.56, Mann-Whitney) but the oxygen consumption in this species was higher in light than dark conditions. The result is thus not due to autotrophy, but could possibly be due to increased activity. *Anthothoe stimpsoni* was the only species that consumed more oxygen in the dark than in the light, but this difference was not statistically significant.

Gut content analysis

A significantly higher percentage (39.4%) of the anemones at Wooley's Pool (n = 1334) contained food compared with those from Blouberg (7.4%, n = 918) ($\chi^2 = 257.0$; $p < 0.001$) (Table 2). Considering the one common species — *Bunodactis reynaudi* — the Wooley's Pool specimens also contained food far more frequently (27.7%, n = 173) than those from Blouberg (7.4%, n = 918) ($\chi^2 = 39.2$; $p < 0.001$).

Table 2 Summary of the proportion of anemones that contained naturally captured prey items at the two study sites in the south-western Cape, South Africa

Species	Number sampled (n)	Number with food in gut	Percentage with food in gut
Wooley's Pool			
Actinia equina	226	81	35.8
Anthothoe stimpsoni	241	57	23.6
Anthopleura michaelseni	103	48	46.6
Bunodosoma capensis	412	30	7.2
Pseudactinia flagellifera	68	53	77.9
Pseudactinia varia	111	63	56.7
Bunodactis reynaudi	173	48	27.7
Total	**1334**	**380**	**39.4**
Blouberg			
Bunodactis reynaudi	918	68	7.4

Coelenteron content analysis

The majority of anemone species consumed prey from a wide spectrum of prey types, but only one or two of these invariably dominated the diet (Table 3). Isopods, pelecypods and gastropods were found in the coelenterons of all species and at both sites, although in very different proportions. Isopods occurred with the lowest frequency in *Bunodactis reynaudi* from Wooley's Pool (2%) and most frequently in *Anthothoe stimpsoni* (62%). Frequency of pelecypods occurrence ranged from 4% in *A. stimpsoni* to 91% in *B. reynaudi* from Blouberg, while the percentage occurrence of gastropods was lowest in *Actinia equina* at 4% and reached a maximum of 67% in *Anthopleura michaelseni*. The percentage occurrence of individual prey species in the guts of each anemone species is shown in Table 4. The diets of each of the species of anemone analysed are described separately below.

Actinia equina

In terms of frequence of occurrence, pelecypods (28%) were the most abundant food items consumed by *A. equina*, followed closely by insects (26%) and then isopods (24%). Because of their larger size gastropods (70%), bryozoans (13%) and chitons (7%) were the most important food items by mass, although all three categories occurred at low frequency. IRI calculations indicate that pelecypods were the most important prey category, followed by insects and then isopods. The low rating given to gastropods by the IRI is surprising considering that they comprise 70% of the diet by mass. This is a function of the low weighting given to mass in Berg's formula (1). The tiny pelecypod *Nucula nucleus* was the most common species consumed (Table 4), but because of their very small size their individual mass was negligible. This also applies to the insects that were eaten. Four insect groups were identified, but only one, *Anurida maritima*, was identified to the species level. Other apparently important prey included nematodes (13% occurrence), the isopods *Exosphaeroma* spp. (11%) and *Cirolana* sp. (4%) and the amphipod *Hyale* sp. (6%).

Anthothoe stimpsoni

A. stimpsoni caught fewer prey types than any of the other anemones found at Wooley's Pool. Numerically the diet was dominated by isopods, which occurred in 62% of the coelenterons examined. Copepods, polychaetes and spiders occurred with equal frequency (8%) and each was represented by a single species *viz.* an unidentified harpacticoid copepod, *Euclymene* sp. and *Desis formidabilis*, respectively. Mites and small gastropods both occurred in 6% of the guts examined. All the captured prey were very small and only two groups — polychaetes (81%) and isopods (19%) — formed a significant proportion of the diet by mass. The index of relative importance (IRI) indicated that isopods were the most important food group, followed by polychaetes. No other groups contributed significantly to the diet. *A. stimpsoni* was the only species that did not consume any Brachyura. The most frequently consumed species were the isopods *Exosphaeroma* spp. and *Jaeropsis stebbingi*, the latter being absent from the diets of the other anemones in the area.

Table 3 The diets of seven species of sea anemone in the south-western Cape (* indicates < 0.5% contribution to mass). IRI = [numerical percentage (%N) + percentage mass (%M)] × frequency of occurrence (%F)

