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Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

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Published online: 17 Feb 2007.

To cite this article: L.M. Kruger & C.L. Griffiths (1998) Sea anemones as secondary consumers on rocky shores in the south-western Cape, South Africa, *Journal of Natural History*, 32:5, 629-644, DOI: [10.1080/00222939800770331](https://doi.org/10.1080/00222939800770331)

To link to this article: <http://dx.doi.org/10.1080/00222939800770331>

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Sea anemones as secondary consumers on rocky shores in the south-western Cape, South Africa

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(Accepted 13 October 1997)

The species composition, abundance and distribution patterns of intertidal sea anemone assemblages were determined at two sites on the Cape Peninsula, South Africa. A single species, *Bunodactis reynaudi* (Milne-Edwards) dominated at Bloubergstrand in Table Bay, with a density of 901 m^{-1} (i.e. per linear metre of coastline). Seven species, with a combined density of 660 m^{-1} , were found at Wooley's Pool in False Bay. Of these *Actinia equina* Linn. and *Anthothoe stimpsoni* (Verr.) occurred primarily in the upper intertidal, *Anthopleura michaelsoni* (Pax), *Bunodosoma capensis* (Less.) and *Bunodactis reynaudi* in the mid- to low intertidal and *Pseudactinia varia* Carlgren and *P. flagellifera* (Hertw.) only in sheltered pools near the sublittoral fringe. Density data are combined with previously reported gut content analyses and digestion rate estimates to calculate total annual consumption rates of natural populations of anemones. At Wooley's Pool the anemones colonizing each linear metre of shore consume an estimated 103 337 isopods, 14 973 amphipods, 21 050 cirripedes, 40 468 pelecypods and 30 102 gastropods annually. At Bloubergstrand the *B. reynaudi* population consume 38 437 polychaetes, 129 744 pelecypods and $116\,229\text{ gastropods m}^{-1}\text{y}^{-1}$. These figures considerably exceed estimated population consumption rates for other major invertebrate predators. However, the bivalves and cirripedes taken by anemones are dislodged individuals, hence anemones are unlikely to play any significant role in structuring populations of these species. By contrast, consumption of motile prey, such as isopods and gastropods, may impact significantly on these populations. Overall annual consumption by naturally occurring anemone assemblages at Bloubergstrand were calculated to be $182\,284\text{ kJ m}^{-2}\text{y}^{-1}$, six times higher than at Wooley's Pool ($30\,851\text{ kJ m}^{-2}\text{y}^{-1}$). These very high rates suggest that anemones are major secondary consumers in rocky intertidal communities in the south-western Cape.

KEYWORDS: sea anemone, diet, consumption rate, South Africa.

Introduction

Several studies have attempted to determine patterns of energy flow through rocky shore ecosystems in the south-western Cape region of South Africa (Branch and Griffiths, 1988; Field and Griffiths, 1991; Griffiths and Branch, 1991). These reports all recognize that anemones form a significant component of rocky shore assemblages in the region, but at the time insufficient information was available on their feeding biology to make estimates of their impact as consumers. Indeed the ecophysiology and feeding ecology of anemones in general remain poorly known.

Some aspects of energetics and feeding biology have been examined, for example oxygen uptake rates in *Actinia equina* Linn. were measured by Griffiths (1977a,b) and in *Metridium senile* (Linn.) and *Anthopleura elegantissima* (Brandt) by Shick *et al.* (1979), while prey capture and absorption efficiencies of *A. elegantissima* under natural conditions were quantified by Zamer (1986). In addition numerous studies, including those by Purcell (1977), Van Praet (1983), Ayre (1984) and Littler *et al.* (1991) have examined the diets of various anemone species. Several components of the energy budget of *A. elegantissima* are quantified by Shick *et al.* (1988), and integrated energy budgets have been measured for *Aiptasia pulchella* (Carlgren) (Hunter, 1984) and *A. elegantissima* (Zamer and Shick, 1987).

The diets of the seven most abundant intertidal anemone species found in the south-western Cape region of South Africa have recently been examined by Kruger and Griffiths (1996), while digestion rates of prey consumed by these same species have been determined by Kruger and Griffiths (in press). None of these anemones contain symbiotic zooxanthellae within their tissues, indicating that all their energy requirements are met by prey capture. This, together with the high densities in which anemones are frequently found in this region suggest that they could have a considerable impact on local prey populations.

Using data on the abundance of sea anemones, together with information on the actual prey consumed by the anemones and the turnover times for the different prey items, an attempt is made here to give the first quantitative estimate of annual consumption rates of each species and of the anemone assemblages as a whole. This, together with the existing information on the population sizes and production rates of prey species, will provide an indication of the overall importance of sea anemones as secondary consumers in rocky shore systems in the south-western Cape.

