Digestion rates of prey eaten by intertidal sea anemones from the south-western Cape, South Africa

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Received 7 May 1997; accepted 28 July 1997

Digestion rates were determined for natural prey items offered to each of seven species of sea anemones found at Wooley's Pool in False Bay and to the single species (*Bunodactis reynaudi*) recorded at Blouberg on the Atlantic coast of the south-western Cape, South Africa.This was done by examining prey items removed from the coelenterons at regular intervals after feeding and assessing their degree of digestion according to a predetermined scale. There was considerable variation in the gut retention times between different anemone species offered the same prey types, with *Actinia equina* consistently showing the shortest gut retention times (12 h for amphipods, 15 h for pelecypods and 23 h for isopods). Of the various prey categories tested, amphipods tended to be the most rapidly digested group, while molluscs and echinoderms usually remained in the coelenteron the longest. Mean gut retention times in *B. reynaudi*, the only species found both in False Bay (17°C) and on the cold west coast (12°C) were markedly longer (72 vs 60 h and 43 vs 30 h for pelecypods and gastropods respectively) at the lower temperature.

Several authors have pointed out that sea anemones are important and conspicuous predators within the rocky intertidal zone of the south-western Cape (McQuaid & Branch 1984, 1985; Field & Griffiths 1991; Griffiths & Branch 1991). However, to date no attempt has been made to quantify their consumption rates, and hence to obtain direct estimates of their importance as secondary consumers within such systems.

Seven species of sea anemones are common on intertidal and shallow subtidal reefs in the region and the natural diets of these species have recently been inferred from analyses of coelenteron contents (Kruger & Griffiths 1996). Gut contents analyses such as these can, however, provide a distorted view of the actual ratios of different prey items consumed. This is because the various food items may be retained in the gut for markedly different periods. The net result is that the relative frequencies of harder, or more resilient materials, such as bone, shell, spines or exoskeleton, tend to be overemphasized, because they persist longer in the gut. Conversely, the rapid digestion rates of soft-bodied prey may result in underestimation of their importance in the diet. These inconsistencies between the results of gut contents analyses and actual diet have been widely addressed in taxa such as fish (Elliott & Persson 1978; Hyslop 1980), birds (Lifjeld 1983; Duffy & Jackson 1986) and mammals (Warner 1981). Gut turnover data for invertebrates are, however, rare, most of the work having been done on crustaceans, particularly crabs (Williams 1981) and lobsters (Carter & Steele 1981). Fortunately anemones make good subjects for such digestion rate estimates, because the prey are usually ingested whole and are retained within the coelenteron until egestion, which is easily observable. A further advantage of measuring gut turnover rates is that they allow consumption rates to be inferred from gut contents analyses taken at random from natural populations, data which are already available for these anemone species (Kruger & Griffiths 1996).

The objective of the present study is to determine gut turnover times of various prey items consumed by each of the seven intertidal anemone species found in the south-western Cape. Such data, taken in conjunction with the earlier dietary studies of Kruger & Griffiths (1996) will permit the calculation of overall consumption rates in the field. These, together with population surveys, in turn can provide a means of quantifying the impact of sea anemones as secondary consumers in the intertidal (Kruger 1995; Kruger & Griffiths, in prep.).

Methods

Anemones to be used for digestion rate studies were collected between February 1993 and December 1994 from two sites: Wooley's Pool in False Bay (34°12'S; 18°43'E) and Blouberg, on the Cape west coast (33°47'S; 18°29'E). All seven species were found at Wooley's Pool, whereas only *Bunodactis reynaudi* occurred at Blouberg. Undamaged animals covering a range of sizes representative of the natural field population were conveyed to the laboratory in individual collecting jars and transferred to aquaria supplied with circulating sea water. Individual anemones were placed in separate sections of compartmentalized tanks and left to reattach. Anemones were maintained at the mean sea water temperature of the site of origin, this being 17°C for Wooley's Pool and 12°C for Blouberg.

To maintain healthy and responsive anemones, the tanks were slowly drained using a narrow-bore siphon hose and then refilled twice daily, simulating tidal action. Anemones were initially allowed to acclimate for at least one week, during which time they were fed every second day with pieces of mussel flesh. They were then starved for a further week prior to the experiments, thus ensuring that no food remained in their coelenterons.