Site	Wooley's Pool																												Blouberg			
Species	*Actinia equina*				*Anthothoe stimpsoni*				*Anthopleura michaelseni*				*Bundosoma capensis*				*Pseudactinia flagellifera*				*Pseudactinia varia*				*Bunodcatis reynaudi*				*Bunodactis reynaudi*			
No. of guts with food	54				52				55				55				51				52				52				67			
Anemone mass range (g)	0.09–8.51				0.03–0.37				15.01–105.14				4.06–70.37				3.16–188.37				0.55–135.28				9.01–178.63				0.37–138.81			
Prey category	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	&F	IRI	%N	%M	%F	IRI
Edible																																
Zooplankton	1	*	2	2	2	*	2	4					4	*	5	20																
Porifera					1	*	2	2					1	*	2	2	1	*	2	2												
Hydrozoa									1	*	2	2	4	*	4	16	3	*	6	18	3	*	6	18					1	*	1	1
Octocorallia																	2	*	4	8												
Actinaria													2	1	4	12													1	*	2	2
Platyhelminthes													12	*	11	132									1	*	2	2	1	*	2	2
Nematoda	7	*	7	49					2	*	4	8	4	*	4	16													7	*	4	28
Polychaeta	2	1	4	12	6	81	8	696	1	*	2	2	4	11	5	75					2	*	4	8					9	*	10	90
Cirripedia									34	39	24	1752	4	10	5	70	2	1	4	12	3	*	6	18	39	45	13	1092				
Copepoda					4	*	8	32					1	*	2	2	1	*	2	2												
Ostracoda																	1	*	2	2	1	*	2	2								
Isopoda	14	5	24	456	33	19	62	3224	7	*	9	63	11	*	16	176	18	*	18	324	9	*	17	153	1	*	2	2	5	*	6	30
Amphipoda	8	1	13	117	1	*	2	2	1	*	2	2	11	*	11	121	4	*	8	32	4	*	6	24					2	*	3	6
Tanaidacea																	1	*	2	2	1	*	2	2								
Macrura																													2	2	3	12
Anomura									3	*	5	15					1	2	2	6	4	2	8	48	1	*	2	2				
Brachyura	1	1	2	4					5	1	9	54	5	5	9	90	4	3	8	56	3	4	6	42	5	2	10	70	3	10	4	52
Acari	1	*	2	2	3	*	6	18																								
Insecta	21	1	26	572									3	*	5	15					2	*	4	8	1	*	2	2				
Araneae	3	*	6	18	4	*	8	32																								
Bryozoa	4	13	7	119					2	*	4	8	3	*	5	15					3	*	6	18	3	*	6	18				
Amphineura	2	7	2	18									3	9	5	60	1	3	2	8	1	*	2	2								
Pelecypoda	42	1	28	1204	2	*	4	8	10	9	18	342	6	*	9	54	11	9	18	360	16	8	23	552	44	42	42	3612	79	88	91	15197
Gastropoda	2	70	4	288	3	*	6	18	68	43	67	7437	6	18	7	168	24	28	43	2236	43	25	42	2856	18	10	25	700	31	*	19	589
Asteroidea									3	1	5	20					1	*	2	2	1	*	2	2	1	*	2	2				
Ophiuroidea																					1	*	2	2	1	*	2	2				
Echinoidea									3	6	5	45	1	6	2	14	6	51	12	684	7	56	12	756	1	1	2	4				
Holothuroidea																									1	*	2	2				
Crinoidea																	1	*	2	2												
Tunicata									1	*	2	2	2	41	4	172	3	3	6	36	1	5	2	12								
Pisces																	1	*	2	2												
Eggs	14	*	7	98	1	*	2	2	3	*	5	15	2	*	4	8					1	*	2	2								
Inedible																																
Algae	7	1	13	104	1	*	2	2	42	5	53	2491	16	1	25	425	14	1	25	375	18	1	25	475	7	5	12	144	2	*	3	6
Other	20	6	35	910	4	*	6	24	56	16	67	4824	30	20	38	1900	35	22	49	2793	32	12	48	2112	37	24	52	3172	12	2	16	224

Anthopleura michaelseni

The most common items in the diet of *A. michaelseni* were gastropods (67%), followed by cirripedes (24%) and pelecypods (18%). Isopods and brachyurans were found in 9% of coelenterons, while anomurans, asteroids and echinoderms were each present in 5%. The same order of importance was reflected in the percentage by mass and IRI calculations. Algae were consumed more frequently (53% occurrence) by

Table 4 Percentage occurrence of the prey items most frequently consumed by sea anemones in the south-western Cape (p = present in less than 5% of coelenterons; – = absent)

	Wooley's Pool							Blouberg
	Actinia equina	*Anthothoe stimpsoni*	*Anthopleura michaelseni*	*Bunodosoma capensis*	*Pseudactinia flagellifera*	*Pseudactinia varia*	*Bunodactis reynaudi*	*Bunodactis reynaudi*
Zooplankton								
Harpacticoidea	–	8	–	p	p	–	–	–
Zoea larva	p	–	–	5	–	–	–	–
Nematoda	13	–	–	–	–	–	–	–
Polychaeta								
Euclymene sp.		–	6	–	–	–	–	–
Scolelepis squamata	–	–	–	–	–	–	–	9
Cirripedia								
Tetraclita serrata	–	–	51	–	p	p	60	–
Balanus algicola	–	–	p	–	p	8	21	–
Octomeris angulosa	–	–	15	–	–	–	12	–
Isopoda								
Cirolana sp.	p	p	5	p	p	p	p	–
Exosphaeroma spp	11	13	p	p	25	p	–	5
Jaeropsis stebbingi	–	33	–	–	–	–	–	–
Amphipoda								
Hyale sp.	6	–	–	p	–	–	–	–
Paramoera capensis	–	–	–	9	–	p	–	–
Anomura								
Paguristes gamianus	p	–	5	p	p	8	p	–
Brachyura								
Ovalipes trimaculatus	–	–	p	p	8	p	p	5
Plagusia chabrus	–	–	–	–	–	p	8	p
Acari		p	6	–	–	–	–	–
Insecta								
Anurida maritima	7	–	–	p	–	–	–	–
Coleoptera	6	–	–	–	–	–	p	–
Diptera	7	–	–	–	–	–	–	–
Formicidae	6	–	–	–	–	–	–	–
Araneae								
Desis formidabilis	p	8	–	–	–	–	–	–
Amphineura								
Acanthochiton garnoti	p	–	–	6	p	p	–	–
Pelecypoda								
Choromytilus meridionalis	–	–	9	–	6	12	21	72
Mytilus galloprovincialis	–	–	5	–	14	6	44	42
Nucula nucleus	76	6	p	9	p	p	10	p
Gastropoda								
Assiminea globulus	–	–	11	p	6	–	p	–
Burnupena spp	–	–	53	p	16	31	15	p
Crepidula porcellana	–	–	15	–	p	6	6	–
Gibbula spp	–	–	5	–	p	8	p	–
Helcion dunkeri	–	–	p	–	6	p	–	–
Nucella spp	–	–	5	–	–	–	–	–
Oxystele spp	–	–	5	–	–	8	–	–
Patella spp	p	–	16	p	–	p	p	p
Tricolia capensis	–	6	5	–	12	33	–	43
Asteroidea								
Patiriella exigua	–	–	5	–	p	p	p	–
Echinoidea								
Parechinus angulosus	–	–	5	p	12	13	p	–