Methods

Study sites

Two sites, one on the east coast (Wooley's Pool) and one on the west coast (Bloubergstrand) of the Cape Peninsula, South Africa (figure 1) were selected for study. This region is a transition zone between the cold-temperate west coast and the warm-temperate south coast of South Africa (Brown and Jarman, 1978; Griffiths and Branch, 1991). Bloubergstrand lies in Table Bay on the Cape west coast (33° 47'S 18° 29'E) and has a mean monthly sea surface temperature of around 14°C. Winter temperatures are fairly constant (11–13°C), but upwelling can cause rapid short-term reductions in temperature from 20°C to as low as 8°C during summer (McQuaid and Branch, 1984; Field and Griffiths, 1991). Although the study site is somewhat sheltered by Table Bay and Robben Island, wave action often results in the deposition of considerable amounts of sand. The rocks consist of Malmesbury Shale, which forms jagged parallel ridges interspersed with stretches of low rock or sand-filled gullies. Much of the low- to mid-shore is covered with mussels, primarily the introduced *Mytilus galloprovincialis* (Lmk), but also *Aulacomya ater* (Molina) and *Choromytilus meridionalis* (Krauss).

Wooley's Pool is situated on the False Bay coastline (34° 12'S 18° 43'E). Mean monthly sea surface temperatures remain within the fairly narrow range 14–19°C (McQuaid and Branch, 1984). The area is partly protected by offshore reefs and rock outcrops close to the shore. The substratum is Table Mountain Sandstone, which forms hard, broad expanses of rock subtidally and large rounded boulders

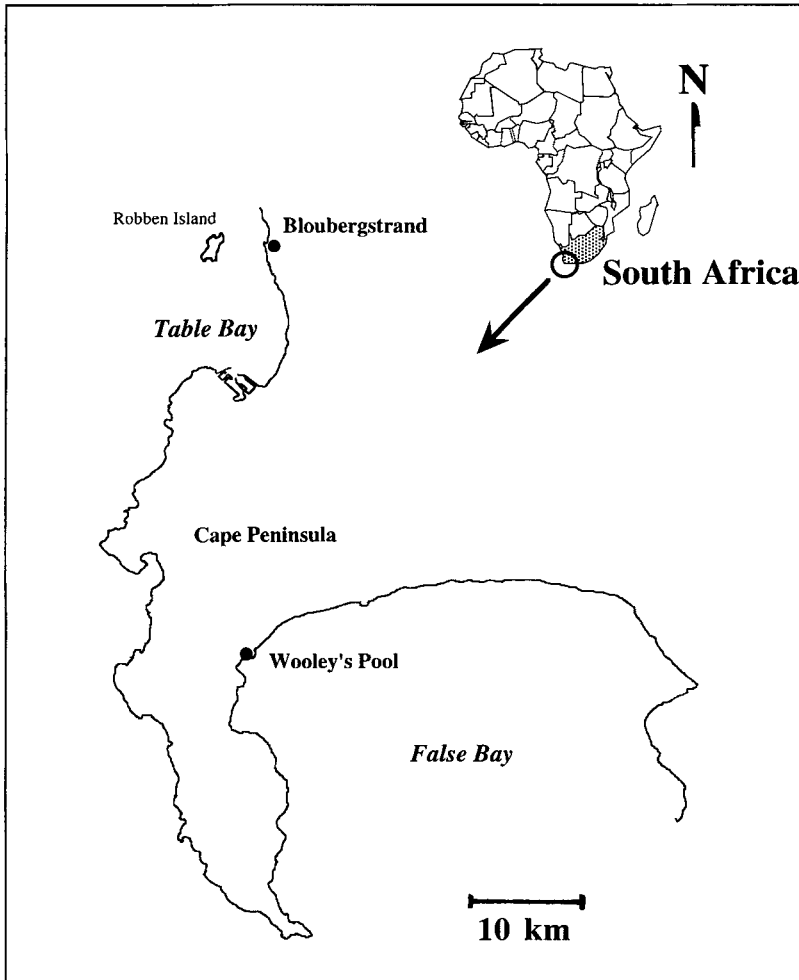


FIG. 1. Map of the south-western Cape showing the study sites.

intertidally. Although present, mussel beds are confined to an offshore rocky outcrop separated from the study site by a water-filled channel.

Population density and distribution

Line transects were used to estimate the abundance and distribution patterns of the various anemone species at each site. Three transects were censused at Wooley's Pool and four at Bloubergstrand. Transects extended from 20 cm below Low Water of Spring Tides (LWS) to an elevation of 2 m above LWS. The length and profile of each transect were recorded and three 0.1 m² quadrats thrown randomly within each 20 cm height stratum. The total number of each species of anemone within the quadrats was recorded. Counts from all transects were pooled for each height at each site. To test the accuracy of the visual counts of anemones, three quadrats were scraped clear at different shore heights at each site, and the anemones within these quadrats sorted, counted and compared with the numbers estimated visually. Anemone abundances are expressed per linear metre of shoreline (m⁻¹), a standard

measure of the abundance of intertidal organisms that takes into account changes in the width of the intertidal zone (Field and Griffiths, 1991).