The rates at which specific prey items were digested by the different anemones were determined by feeding replicate specimens of each species with individual food items. Live, undamaged prey were used to ensure that no deterioration of the tissues occurred prior to ingestion. The mass of each prey

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item was recorded and smaller-sized prey fed to smaller-sized anemones, to simulate natural feeding behaviour (Purcell 1977; Sebens & Koehl 1984). To initiate ingestion prey were held with forceps and dropped onto the tentacles or oral disc of expanded anemones. Handling times prior to actual ingestion were extremely short (< 2 min) and were included in the measures of turnover rate.

At regular intervals after ingestion three anemones were selected randomly from each of the groups fed with a particular prey item and anaesthetised in a plastic jar containing 10% $MgCl_2$ mixed 1:1 with sea water. They were then frozen rapidly at –80°C to prevent further digestion, and left for a minimum of 2 h. The anemones were then dissected to reveal the ingested food. The degree of digestion of each prey item was assessed and recorded according to the predetermined scale shown in Table 1. This process was continued until egestion had taken place. Since there was considerable variation in the digestion states of the prey items removed from the three replicate anemones in each sample a three point weighted running mean was used when plotting results. The specific prey items used in the digestion rate experiments are listed in Table 2. Three different prey categories were offered to each anemone species, but as *Anthothoe stimpsoni* and *Bunodosoma capensis* frequently rejected food presented to them, results could only be obtained for two food types in these species.

The anemone species considered here differ greatly in size (Kruger 1995) — *A. stimpsoni* being the smallest form (9.1 mm mean basal diameter) and *Pseudactinia flagellifera* (60.2 mm mean basal diameter) the largest. Partially as a result of these size differences, the prey items in the natural diets of the various species vary considerably in both size and taxonomic composition (Kruger & Griffiths 1996). To make estimates of gut retention times ecologically meaningful, anemones of different sizes were thus offered prey representative of their natural diets. In some cases this involved offering the various anemone species different prey taxa. Some interspecific comparisons of digestion rates can, however, still be made in these cases by comparing the gut residence times for prey of the same taxonomic class for example between *A. stimpsoni* presented with the small gastropod *Tricolia capensis* and *P. flagellifera* fed with the larger whelk *Burnupena cincta*.

Table 1 Key used to determine the digestion rates of the various prey taxa fed to the seven species of sea anemones. The digestion state index represents progressive changes in the condition of the food item from ingestion (6) to egestion (0)

Digestion state	Prey category			
	Arthropoda	Mollusca	Echinodermata	Annelida
6	Ingested	Ingested	Ingested	Ingested
5	Mucus-covered	Mucus-covered	Mucus-covered	Mucus-covered
4	Exoskeleton damaged	Shell opening	Spines detaching	Surface damage
3	Limbs off	Shell open, flesh intact	All spines off	Breaking up
2	Exoskeleton empty	Flesh liquefied	Flesh liquefied	Flesh liquefied
1	Exoskeleton in pieces	Shell empty	Shell empty	Jaws + setae
0	Egested	Egested	Egested	Egested

Table 2 Prey species fed to seven anemone species in the digestion rate experiments

Anemone species	Prey category	Prey species
Actinia equina	Isopoda	*Cirolana* sp.
	Amphipoda	*Paramoera capensis*
	Pelecypoda	*Nucula nucleus*
Anthothoe stimpsoni	Isopoda	*Cirolana* sp.
	Gastropoda	*Tricolia capensis*
Anthopleura michaelseni	Cirripedia	*Tetraclita serrata*
	Pelecypoda	*Mytilus galloprovincialis*
	Gastropoda	*Burnupena cincta*
Bunodosoma capensis	Isopoda	*Cirolana* sp.
	Amphipoda	*Paramoera capensis*
Pseudactinia flagellifera	Isopoda	*Cirolana* sp.
	Pelecypoda	*Mytilus galloprovincialis*
	Gastropoda	*Burnupena cincta*
Pseudactinia varia	Isopoda	*Cirolana* sp.
	Gastropoda	*Burnupena cincta*
	Echinoidea	*Parechinus angulosus*
Bunodactis reynaudi	Cirripedia	*Tetraclita serrata*
(Wooley's Pool)	Pelecypoda	*Mytilus galloprovincialis*
	Gastropoda	*Burnupena cincta*
Bunodactis reynaudi	Polychaeta	*Pseudonereis variegata*
(Blouberg)	Pelecypoda	*Mytilus galloprovincialis*
	Gastropoda	*Burnupena cincta*

Results

Time-series illustrating the digestion state of various prey items following ingestion by each of the anemone species all demonstrate a steady decline in prey condition over time, although the signals do contain considerable noise, perhaps partly as a result of the artificial scale used. To save space Figure 1 gives these data for only two of the anemone species, *Actinia equina* and *Bunodactis reynaudi* (Blouberg population). These represent the fastest and slowest digestion rates recorded respectively. The remaining data can be obtained from the authors, but are given here simply in terms of the time to egestion for each prey category (Table 3). These results can be used both to compare gut residence times of different prey items consumed by a single anemone species and to compare the digestive abilities of various anemone species fed on the same or similar prey. In the case of *B. reynaudi* there is also information on the effects of temperature on gut residence times.