this species than by any other anemone, but contributed only 5% of the mass eaten.

Nine species of gastropods were identified from gut contents. Of these, *Burnupena* spp occurred most frequently (53%). Three species of cirripedes, *Tetraclita serrata* (51%), *Balanus algicola* (4%) and *Octomeris angulosa* (15%) were also found.

Bunodosoma capensis

Nineteen prey categories occurred in more than 5% of the *B. capensis* examined (Table 3) and no particular group dominated the diet. Isopods (16%), amphipods (11%) and platyhelminths (11%) occurred most frequently — the last being a food category particular to this anemone species. Tunicates were found in very few guts (4%), yet contributed substantially to the mass (41%). Gastropods made up 18% of the diet by mass and polychaetes, cirripedes and amphineurans 11%, 10% and 9% respectively. The IRI calculations gave the order of importance as: isopods, tunicates and then gastropods. This resulted from the relatively high frequency of occurrence of isopods (16%) and large contribution to the mass of the prey items by tunicates and gastropods. Three species occurred in more than 5% of the anemones examined, the amphipod *Paramoera capensis* (9%), the pelecypod *Nucula nucleus* (9%), and the amphineuran *Acanthochiton garnoti* (Table 4).

Pseudactinia flagellifera

Gastropods (43%) occurred most frequently in the guts of *P. flagellifera*, followed by pelecypods (18%) and isopods (18%). Echinoderms occurred in 12% of the guts examined and contributed substantially to the mass (51%) of prey items. Gastropods accounted for 28% of the mass and pelecypods 9%. The mass of isopods was negligible and consequently the IRI result was low for this category. The order of importance from the IRI calculations was gastropods, followed by echinoderms and then pelecypods. This was the only species of anemone found to consume crinoids, octocorals and fish. Two species of isopods identified only as *Exosphaeroma* spp. were frequently consumed (25%). Of the six species of gastropods identified, *Burnupena* spp. (16%) and *Tricolia capensis* (12%) were the most common. *Mytilus galloprovincialis* (14%) was the most commonly consumed pelecypod.

Pseudactinia varia

As with *P. flagellifera*, gastropods (42%) occurred with the highest frequency in the coelenteron contents of *P. varia*, again followed by pelecypods (23%) and isopods (17%). Echinoderms were less common (12%) and yet counted for most of the mass (56%). Gastropods contributed 25% to the mass and pelecypods 8%. Consequently the order of importance resulting from the IRI calculations was gastropods, echinoderms and then pelecypods. The most important gastropod species were *Burnupena* spp. (31% occurrence) and *Tricolia capensis* (33%). Of the pelecypods consumed, *Choromytilus meridionalis* occurred in 12% of the guts examined. The most important echinoderm in the diet was *Parechinus angulosus* (13%).

Bunodactis reynaudi

(a) Wooley's Pool

The most frequently occurring food categories in the gut contents of *B. reynaudi* from Wooley's Pool were pelecypods (42%), gastropods (25%) and cirripedes (13%). Cirripedes (45%) were the most important contributors to the percentage mass, followed by pelecypods (42%) and gastropods (10%) This resulted in cirripedes receiving the highest ranking in terms of the IRI, followed by pelecypods and then gastropods. Three cirripede species, *Tetraclita serrata* (60%), *Balanus algicola* (21%) and *Octomeris angulosa* (12%), and three pelecypods — namely *Mytilus galloprovincialis* (44%), *Choromytilus meridionalis* (21%) and *Nucula nucleus* (10%) — were the most commonly consumed items. *B. reynaudi* at Wooley's Pool was the only anemone examined that did not consume amphipods in appreciable amounts. It was also the only species that fed on holothurians.

(b) Blouberg

Relative to all the species at Wooley's Pool, *B. reynaudi* from Blouberg had a very restricted diet. Coelenteron contents comprised only 10 prey categories and only four of these were consumed by more than 5% of the anemones examined. Pelecypods dominated the diet both in terms of occurrence (91%) and contribution to mass (88%) and were consequently by far the most important item eaten. Other items that occurred in the guts were gastropods (19%) and polychaetes (10%), yet both of these groups contributed less than 0.5% to the mass. Brachyura (10%) and Macrura (2%) accounted for the remaining mass, but occurred at low frequencies and were therefore less important than gastropods and polychaetes in the IRI. Of the pelecypods *Choromytilus meridionalis* (72%) and *Mytilus galloprovincialis* (42%) were found most frequently in the guts. The only other common species was the gastropod *Tricolia capensis* (43%).