Composition of the diets

The diets of the anemones at the two sites were investigated by means of gut content analysis, as detailed by Kruger and Griffiths (1996). This provided information on the species of prey most frequently consumed by each anemone and also the mean numbers and mass of prey items found in the coelenteron.

Gut turnover time

To estimate the quantity of natural prey consumed per unit time, it is necessary to determine the turnover times of each of the categories of prey found in the coelenteron. This has been dealt with in a companion paper (Kruger and Griffiths, in press). Gut retention times of the most frequently consumed prey items were assessed by feeding the anemones with each prey type in the laboratory and noting the length of time taken before the food bolus was egested. Anemones used in these experiments were maintained at the mean sea water temperature of the site from which they were collected. These rates were then used to estimate number of turnovers per year and hence annual consumption rates. In these calculations the digestion rate of each prey item was assumed to be constant throughout the year and the prey turnover time within each prey category to be independent of the relative size of prey to anemone.

The total annual consumption of a particular prey item by each anemone species was estimated as: average number of each prey item in coelenteron \times turnovers per year \times anemone abundance (m^{-1}). The overall annual consumption of anemones as a group was then determined by summing the annual consumption estimates of the different species at each site. Numerical results were converted to energy equivalents using the energy values given by Field *et al.* (1980).

Results

The mean width of the intertidal zone at the two sites was similar (Wooley's Pool: $x = 17.9 \pm 3.02$ m, Bloubergstrand: $x = 18.4 \pm 5.40$ m). However, because the slope at Bloubergstrand is more even, and the area more exposed to wave action, the waves swash higher up the shore than at the more sheltered and irregular stepped shore at Wooley's Pool, and hence the biological zones extend further upshore at this site.

The counts of anemones obtained from the cleared quadrats indicated that only approximately 3.8% of individuals were missed in visual counts (table 1) indicating that they provide an acceptable accuracy of anemone densities.

Abundance and distribution

The intertidal distribution and abundance of sea anemones at the two sites are depicted in figure 2. The overall abundance of anemones was 660 per linear metre (m^{-1}) at Wooley's Pool and 901 m^{-1} at Bloubergstrand. At Bloubergstrand the diversity was low, with only *Bunodactis reynaudi* (Milne-Edwards) being present. Seven species were found at Wooley's Pool.

At Wooley's Pool the species can be divided into three groups according to their zonation on the shore. The first group, *Actinia equina* Linn. and *Anthothoe stimpsoni* (Verr.), were absent from the lower shore and are referred to as high-shore species.

Table 1. Visual counts of sea anemones and corresponding quadrat samples cleared at each site.

Site	Anemones counted visually in quadrat (0.1 m ²)	Total anemones in cleared quadrat (0.1 m ²)	Underestimate in visual count (%)
Blouberg	335	355	6
	650	684	5
	132	134	2
Wooley's Pool	24	24	0
	79	80	1
	85	89	5

The second group, consisting of *Anthopleura michaelseni* (Pax), *Bunodosoma capensis* (Less.) and *B. reynaudi*, occupied the widest range in the intertidal zone, but did not extend above 100 cm above LWS. They are identified as mid-shore species. The two *Pseudactinia* species—*P. flagellifera* (Hertw.) and *P. varia* Carlgren—comprised a low-shore group, both of which are common subtidally and in extreme lowshore pools, but absent more than 20 cm above LWS.

The overall abundance of *A. equina* was 60 m⁻¹, with maximum density occurring in shaded crevices 80–100 cm above LWS. This is the only species regularly found out of water at low tide (Branch *et al.* 1994). *A. stimpsoni* had a narrower range than *A. equina*, occurring only in pools in the upper balanoid and *Littorina* zones, 60–120 cm above LWS. It was nonetheless the most abundant species ($x = 466 \text{ m}^{-1}$) at Wooley's Pool, reaching maximal densities of 1450 m⁻². *A. michaelseni*, *B. capensis* and *B. reynaudi* had similar vertical distributions, extending from the shallow subtidal to the upper balanoid zone about 100 cm above LWS. *A. michaelseni* had the lowest overall abundance of the mid-shore species (25 m⁻¹), compared to 35 m⁻¹ for *B. capensis*. *B. reynaudi* was the most abundant mid-shore species (49 m⁻¹) with a maximum density of 147 m⁻² in the lower balanoid zone (20–40 cm above LWS). The two low-shore species had the narrowest intertidal ranges (although they do extend into deeper waters not surveyed in this study) and occurred in the lowest densities. *P. flagellifera* was only found on the subtidal fringe, where it had a density of 10 m⁻². Its overall abundance at Wooley's Pool was 18 m⁻¹. *P. varia* had an overall abundance of only 5 m⁻¹, yet reached a maximum density of 43 m⁻² in the shallow subtidal.