Gut residence time vs prey category

Plots showing progressive changes in the state of digestion of three types of prey eaten by *Actinia equina* from Wooley's Pool and *Bunodactis reynaudi* from Blouberg are shown in Figure 1. In the case of *A. equina* amphipods (*Paramoera*

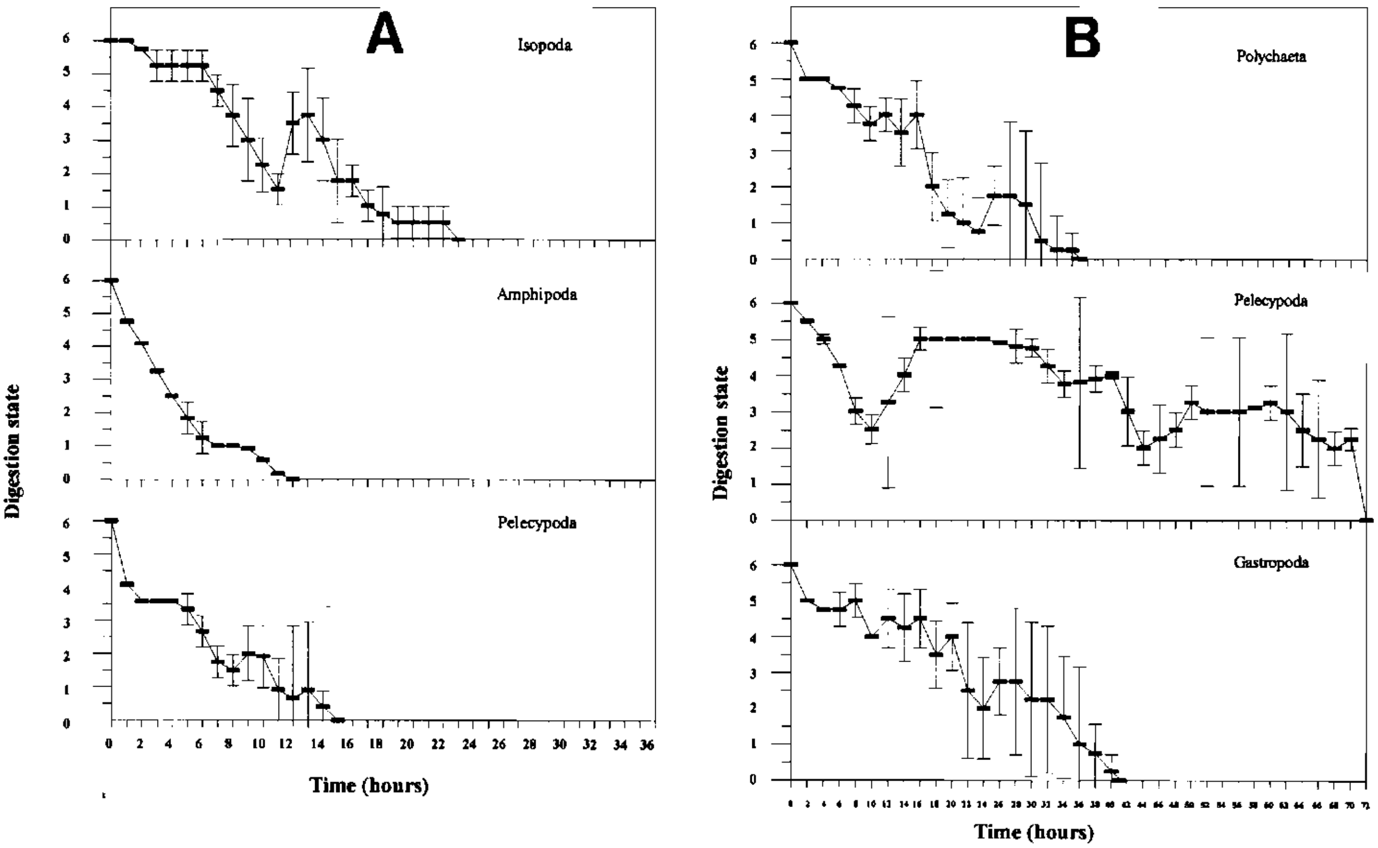

Figure 1 Time series showing progressive stages in digestion state of three categories of food item consumed by (A) *Actinia equina* from Wooley's Pool and (B) *Bunodactis reynaudi* from Blouberg. Data are shown as three point running means (± *SD*) of the digestion states for three anemones sacrificed at each of the time iintervals shown. Indices of digestion state are as shown in Table 1 and the prey species used are listed in Table 2.

Table 3 Time taken (h ± *SD*) for seven species of sea anemone at Wooley's Pool and the single species at Blouberg to egest various categories of prey. The species fed to each anemone are listed in Table 2

	Prey category						
Anemone species	Amphipoda	Isopoda	Pelycypoda	Gastropoda	Cirripeda	Echinoidea	Polychaeta
Wooley's Pool							
Actinia equina	12 ± 0.6	23 ± 0.6	15 ± 0.5				
Anthothoe stimpsoni		28 ± 0.7		30 ± 0.9			
Anthopleura michaelseni			32 ± 1.2	26 ± 1.1	29 ± 1.4		
Bunodosoma capensis	23 ± 0.9	27 ± 1.2					
Pseudactinia flagellifera		29 ± 0.7	47 ± 1.4	33 ± 0.4			
Pseudactinia varia		30 ± 0.6		38 ± 0.6		34 ± 0.3	
Bunodactis reynaudi			60 ± 1.5	30 ± 0.7	25 ± 0.2		
Blouberg							
B. reynaudi			72 ± 1.1	43 ± 1.1			37 ± 0.9

capensis — see Table 2) were the most rapidly digested prey and were egested on average after 12 h — the shortest time of any prey item in the study. Pelecypods (*Nucula nucleus*) took 15 h to be fully digested, while isopods (*Cirolana* sp.) were egested after 23 h. There were few other noteworthy prey-related variations in gut residence time within the remaining anemone species from Wooley's Pool. *Anthothoe stimpsoni* took an average of 28 h to egest isopods (*Cirolana* sp.) and 30 h for gastropods (*Tricolia capensis*). The time taken for *Anthopleura michaelseni* to egest prey items