The results of the cluster and ordination analyses comparing the diets of the different anemone species are shown in Figures 1 and 2. Four main groups were distinguished in the dendrogram (Figure 1) at an arbitrary similarity level of 55%. *Anthothoe stimpsoni* clustered separately as it ate only small prey items, including more mites and spiders than any other species. The diet of *Bunodosoma capensis* and *Actinia equina* were sufficiently distinct to form a separate group. These species are both generalists, with no particular prey category dominating their diets. *B. capensis* was the only species that consumed platyhelminths, and *A. equina* the only species where insects formed a large proportion of the prey captured. The two *Pseudactinia* species grouped together with *Anthopleura michaelseni* and *Bunodactis reynaudi* from Wooley's Pool to form a cluster of macro-predators. These species fed mostly on pelecypods and gastropods, and were the only species that ate echinoderms, asteroids and cirripedes. *B. reynaudi* at Blouberg also formed a separate group, as pelecypods were so dominant in its diet. This was also the only species found to contain macrurans (*Jasus lalandii*). The stress level (three-dimensionality) of the plot was acceptably low (0.02).

Discussion

The rate of oxygen consumption by anemones is determined by, amongst other things, their size, state of expansion or contraction, temperature and illumination intensity (Sebens 1987; Shick 1991). From the results of the oxygen consumption readings under light and dark conditions it is apparent that none of the anemone species examined show any detectable autotrophic activity. *Bunodactis reynaudi* was the only species in which there was a significant difference in oxygen consumption under the different light intensities. However, the rate of oxygen consumption was higher in the light than in the dark, so the difference is not the result of autotrophic

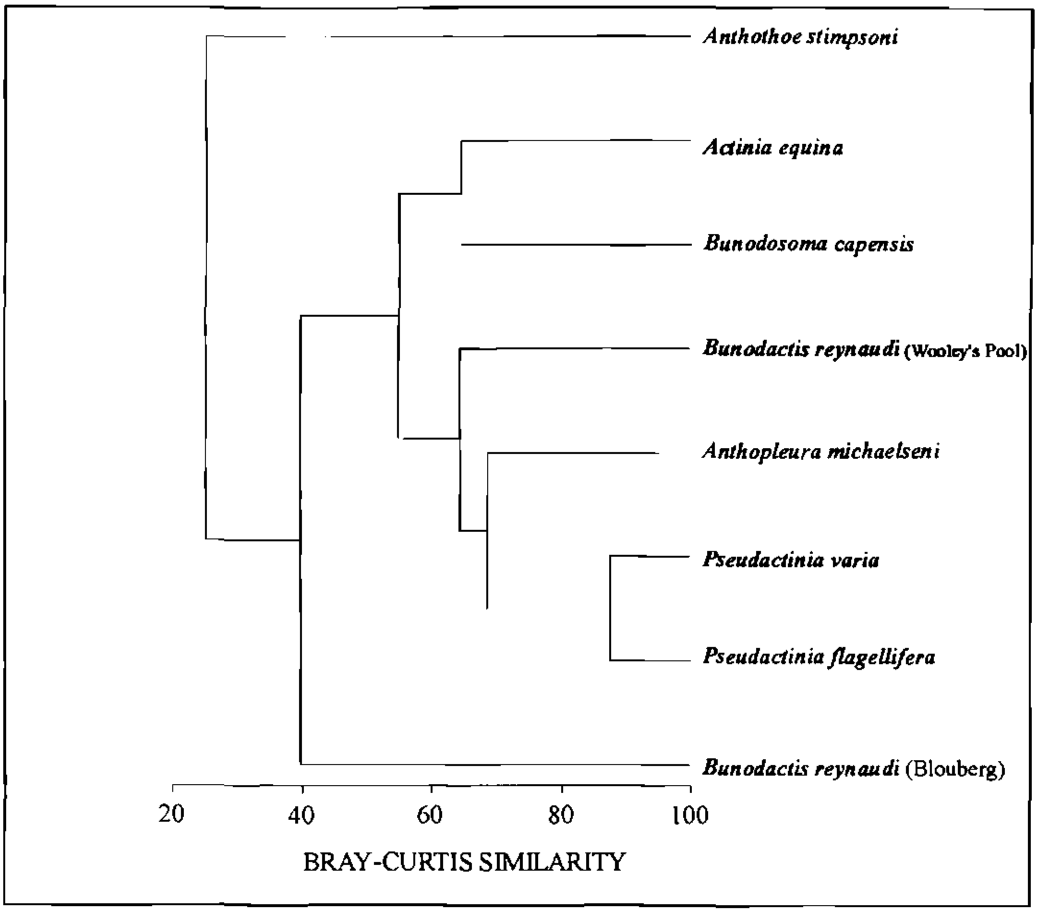

Figure 1 Dendrogram showing the degree of similarity between the diets of seven species of sea anemones in the south-western Cape based on the Index of Relative Importance (IRI) of the prey items consumed.

activities. Very few studies by other authors have measured respiration rates in any of the species from this study. Our results are, however consistent with those of Sebens & De Reimer (1977) who found that *Bunodactis* sp. did not possess any zooxanthellae and Griffiths (1977a) and Shick, Widdows & Gnaiger (1988) who ascertained that *Actinia equina* does not contain endosymbiotic algae.