Bunodactis reynaudi was the only species recorded at Bloubergstrand, and had a very different vertical distribution to that recorded at Wooley's Pool, the upper limit of distribution being 200 cm above LWS at Bloubergstrand and only 80 cm above LWS at Wooley's Pool. At Bloubergstrand *B. reynaudi* were abundant across almost the entire shore, but especially from 0–100 cm above LWS, where the average density was 1380 m⁻². This high density is largely attributable to juveniles packed within the mussel beds, where the maximum density was 2310 m⁻². This declined to 37 m⁻² at the upper limit of the mussel beds (140 cm above LWS). In the more exposed upper levels anemones were usually confined to rock pools or crevices.

Diet composition

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, however cluster and ordination analysis distinguished four main feeding groups

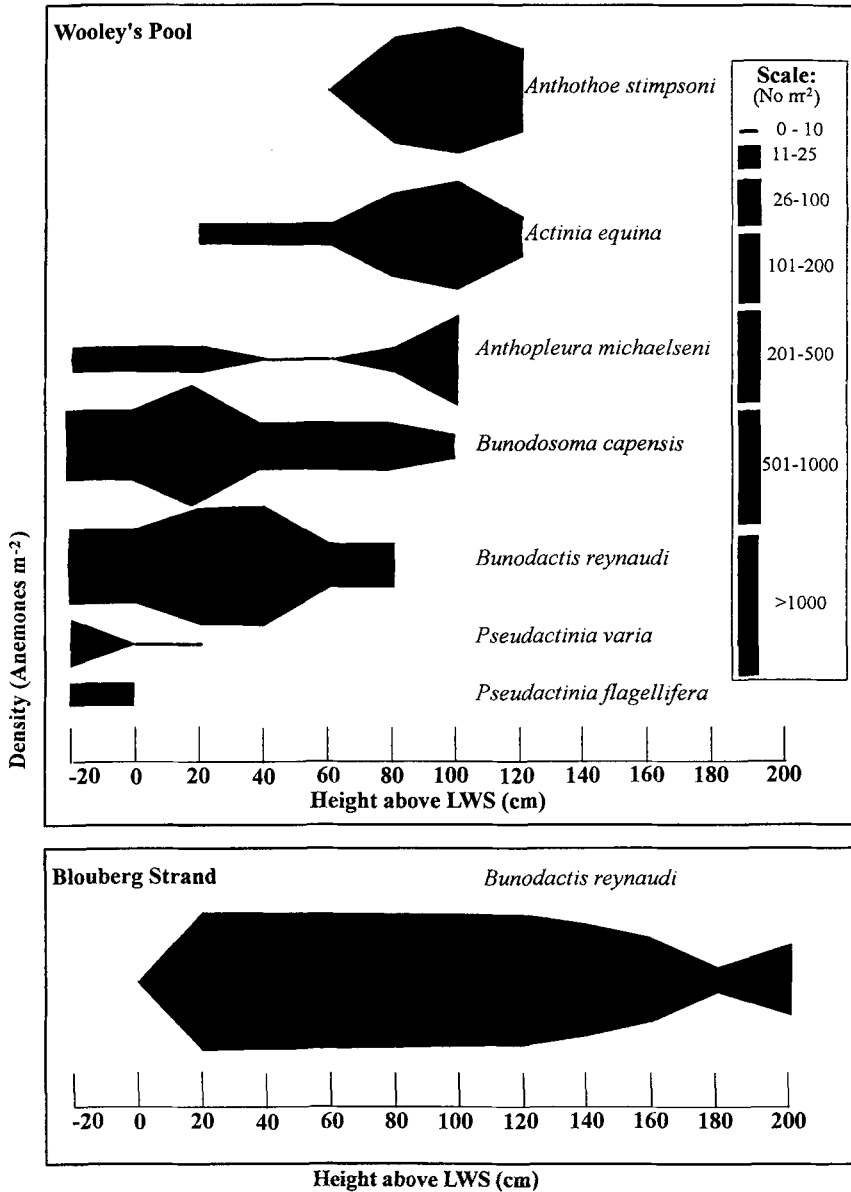


FIG. 2. Vertical zonation and abundance of intertidal sea anemones at the two study sites in the Cape Peninsula.

among anemone assemblages (Kruger and Griffiths, 1996). These were identified as microphagous (*A. stimpsoni*), generalist (*B. capensis* and *A. equina*), macrophagous (*B. reynaudi* from Wooley's Pool, *A. michaelseni*, *P. flagellifera* and *P. varia*) and specialist bivalve-feeder (*B. reynaudi* from Bloubergstrand).

Gut turnover times

A wide variation in both intra- and interspecific prey digestion times was evident (Kruger and Griffiths, in press; table 2). *A. equina* had the fastest throughput times

of the seven species examined. Turnover times for prey consumed by *Bunodactis reynaudi* maintained at 12°C (Bloubergstrand) were consistently longer than those kept at 17°C. The digestibility of the various prey items also determines the time for which they were retained within the coelenteron. Soft-bodied prey were digested fairly rapidly and the rate of deterioration was also faster. Crustaceans were generally digested more rapidly than hard-shelled prey (molluscs and echinoderms), which tended to have the longest gut-turnover times.