varied from 26 h for the gastropod *Burnupena cincta*, to 29 h for the cirripede *Tetraclita serrata* and 32 h for the pelecypod *Mytilus galloprovincialis*. *Bunodosoma capensis* took an average of 23 h to egest the amphipod *Paramoera capensis* and 27 h for the isopod *Cirolana* sp. *P. flagellifera* voided the gastropod *B. cincta* 33 h after ingestion, the isopod *Cirolana* sp. after 29 h, and the pelecypod *M. galloprovincialis* after 47 h. Gut turnover rates for *P. varia* were similar at 38 h for *B. cincta*, 30 h for *Cirolana* sp. and 34 h for the echinoid *Parechinus angulosus*. The average time taken for *B. reynaudi* from Wooley's Pool to digest the cirripede *T. serrata* was 25 h, and for *B. cincta* (gastropod) 30 h. The time taken to egest *M. galloprovincialis* was much longer (60 h). A similar pattern was evident in specimens from Blouberg, although turnover times were even longer under these colder conditions. The remains of the polychaete *Pseudonereis variegata* were voided after an average of 37 h at this site, whereas the pelycypod *M. galloprovincialis* persisted for almost twice as long at 72 h.

Comparisons between anemone species

Actinia equina appeared to digest prey considerably faster than any of the other species (Table 3) and were the only anemones to produce egesta of all items eaten within 24 h of ingestion (Figure 1A). Comparisons between the remaining results for species tested at 17°C (Table 3) show most prey items to be egested within the fairly narrow time frame of 26–38 h following ingestion. The only exceptions were for pelycepods consumed by *Pseudactinia flagellifera* (47 h) and *Bunodactis reynaudi* (60 h). More detailed interpretation is confounded by the fact that the various anemones were fed prey representative of their natural diets, which often differed between anemone species (Tables 2, 3). There does, however, appear to be a tendency for the longer gut retention times to occur amongst *Pseudactinia* spp. and *Bunodactis reynaudi*, relative to *Anthothoe stimpsoni*, *Anthopleura michaelseni* and *Bunodosoma capensis*.