Under similar climatic and tidal conditions, more of the anemones at Wooley's Pool contained food items, than at Blouberg (Table 2). This result is surprising since Blouberg is an exposed site and subject to much stronger wave action than Wooley's Pool. Strong wave action is often associated with increased amounts of food for sea anemones (Robbins & Shick 1980) — not only because the volume of food-laden water reaching the anemones is increased, but also because the waves dislodge organisms, making them available as prey (Sebens & Paine 1978; Sebens 1981a; Koehl 1982; Denny 1987). The number of anemones feeding might therefore be expected to be higher at Blouberg than at Wooley's Pool. The low percentage occurrence of food at the Blouberg site may be due to the much higher density of anemones at Blouberg (901 m^{-1}), compared with Wooley's Pool (49 m^{-1}). Adult anemones at Blouberg are crowded on the rocks above the mussel beds that provide their major food source. Larger or optimally positioned individuals may thus shield those further up the shore and reduce availability of prey to them. This is supported by the fact that anemones that had captured prey frequently contained numerous prey items within the coelenteron. The calmer conditions at Wooley's Pool could also contribute to a higher prey capture efficiency at this site. Low flow reduces the amount of prey swept along helplessly in strong currents, but can make more motile prey more available to the anemones (Sebens & Koehl 1984).

Gut content analyses indicated that sea anemones exploit a wide spectrum of prey items. There was a large degree of overlap in the diets of the various species examined. Isopods, gastropods and pelecypods (bivalves) were eaten by all seven species, but their importance in the diets varied considerably. Isopods were the most important food item in the diet of *Anthothoe stimpsoni*, while *Bunodosoma capensis, Anthopleura michaelseni, Pseudactinia flagellifera* and *P. varia* all ate mainly gastropods. *Actinia equina*, and the *Bunodactis reynaudi* populations at both Wooley's Pool and Blouberg consumed mostly pelecypods. In terms of mass, hard-shelled prey such as gastropods, cirripedes and pelecypods may have been disproportionally represented because of the inclusion of the shells in the wet weight measurements. Although it has been shown that at least 50% of the wet mass of molluscs is shell (Griffiths 1981), prey items were weighed with their shells because many were very small and the flesh could not be separated from the shell. Also, shell contents occurred in various stages of digestion, from intact to completely digested.

High-shore pools support very little life (Branch & Grif-

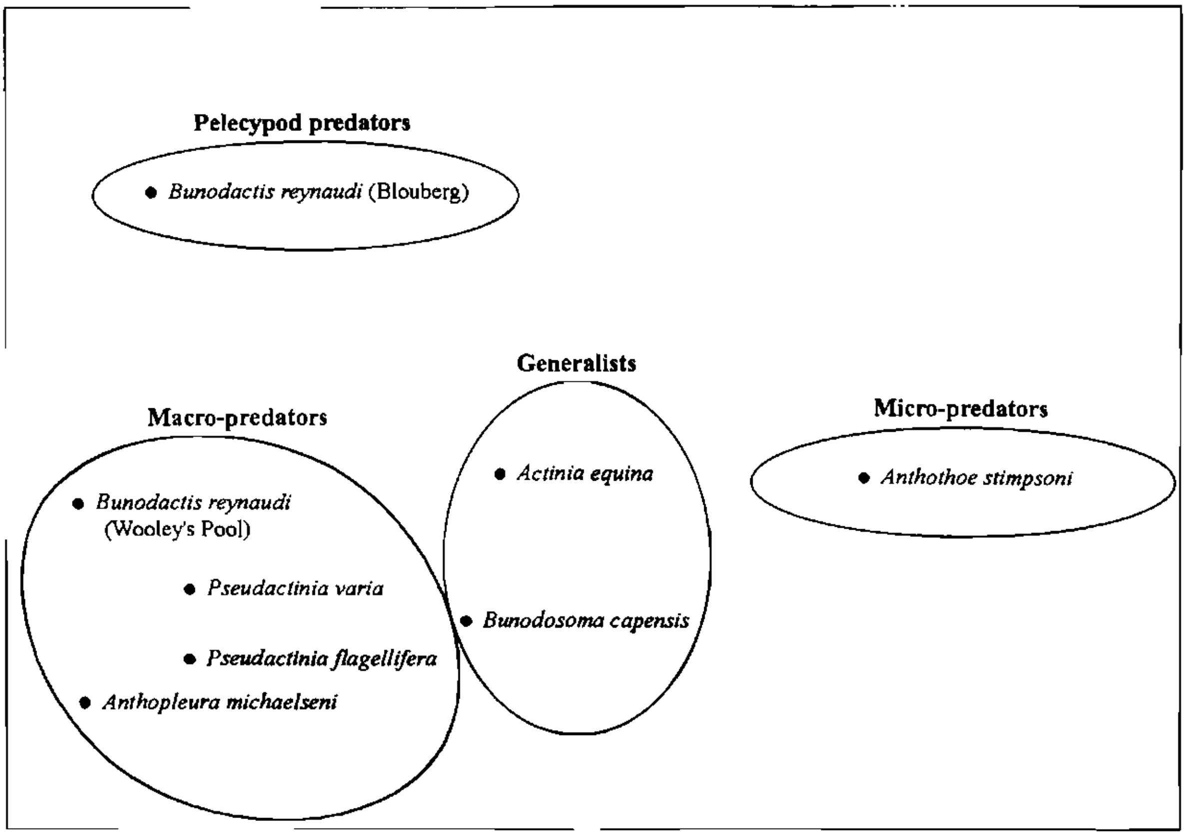

Figure 2 The relationship between the diets of the different anemone species at the two study sites. The ordination was obtained using multidimensional scaling on the same similarity matrix as Figure 1. *Bunodactis reynaudi* (Blouberg) was the only species that occurred at Blouberg, the remaining species were found at Wooley's Pool. (Stress = 0.02.)

fiths 1988) and diversity within them is low (Dethier 1980; Huggett & Griffiths 1986). It is not surprising therefore, that *Anthothoe stimpsoni*, which tended to inhabit these pools, consumed fewer prey categories than any of the other species examined. Prey size increases with anemone size (Sebens 1982a), so that *A. stimpsoni's* small size might therefore also limit the range of prey available to it.