Diets and consumption rates of individual species

Parameters used to determine the annual consumption rates of various prey types by the seven species of sea anemones examined are presented in table 2. The consumption patterns of the anemone species at each site are compared individually below:

Actinia equina. Pelecypods were the most abundant item in the diet of this species, followed by isopods and then amphipods. However, because digestion times for isopods were almost double those of amphipods, the annual consumption rate of amphipods (110 per annum) exceeded that of isopods (95 per annum). Bivalves, mostly the tiny *Nucula nucleus* Linn., remained by far the most commonly eaten items (450 per anemone y^{-1}). The relative high abundance of *A. equina* of 60 m^{-1} shoreline resulted in a population consumption of 39 315 items $m^{-1} y^{-1}$, of which 69% were bivalves.

Anthothoe stimpsoni. Isopods were the most abundant component in the diet of *A. stimpsoni*, while gastropods were much less frequent. Turnover times were similar for the two groups and consequently isopods (197 per anemone) emerged as by far the most frequently consumed item, greatly exceeding gastropods (18 per anemone). *A. stimpsoni* was the most abundant anemone at Wooley's Pool (466 m^{-1}) and as a result has the highest population consumption (100 055 prey items $m^{-1} y^{-1}$) isopods accounted for 92% of this.

Anthopleura michaelsoni. Gastropods were the most important group in the coelenteron contents of *A. michaelsoni*, occurring twice as frequently as cirripedes. Pelecypods were relatively scarce. Turnover times were not markedly different, although gastropods were digested slightly faster than cirripedes. Because of this quicker digestion rate, gastropods remained the most abundant item consumed (415 per anemone y^{-1}) forming 64% of the total annual population consumption (10 363 $m^{-1} y^{-1}$), while cirripedes contributed only 28% (4 600 $m^{-1} y^{-1}$). Overall *A. michaelsoni* was the most important consumer of gastropods at Wooley's Pool.

Bunodosoma capensis. Isopods and amphipods were consumed in relatively low quantities and with equal frequency by this species. Turnover times for the two prey items were similar—amphipods being digested in 23 h, and isopods in 27 h. Because of the low frequency of occurrence of prey items in the guts, the estimated annual prey consumed annually is low (62 isopods and 72 amphipods per anemone). The overall population of 35 *B. capensis* m^{-1} thus consumed 2 520 amphipods and 2 155 isopods $m^{-1} y^{-1}$.

Pseudactinia flagellifera. Gastropods were the most abundant prey item in the guts of this species, followed by isopods and then pelecypods. Pelecypods had the longest turnover time and consequently contributed only 14% of the annual population consumption of 5 323 prey items. Gastropods made up nearly half of the dietary items (49% or 2 628 m^{-1}) consumed by the population. Because isopods were digested relatively rapidly (29 h) their proportional contribution to the diet was

Table 2. Consumption rates of seven species of intertidal sea anemone from two sites in the south-western Cape.

Wooley's Pool	Anemone species (No. of guts examined)	Major prey categories	Average prey per anemone	Turnover time (hours) \pm SD	Turnovers y^{-1}	No. consumed per anemone per year	Anemone abundance (m^{-1})	Population consumption ($No. m^{-1} y^{-1}$)	
Wooley's Pool	<i>Actinia equina</i> (N=87)	Isopoda Amphipoda Pelecypoda	0.25 0.15 0.77	23 \pm 0.61 12 \pm 0.58 15 \pm 0.48	381 730 584	95 110 450	60 60 60	5715 6600 27000	
	<i>Anothoe stimpsoni</i> (N=185)	Isopoda Gastropoda	0.63 0.06	28 \pm 0.67 30 \pm 0.91	313 292	197 18	466 466	91891 8164	
	<i>Anthopleura michaelsoni</i> (N=57)	Cirripedia Pelecypoda Gastropoda	0.61 0.18 1.23	29 \pm 1.36 32 \pm 1.23 26 \pm 1.09	302 274 337	184 49 415	25 25 35	4600 1225 10363	
	<i>Bunodosoma capensis</i> (N=72)	Isopoda Amphipoda	0.19 0.19	27 \pm 1.24 23 \pm 0.85	324 381	62 72	35 35	2155 2520	
	<i>Pseudactinia flagellifera</i> (N=59)	Isopoda Pelecypoda Gastropoda	0.36 0.22 0.55	29 \pm 0.66 47 \pm 1.44 33 \pm 0.37	302 186 265	109 41 146	18 18 18	1957 738 2628	
	<i>Pseudactinia varia</i> (N=60)	Isopoda Gastropoda	0.19 0.96	30 \pm 0.63 38 \pm 0.61	292 231	55 222	5 5	275 1110	
	Blouberg	<i>Bunodactis reynaudi</i> (N=90)	Echinoidea	0.15	34 \pm 0.34	258	39	5	195
			Cirripedia	0.94	25 \pm 0.16	350	329	49	16121
			Pelecypoda	0.85	60 \pm 1.51	146	124	49	6076
			Gastropoda	0.44	30 \pm 0.69	292	128	49	6272
Blouberg	<i>Bunodactis reynaudi</i> (N=90)	Polychaeta	0.18	37 \pm 0.93	237	43	901	38437	
		Pelecypoda	1.18	72 \pm 1.11	122	144	901	129744	
		Gastropoda	0.63	43 \pm 1.09	204	129	901	116229	