Effects of temperature

Specimens of *Bunodactis reynaudi* collected from Blouberg, and held at 12°C, digested their prey considerably more slowly than those from Wooley's Pool, which were held at 17°C. The gut retention times of both the pelecypod *Mytilus galloprovincialis* (72 vs 60 h) and the gastropod *Burnupena cincta* (43 vs 30 h) at the two different sites were significantly different ($p < 0.001$, Mann-Whitney; Zar 1984).

Discussion

A fairly wide range in both intra- and interspecific prey digestion times spanning a range of 12–72 h were evident from our results. *Actinia equina* had the fastest gut turnover times of the seven anemone species. The remaining species showed similar ranges, with a tendency for the longer times to occur in the *Pseudactinia* spp. and in *Bunodactis reynaudi*. The colder water temperatures at Blouberg, where only *Bunodactis reynaudi* was found, resulted in considerably slower rates of prey digestion at this site.

Comparisons between prey categories

The digestibility of prey items would be expected to be the primary factor determining the time for which they are retained within the coelenteron (Shick 1991) and indeed earlier studies of sea anemones have shown that soft-bodied prey are digested comparatively rapidly (Sebens & Koehl 1984). This is supported by our data for polychaetes, which deteriorated more rapidly and were egested far sooner than any of the shelled prey items consumed by *Bunodactis reynaudi* at Blouberg (Figure 1B). The shorter throughput time for amphipods compared with isopods (Figure 1A) can be explained in the same way. *Paramoera capensis* is a fairly delicate amphipod (Branch, Griffiths, Branch & Beckley 1994) compared to the more heavily chitinized isopod, *Cirolana* sp. The isopods also roll up into a ball when disturbed, which may assist in protecting the delicate ventral surface and also reduce the surface area of the prey exposed to the 'chitinase activity' (Shick 1991), hence retarding digestion. The isopods fed to the anemones were also larger (mean wet weight 0.04 g) than the amphipods (mean wet weight 0.01 g) and this might have resulted in their longer digestion time.

Crustaceans were generally digested more rapidly than hard-shelled molluscs and echinoderms. This is not surprising. Besides the protection provided by the shell and the frequently larger biomass of the pelecypods used, anemones have been demonstrated to have extremely powerful enzymes capable of digesting the chitinous exoskeleton of crustaceans (Elyakova 1972). Even cirripedes eaten by *Anthopleura michaelseni* and *Bunodactis reynaudi* from Wooley's Pool took less time to be digested than similarly sized mussels eaten by the same species. Pelecypods eaten by *Actinia equina* were the small, thin-shelled bivalve *Nucula nucleus*. These were digested far more rapidly than the larger, more heavy-shelled mussel *Mytilus galloprovincialis*, which was fed to the other species.

Throughput times determined for the anemones in this study were generally longer than those obtained by other authors. For example Zamer (1986) found that *Artemia* sp. consumed by *Anthopleura elegantissima* were digested within 4 h. Purcell (1977) found that zooplankton remains were egested by *Metridium senile* in 24–48 h, while Sebens & Koehl (1984) noted digestion times of only 2–6 h in this species. The medusivorous anemone *Entacmaea medusivora* digested its prey in 2–24 h (Fautin & Fitt 1991). Scallops were egested 7–15 h after ingestion by *Anthopleura ballii* (Minchin 1983), and the remains of crustaceans and echinoderms less than 24 h after ingestion by *Stoichactis giganteum* (Herndl, Velimirov & Krauss 1985). The latter species is one of the largest anemones and was maintained at a water temperature of 23°C, a factor which may have reduced the digestion time, compared with those in the present study. The only study reporting longer retention times than those documented here was the population of *Actinia tenebrosa* studied by Ayre (1984), which still contained remains of terrestrial moths consumed three weeks previously! The wide variation in these results illustrates the difficulty in determining accurate digestion rates for sea anemones, because of the plethora of interacting factors such as temperature, digestibility of the prey and ration size which may potentially affect this parameter.