The high proportion of gastropods in the diet of *Anthopleura michaelseni* and the two *Pseudactinia* species, may be explained in terms of their morphology and the habitats that they occupy. *A. michaelseni* are often found partially buried in sandy crevices with only the tentacles exposed. Gastropods such as *Burnupena* spp. that scavenge in crevices may thus blunder directly into their tentacles. The two *Pseudactinia* species are known to have extremely high toxicity levels (Bernheimer, Avigad, Branch, Dowdle & Lai 1984) and very 'sticky' tentacles that enable them to capture and hold large and active prey (Fautin & Fitt 1991). Their large size also increase the chances of these species capturing large prey (Herndl, Velimirov & Krauss 1985), such as cirripedes (*A. michaelseni*) and pelecypods (*A. michaelseni* and *Pseudactinia* spp.).

The components of the diets of the two *Pseudactinia* spp. were remarkably similar (Table 3). The guts of each species contained 19 prey categories, 14 of which were common to both species. These similarities are not surprising, as both species occupy very similar habitats and are morphologically alike. There is a predominance of motile prey in the diet (Table 3). This is to be expected because of the sheltered environment that these anemones inhabit (Branch & Griffiths 1988). In calm conditions prey capture may increase because larger prey can be held without being 'wrenched' from the tentacles by water movements. The low-shore position occupied by the two *Pseudactinia* species was adjacent to mussel beds. It is not surprising therefore that, contrary to the findings of Krijgsman & Talbot (1953), mussels were found in the gut content of both these species.

The main components of the diets of *Bunodactis reynaudi* from the two sites were the same, but pelecypods formed a higher proportion of the diet at Blouberg (Table 3). *Choromytilus meridionalis* and *Mytilus galloprovincialis* were the most common species eaten at both sites (Table 4). Wave tumbled mussels are frequently washed into the cracks and crevices occupied by *B. reynaudi* and the more than 300 short tentacles and the highly contractile sphincter muscle of this species ensure that prey can be firmly held and rapidly transferred to the mouth. Exposed sites, such as Blouberg, are known to have a much higher filter-feeder biomass than more sheltered sites (Field & Griffiths 1991; Emanuel, Bustamante, Branch, Eekhout & Odendaal 1992). It is not surprising thus that pelecypods dominated the diet at the latter site.

Four feeding groups were revealed by the cluster analysis and MDS-ordination (Figures 1, 2). *Anthothoe stimpsoni*, which are small and consume only small prey items, are regarded as micro-predators. *Actinia equina* and *Bunodosoma capensis* are generalists as neither appeared to favour any particular prey category. Both species are of intermediate size (Table 3) and consume prey covering a wide size range. The macro-predator group consists of the largest anemone species at Wooley's Pool *viz.*, *Bunodactis reynaudi, Anthopleura michaelseni, Pseudactinia flagellifera* and *Pseudactinia varia*. Because of their large size, these species are able to capture large prey. Their diets consisted largely of cirripedes, large gastropods and the mussels *C. meridionalis* and *M. galloprovincialis* and, in the case of *Pseudactinia* spp., sea urchins (Table 4). These macro-predators are probably the only anemones large enough to catch and utilize these prey. The diet of *B. reynaudi* at Blouberg was dominated by mussels and consequently they may be considered as specialist bivalve-feeders at this site.

In terms of taxonomic prey categories, the coelenteron contents of all the anemones examined were similar to those of other temperate anemones (Sebens & Koehl 1984; Shepherd & Gray 1985). Prey items from the *Actinia equina* population at Wooley's Pool are similar to those taken by this species in the U.K. (Rostron & Rostron 1978) and from Europe (Van-Praët 1985; Chintiroglou & Koukouras 1992). In each case, small crustaceans formed the bulk of the diet. Interestingly, insects formed a substantial part of the diet (Table 3) in the present study and in those of Van-Praët (1985) and of Chintiroglou & Koukouras (1992). Insects were also important constituents in the diet of *Actinia tenebrosa* from Australia (Ayre 1984). Because insects are only present during certain periods of the year, Ayre (1984) concluded that sea anemones are opportunistic predators. Our results confirm this. Most of the anemones that contained insects were collected in late spring (October and November, 1993), which is when Ayre made his collections. Van-Praët (1983) recorded that the mussel *Mytilus edulis* constituted most of the biomass in the coelenterons of *A. equina*. However, although pelecypods were the most important items in terms of frequency of occurrence (Table 3), they were almost all the tiny *Nucula nucleus* (Table 4). Mussels were completely absent from the gut contents of *A. equina* in this study.

Sea anemones are passive feeders that depend to a large extent on ambient water motion to bring prey to them. As the degree of wave action decreases therefore, anemones must rely increasingly on the mobility of the prey themselves (Shick 1991). This was reflected in the results. At Blouberg, which is an exposed site, sessile organisms, particularly the mussels *C. meridionalis* and *M. galloprovincialis*, formed the bulk of the prey (Table 4). Wooley's Pool is a more sheltered site and here mobile forms, such as gastropods and crustaceans, were more prevalent (Table 3).