The average time taken for prey to be digested by the different species was divided into one year to estimate number of turnovers per year (SD is also given). The average number of each prey type per anemone, in a random sample of (N) anemones as derived from Kruger and Griffiths (1996a), is also included. The number of prey eaten per anemone per year is the product of turnovers per year (from Kruger and Griffiths, 1996b) and the average number of prey per anemone. Population consumption was calculated by multiplying the number of prey consumed by a single anemone, by the number of anemones per linear metre of shoreline.

relatively higher (37% or $1957\text{ m}^{-1}\text{ y}^{-1}$) than indicated by their frequency of occurrence in the coelenteron.

Pseudactinia varia. Gastropods were by far the most common items in the guts of this species, occurring more than five times as abundantly as either isopods or echinoderms. Isopods had the fastest turnover time (30 h) and gastropods the slowest (38 h). Despite this slow turnover time, gastropods remained by far the most commonly consumed food item (222 per individual y^{-1}). *P. varia* was the least abundant of the anemones at Wooley's Pool and hence the annual consumption by this population was the lowest of any species at $1\,580\text{ items m}^{-1}\text{ y}^{-1}$, 70% of this comprising gastropods.

Bunodactis reynaudi. Cirripedes were the most frequently encountered prey item in the guts of *B. reynaudi* from Wooley's Pool, followed closely by pelecypods, and then gastropods. However, because pelecypods took twice as long as the other items to be digested, their annual consumption rate (124 per anemone y^{-1}) was considerably less than that of cirripedes (329 per anemone) or even gastropods (128). Total annual population consumption was $28\,469\text{ items m}^{-1}$, of which cirripedes made up 57%, pelecypods 21% and gastropods 22%.

B. reynaudi was the only anemone also found at Bloubergstrand, where pelecypods were the dominant item found in the gut, occurring more than twice as often as gastropods. Polychaetes made up only 10% of items in the coelenteron. Despite the fact that these soft-bodied prey were digested in half the time of the shelled pelecypods, their annual consumption remained low (43 per anemone y^{-1}). Pelecypods remained the most frequently ingested item (144 y^{-1}), while gastropods were consumed at a rate of 129 per annum. Because of the very high abundance of *B. reynaudi* at Bloubergstrand (901 m^{-1}), population consumption was exceedingly high at $28\,4410\text{ prey items m}^{-1}\text{ y}^{-1}$. The diet was dominated by pelecypods and gastropods, both of which were consumed in very large quantities of $129\,744\text{ m}^{-1}\text{ y}^{-1}$ and $116\,229\text{ m}^{-1}\text{ y}^{-1}$ respectively.

Total annual consumption

Total annual consumption rates of each of the major prey groups, summarized by anemone species, are shown in table 3. Only groups that occurred in at least 10% of the gut contents of at least one anemone species are considered. Digestion rates of most prey groups were determined experimentally by Kruger and Griffiths (in press). The turnover times of food items not established experimentally were calculated as follows:

- 1) If the digestion rate had been determined experimentally for other anemone species, the turnover time was taken to be the mean rate obtained from all the anemones tested.
- 2) If the turnover time of a particular prey item had not been determined experimentally for any of the anemone species, then it was assumed to equal the mean digestion rate of prey groups within the same taxonomic phylum consumed by all the anemone species.

While prey from each taxonomic group were eaten by a variety of anemone species, in most cases only one or two anemone species were responsible for most of the mortality of that prey group. For example at Wooley's Pool, the number of isopods eaten by *A. stimpsoni* ($91\,891\text{ m}^{-1}\text{ y}^{-1}$) far exceeded those consumed by other species. This is in part due to the high abundance of *A. stimpsoni* (466 m^{-1})

Table 3. Total annual consumption rates (no. of prey items) of the most abundant prey items consumed by the different sea anemone species at the two study sites. The rates are expressed per linear metre of shoreline. Results given in brackets () were derived using estimated prey turnover times, as described previously.