Interspecific differences

The rapid rate of digestion of prey by *Actinia equina* is not easily explained, although these anemones do differ in their habits from the other species considered here, in that they live high in the intertidal zone (Kruger 1995) and are therefore frequently subjected to aerial exposure. *Actinia equina* is also the only species in this study that broods its young. Sufficient food must therefore be assimilated, not only to sustain the adults, but to meet the requirements of their broods. Because of this and perhaps also because larger individuals are less susceptible to desiccation than smaller ones (Ottaway & Thomas 1971), rapid energy turnover and concomitant high growth rates may be strongly selected for in these anemones and this may have resulted in the evolution of rapid digestion rates.

Temperature-related differences

Turnover times of prey consumed by *Bunodactis reynaudi* maintained at 12°C were consistently longer than in those kept at 17°C. Digestion rate is reduced at lower temperatures owing to both a decrease in the metabolic rate of the anemones (Sebens 1980) and the thermal sensitivity of digestive enzymes (Shick 1991). An increase in temperature may lead to a reduced throughput time, as the metabolic cost to the anemone increases (Sebens 1982). Absorption is also temperature dependent. Anemones at lower temperatures gain less weight than those in warmer conditions (Sebens 1980).

Taking into account their relatively fast digestion rates and the high densities in which they often occur (Kruger 1995), it is suggested that anemones are capable of consuming considerable amounts of prey and could therefore impact significantly on their prey populations. In order to ascertain the impact of this group as consumers in rocky shore ecosystems, the abundance of each anemone species must be known, as well as the natural diets of each species at the different sites and the gut turnover times provided above. Overall estimates of population consumption rates will be the subject of a subsequent paper currently in preparation.

Acknowledgments

Financial assistance in the form of postgraduate bursaries for the senior author from the Foundation for Research Development (FRD) and an FRD Core Program grant to G.M. Branch, J.G. Field and C.L. Griffiths is gratefully acknowledged.

References

AYRE, D.J. 1984. The sea anemone *Actinia tenebrosa*: an opportunistic insectivore. *Ophelia* 23(2): 149–153.

BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L. & BECKLEY, L.E. 1994. Two Oceans. A guide to the marine life of Southern Africa. David Philip, Cape Town. 360pp.

CARTER, J.A. & STEELE, D.H. 1982. Stomach contents of immature lobsters (*Homarus americanus*) from Placentia Bay, Newfoundland. *Can. J. Zool.* 60: 337–347.

DUFFY, D.C. & JACKSON, S. 1986. Diet studies of seabirds: a review of methods. *Colonial Waterbirds.* 9: 1–17.

ELLIOTT, J.M. & PERSSON, L. 1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47: 977–991.

ELYAKOVA, L.A. 1972. Distribution of cellulases and chitinases in marine invertebrates. *Comp. Biochem. Physiol.* 43B: 67–70.

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, London, New York, Tokyo. pp. 323–346.

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

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.

HYSLOP, E.J. 1980. Stomach contents analysis — a review of methods and their application. *J. Fish. Biol.* 17: 411–429.

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.

KRUGER, L.M. & GRIFFITHS, C.L. 1996. Sources of nutrition in intertidal sea anemones from the south-western Cape, South Africa. *S Afr. J. Zool.* 31: 110–119.

LIFJELD, J. 1983. Stomach content analyses of the Dunlin *Calidris alpina*: bias due to differential digestibility of prey items. *Fauna norv. Ser. C. Cinclus.* 6: 43–46.

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.

MCQUAID, C.D. & BRANCH, G.M. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Mar. Ecol. Prog. Ser.* 22: 153–161.

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

OTTAWAY, J. R. & THOMAS, I.M. 1971. Movement and zonation of the intertidal anemone *Actinia tenebrosa* Farqu. (Cnidaria: Anthozoa) under experimental conditions. *Aust. J. Freshw. Res.* 22: 63–78.

PURCELL, J.E. 1977. The diet of large and small individuals of the sea anemone *Metridium senile*. *Bull. S. Cal. Acad. Sci.* 76(3): 168–172.

SEBENS, K.P. 1980. The regulation of asexual reproduction and indeterminate body size in the sea anemone *Anthopleura elegantissima* (Brandt). *Biol. Bull.* 158: 370–382.

SEBENS, K.P. 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* 63(1): 209–222.

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.

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

WARNER, A.C.I. 1981. Rate of passage of digesta through the gut of mammals and birds. *Nutrition Abstracts and Reviews Series B.* 51(12):789–820.

WILLIAMS, M.J. 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *J. Exp. Mar. Biol. Ecol.* 52: 103–113.

ZAMER, W.E. 1986. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima* I. Prey capture, absorption efficiency and growth. *Mar. Biol.* 92: 299–314.

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