Macroalgal fragments were present in the gut contents of all the species and were consumed particularly frequently by *Anthopleura michaelseni* (Table 3). It is, however not known whether sea anemones derive any nutritional benefit from plant material, which is also common in the diets of other species such as *A. elegantissima* (Sebens 1981b) and *A. ballii* (Cocks) (Minchen 1983). Gastric juices of *Actinia equina* (Van-Praët 1982) and *P. flagellifera* are known to contain amylase (Krijgsman & Talbot 1953), that can digest the cell walls of marine algae, but whether they posses the enzymes to utilize the cell contents is unknown. It is possible that bacteria or epiphytic diatoms, that are frequently associated with algal and other detritus, may be nutritionally important to the anemones that consume them (Herndl *et al.* 1985; Zamer, Robbins & Shick 1987).

The vast quantities of totally indigestible items found in coelenteron contents (Table 3) indicate that sea anemones are unselective in what they ingest (Shick 1991). Scarcity of prey and limited feeding time in the intertidal, are likely to have resulted in the selection of a numbers-maximizing feeding strategy (Griffiths 1975). The metabolic cost of prey capture is low for anemones (Shick 1991), and because egestion need not eliminate food still in the process of being digested, all material encountering the tentacles is ingested. Bursey & Guanciale (1977) noted that *Condylactis gigantea* continues to accept prey after ingestion has already taken place, as does *P. flagellifera* (Krijgsman & Talbot 1953).

The opportunistic feeding behaviour of sea anemones (Ayre 1984) makes a wide range of prey available to them. Given the high density of anemones in this and other regions they may have a considerable impact on the invertebrate prey populations that they exploit (MacKenzie 1977; Minchin 1983; Mathieson, Penniman & Harris 1991). In order to determine this, it is necessary to know the abundance of anemones on the shore and to estimate their consumption rates of the live prey that they ingest. This will be the subject of a subsequent paper that is presently in preparation.

Acknowledgements

This work was made possible by a postgraduate bursary to the senior author from the Foundation for Research Development (FRD) and further financial support was provided through a Foundation for Research Development Core-Programme Grant to Professors G.M. Branch, J.G. Field and C.L. Griffiths.

References

AYRE, D.J. 1984. The sea anemone *Actinia tenebrosa*: an opportunistic insectivore. *Ophelia* 23: 149–153.

BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Mar. Biol.* 50: 263–273.

BERNHEIMER, A.W., AVIGAD, L.S., BRANCH, G.M., DOWDLE, E. & LAI, C.Y. 1984. Purification and properties of a toxin from the South African sea anemone, *Pseudactinia varia*. *Toxicon* 22: 183–191.

BRANCH, G.M. & GRIFFITHS, C.L. 1988. The Benguela ecosystem. Part V. The coastal zone. *Oceanogr. Mar. Biol. Ann. Rev.* 26: 395–486.

BURSEY, C.R. & GUANCIALE, J.M. 1977. Feeding behavior of the sea anemone *Condylactis gigantea*. *Comp. Biochem. Physiol.* 57A: 115–117.

CHINTIROGLOU, Ch. & KOUKOURAS, A. 1992. The feeding habits of three Mediterranean sea anemone species, *Anemonia viridis* (Forskål), *Acinia equina* (Linnaeus) and *Çereus pedunculatus* (Pennant). *Helgoländer Meeresunters.* 46: 53–68.

DAYTON, P.K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Amer. Nat.* 107: 662–670.

DENNY, M.W. 1987. Life in the maelstrom: the biomechanics of wave-swept rocky shores. *TREE.* 2: 61–66.

DETHIER, M.N. 1980. Tidepools as refuges: predation and the limits of the harpacticoid copepod *Tigriopus californicus* (Baker). *J. Exp. Mar. Biol. Ecol.* 42: 99–111.

EMANUEL, B.P., BUSTAMANTE, R.H., BRANCH, G.M., EEKHOUT, S. & ODENDAAL, F.J. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *S. Afr. J. mar. Sci.* 12: 341–354.

FAUTIN, D.G. & FITT, W.K. 1991. A jellyfish-eating sea anemone (Cnidaria, Actiniaria) from Palau: *Entacmaea medusivora* sp. nov. *Hydrobiologia* 216/217: 453–461.

FIELD, J.G. & GRIFFITHS, C.L. 1991. Littoral and sublittoral ecosystems of Southern Africa. In: Ecosystems of the World 24. A.C. Mathieson and P.H. Nienhuis, (eds.). Elsevier, Amsterdam. pp. 323–346.

FIELD, J.G., CLARKE, K.R. & WARWICK, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8: 37–52.

GRIFFITHS, C.L. & BRANCH, G.M. 1991. The macrofauna of rocky shores in False Bay. *Trans. Roy. Soc. S. Afr.* 47: 575–594.

GRIFFITHS, D. 1975. Prey availability and the food of predators. *Ecology* 56: 1209–1214.

GRIFFITHS, R.J. 1977. Thermal stress and the biology of *Actinia equina* L. (Anthozoa). *J. Exp. Mar. Biol. Ecol.* 27: 141–154.

GRIFFITHS, R.J. 1981. Population dynamics and growth of the bivalve *Choromytilus meridionalis* (Kr.) at different tidal levels. *Estuar. cstl Shelf Sci.* 12: 101–118.

HARRIS, L.G. 1991. Comparative ecology of subtidal actiniarians from the coasts of California and the Gulf of Maine, USA. *Hydrobiologia* 216/217: 271–278.

HERNDL, G.J., VELIMIROV, B & KRAUSS, R.E. 1985. Heterotrophic nutrition and control of bacterial density in the coelenteron of the giant sea anemone *Stoichactis giganteum*. *Mar. Ecol. Prog. Ser.* 22: 101–105.

HUGGETT, J. & GRIFFITHS, C.L. 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. *Mar. Ecol. Prog. Ser.* 29: 190–197.