Anemone species	Isopoda	Amphipoda	Cirripedia	Pelecypoda	Gastropoda	Echinoidea	Polychaeta	Insecta	Brachyura
Woolley's Pool									
<i>Actinia equina</i>	5715	6600	—	27000	(480)	—	(660)	(9060)	—
<i>Anthothoe stimpsoni</i>	91891	(4660)	—	(4194)	8164	—	(16398)	—	—
<i>Anthopleura michaelseni</i>	(1050)	(250)	4600	1225	10363	(375)	(175)	—	—
<i>Bunodosoma capensis</i>	2155	2520	—	(875)	(1085)	(210)	(875)	(630)	—
<i>Pseudactinia flagellifera</i>	1957	(738)	(234)	738	2628	(954)	—	—	—
<i>Pseudactinia varia</i>	275	(205)	(95)	(360)	1110	195	(70)	(70)	(105)
<i>Bunodactis reynaudi</i>	(294)	—	16121	6076	6272	(294)	—	(343)	(1715)
Total	103337	14973	21050	40468	30102	2028	3178	10103	1820
Bloubergstrand									
<i>Bunodactis reynaudi</i>	(14416)	(8109)	—	129744	116229	—	38437	—	(8109)

at this site, although the number of isopods consumed per anemone still surpasses that of the other species (table 2). The important consumers of amphipods were *A. equina* followed by *A. stimpsoni* and *B. capensis*. Only two anemone species were significant consumers of cirripedes, with *B. reynaudi* by far the most important followed by *A. michaelsoni*. The greatest proportion of pelecypods ingested at Wooley's Pool were taken by *A. equina* and the most important consumer of gastropods was *A. michaelsoni*.

Turning to the overall numbers of prey items consumed by the anemone assemblage as a whole isopods emerge as the prey group most heavily exploited by anemones at Wooley's Pool ($103\,337\text{ m}^{-1}\text{ y}^{-1}$), followed by pelecypods, gastropods, cirripedes, amphipods and then insects.

At Bloubergstrand, where *Bunodactis reynaudi* is the only anemone, pelecypods were the most important prey group ($129\,744\text{ m}^{-1}\text{ y}^{-1}$) followed by gastropods ($116\,229\text{ m}^{-1}\text{ y}^{-1}$). These were consumed three times more frequently than polychaetes and eight times more often than isopods, while amphipods and crabs were relatively infrequently eaten.

In terms of anemone nutrition, or of community energetics, it is perhaps more meaningful to examine the contributions of the various prey items in energetic terms (table 4). In terms of the energetic contribution to the requirements of anemones at Wooley's Pool, gastropods were the most important prey group ($17\,230\text{ kJ m}^{-2}\text{ y}^{-1}$ or 56%), followed by Brachyura ($7\,505.5\text{ kJ m}^{-2}\text{ y}^{-1}$ or 24%) and echinoderms ($3\,050.9\text{ kJ m}^{-2}\text{ y}^{-1}$ or 10%). By comparison, the most frequently consumed, but smaller isopods, yielded only $357.2\text{ kJ m}^{-2}\text{ y}^{-1}$.

At Bloubergstrand pelecypods (45%) and gastropods (36%) contributed most to the energetic requirements of anemones ($82\,483\text{ kJ m}^{-2}\text{ y}^{-1}$ and $66\,527\text{ kJ m}^{-2}\text{ y}^{-1}$ respectively). Crabs (Brachyura) were also important (18% or $33\,010\text{ kJ m}^{-2}\text{ y}^{-1}$), whereas polychaetes, which were the third most frequently consumed group, supplied only $196\text{ kJ m}^{-2}\text{ y}^{-1}$ or 0.1% of the overall energy content of the diet.

The total overall ingestion rates of all the major prey items consumed by anemones are estimated as $30\,851\text{ kJ m}^{-2}\text{ y}^{-1}$ and $182\,284\text{ kJ m}^{-2}\text{ y}^{-1}$ for Wooley's Pool and Bloubergstrand respectively.

Discussion

Most feeding studies simply document gut contents and assume these provide a realistic reflection of diet. Examining the remains of prey in the gut may not, however, provide an accurate reflection of diet, since different prey items may exhibit quite different turnover times (Peterson and Bradley, 1978). By incorporating the turnover times of the various prey items, actual diet can be estimated much more accurately (Sullivan and Reeve, 1982).

Our earlier, detailed analysis of the diets of intertidal sea anemones from two sites in the south-western Cape, led to the conclusion that they could be separated into four distinct feeding groups (Kruger and Griffiths, 1996). *Anthothoe stimpsoni* was considered to be a microphagous feeder, *Actinia equina* and *Bunodosoma capensis* were regarded as generalists, *Bunodactis reynaudi* (from Wooley's Pool), *Anthopleura michaelsoni*, *Pseudactinia flagellifera* and *P. varia* were deemed to be macrophagous feeders, and *B. reynaudi* from Bloubergstrand was found to be a specialist bivalve-feeder. When the turnover times of the different prey items (Kruger and Griffiths, in press) are taken into account, however, some of these conclusions need to be modified. *A. stimpsoni* remains essentially microphagous, depending to a large extent

Table 4. Overall annual consumption ($\text{kJ m}^{-2} \text{y}^{-1}$) of the most abundant prey groups consumed by anemone assemblages at both study sites. Calculations were made using the conversion figures in Field *et al.* (1980). No data were available for insects and hence they have been excluded from the final consumption estimates.