KELLOGG, R.B. & PATTON, J.S. 1983. Lipid droplets, medium of energy exchange in the symbiotic anemone *Condylactis gigantea*: a model coral polyp. *Mar. Biol.* 75: 137–149.

KOEHL, M.A.R. 1982. The interaction of moving water and sessile organisms. *Sci. Am.* 247: 110–120.

KRIJGSMAN, B.J. & TALBOT, F.H. 1953. Experiments on digestion in sea-anemones. *Arch. Int. Physiol.* 61: 277–291.

KRUGER, L.M. 1995. Feeding biology of intertidal sea anemones in the south-western Cape. M.Sc. thesis. University of Cape Town, Cape Town, South Africa. 98pp.

MACKENZIE, C.L. Jr. 1977. Sea anemone predation on larval oysters in Chesapeake Bay (Maryland). *Proc. Natl Shellfish. Assoc.* 67: 113-117.

MATHIESON, A.C., PENNIMAN, C.A. & HARRIS, L.G. 1991. Northwest Atlantic Rocky Shore Ecology. In: Ecosystems of the World 24. A.C. Mathieson and P.H. Niehuis, (eds.). Elsevier, Amsterdam. pp 109–191.

MINCHIN, D. 1983. Predation on young *Pecten maximus* (L.) (Bivalvia), by the anemone *Anthopleura ballii* (Cocks). *J. moll. Stud.* 49: 228–231.

MCQUAID, C.D. & BRANCH, G.M. 1984. Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Mar. Ecol. Prog. Ser.* 19: 145–151.

ROBBINS, R.E. & SHICK, J.M. 1980. Expansion-contraction behavior in the sea anemone *Metridium senile*: environmental cues and energetic consequences. In: Nutrition in the Lower Metazoa, D.C. Smith and Y. Tiffon, (eds.). Pergamon Press, Oxford, UK. pp 101–116.

ROSTRON, M.A. & ROSTRON, J. 1978. Fecundity and reproductive ecology of a natural population of *Actinia equina* L. (Cnidaria: Anthozoa). *J. Exp. Mar. Biol. Ecol.* 33: 251–259.

SEBENS, K.P. 1981a. Recruitment in a sea anemone population: juvenile substrate becomes adult prey. *Science* 213: 785–787.

SEBENS, K.P. 1981b. The allometry of feeding, energetics, and body size in three sea anemone species. *Biol. Bull.* 161: 152–171.

SEBENS, K.P. 1982a. Recruitment and habitat selection in the intertidal sea anemones, *Anthopleura elegantissima* (Brandt) and *A. xanthogrammica* (Brandt). *J. Exp. Mar. Biol. Ecol.* 59: 103–124.

SEBENS, K.P. 1982b. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* 63: 209–222.

SEBENS, K.P. 1987. Coelenterata. In: Animal Energetics, Vol. 1, Protozoa through Insecta. T.J. Pandian & F.J. Vernberg (eds.). Academic Press. New York. pp. 55–120.

SEBENS, K.P. & DEREIMER, K. 1977. Diel cycles of expansion and contraction in coral reef anthozoans. *Mar. Biol.* 43: 247–256.

SEBENS, K.P. & KOEHL, M.A.R. 1984. Predation on zooplankton by two benthic anthozoans, *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria), in the New England subtidal. *Mar. Biol.* 81: 255–271.

SEBENS, K.P. & PAINE, R.T. 1978. Biogeography of anthozoans along the west coast of South America: habitat, disturbance, and prey availability. In: *Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere,* Auckland, New Zealand, N.Z. DSIR Inf. (Ser. 137). 1: 219–237.

SHEPHERD, S.A. & GRAY, J.D. 1985. Food of the anemone *Anthothoe albocincta* at West Island, South Australia. *Trans. R. Soc. S. Aust.* 109: 191–192.

SHICK, J.M. 1991. A Functional Biology of Sea Anemones. Chapman and Hall, London. 395 pp.

SHICK, J.M., WIDDOWS, J. & GNAIGER, E. 1988. Calorimetric studies of behavior, metabolism and energetics of sessile intertidal animals. *Amer. Zool.* 28: 161–181.

TSUCHIDA, C.B. & POTTS, D.C. 1994. The effects of illumination, food and symbionts on growth of the sea anemone *Anthopleura elegantissima* (Brandt, 1835). I. Ramet growth. *J. Exp. Mar. Biol. Ecol.* 183: 227–242.

TYTLER, E.M. & SPENCER DAVIES, P. 1984. Photosynthetic production and respiratory energy expenditure in the anemone *Anemonia sulcata* (Pennant). *J. Exp. Mar. Biol. Ecol.* 81: 73–86.

VAN-PRAËT, M. 1982. Amylase and trypsin- and chymotrypsin-like proteases from *Actinia equina* L.; their role in the nutrition of this sea anemone. *Comp. Biochem. Physiol.* 72A: 523–528.

VAN-PRAËT, M. 1983. Régime alimentaire des Actines. *Bull. Soc. Zool. France* 108: 403–407.

VAN-PRAËT, M. 1985. Nutrition of sea anemones. *Adv. Mar. Biol.* 22: 65–99.

ZAMER, W.E., ROBBINS, R.E. & SHICK, J.M. 1987. β-Glucuronidase activity and detritus utilization in the sea anemone *Metridium senile* and *Anthopleura elegantissima*. *Comp. Biochem. Physiol.* 87B (2): 303–308.

ZAR, J.H. 1984. Biostatistical Analysis, 2nd ed. Prentice Hall. Englewood Cliffs, New Jersey. 718pp.