Site	Isopoda	Amphipoda	Cirripedia	Pelecypoda	Gastropoda	Echinoidea	Polychaeta	Brachyura	Total
Wooley's Pool	357.2	32.8	72.5	2586.2	17 229.8	3050.9	16.2	7505.5	30 851.1
Bloubergstrand	49.8	17.7	—	82 482.6	66 527.3	—	196.4	33 010.1	182 283.9

on isopods. *B. capensis* is still very definitely a generalist, showing no preference towards any particular prey item. The number of pelecypods consumed by the population of *A. equina* was however, found to greatly exceed the quantity of isopods and amphipods taken (table 2), making this species more of a bivalve predator. The pelecypods taken were exclusively the tiny bivalve *Nucula nucleus* (Kruger and Griffiths, 1996). The macrophagous group remained unaltered and generally capture fewer prey than the microphagous or generalist species—presumably because fewer of these larger items need to be consumed to meet the energy requirements of the anemones. Taking turnover time into account suggests that gastropods are a more important component in the diet of *B. reynaudi* from Bloubergstrand than originally proposed. The quantity of mussels consumed by this species annually is exceedingly high ($129\,744\text{ m}^{-1}$), but the shorter turnover time of gastropods also results in a very large consumption estimate of $116\,229\text{ m}^{-1}$.

Although only the one species, *B. reynaudi*, occurred at Bloubergstrand, its density greatly exceeded the combined densities of all the anemones at Wooley's Pool (table 2). This enormous abundance may be attributed to a greater availability of food at this site. Pelecypods (mainly the fast growing invasive alien mussel *Mytilus galloprovincialis*) are extremely abundant in this area (van Erkom Schurink and Griffiths, 1990). The shore at Bloubergstrand is also exposed, a feature which enhances the biomass of filter-feeders (McQuaid and Branch, 1985; Field and Griffiths, 1991; Emanuel *et al.*, 1992). Also, because of the increased wave action at this site, mussels are more likely to be dislodged and tumbled around, making them more available as prey to the anemones (Branch and Griffiths, 1988).

It is of interest to compare the overall consumption rates of sea anemones with those of other predators in the same system. Population consumption rates are available for three of the most important invertebrate predators in the region, the rock lobster *Jasus lalandii* (Milne-Edwards), the starfish *Marthasterias glacialis* (Linn.) and the gastropod *Trochia* (formerly *Nucella*) *cingulata* (Linn.), all of which feed largely on mussels (Penney and Griffiths, 1984; Wickens and Griffiths, 1985). Rates of mussel consumption by these predators and by anemones are compared in table 5. While it is recognized that each predator population has tended to be studied in those areas in which its abundance is maximal, it is evident that anemones emerge as very important consumers of mussels. In particular the dense *B. reynaudi* population at Bloubergstrand is capable of consuming at least five times more mussels than *J. lalandii*, one of the most conspicuous predators of mussels in the south-western

Table 5. Predator density and consumption rates of mussels (*Mytilus galloprovincialis* or *Choromytilus meridionalis*) by anemones and other invertebrate predators at various sites in the south-western Cape. Data for *Jasus lalandii* from Zoutendyk (1988), *Marthasterias glacialis* from Penney and Griffiths (1984) and *Trochia* (= *Nucella*) *cingulata* from Wickens and Griffiths (1985).

Predator	Density per square metre	Number of prey per predator per day	Population consumption ($\text{No m}^{-2} \text{y}^{-1}$)
Anemones (Wooley's Pool)	16.5	0.17	1024
Anemones (Bloubergstrand)	712	0.39	101 353
<i>Jasus lalandii</i>	0.5	107	19 528
<i>Marthasterias glacialis</i>	6	0.84	1840
<i>Trochia cingulata</i>	492	0.08	14 366

Cape (Griffiths and Hockey, 1987). However, because anemones are passive sessile feeders (Sebens, 1982) and the vast majority of the mussels that they capture are loose individuals with virtually no chance of survival (Branch and Griffiths, 1988), they are not likely to have any effect on the structuring of mussel populations.

A similar situation applies to barnacles, which are consumed by *B. reynaudi* and *A. michaelsoni* from Wooley's Pool at rates of 1314 and 368 barnacles $\text{m}^{-2} \text{y}^{-1}$ respectively, twice that taken by the abundant predatory gastropod *Nucella dubia* (Krauss), which consumes 678 barnacles $\text{m}^{-2} \text{y}^{-1}$ (McQuaid, 1985). Again, however, the barnacles accessible to anemones will have been dislodged from the rocks, with little chance of survival, and hence anemone consumption will have no impact on the barnacle population.

The situation concerning motile prey is, however, very different, as these are often ingested alive and healthy, and are thus actually removed from the population. In numerical terms the most abundant such group were the isopods (table 3). By contrast, in energetic terms gastropods were by far the most important of the motile groups of prey (table 4). Insufficient information on the other predators of these groups is available to evaluate the significance of anemones on their populations, relative to other potential consumers.

Total overall consumption of anemones (table 4) at Wooley's Pool ($30851 \text{ kJ m}^{-2} \text{ y}^{-1}$) and Bloubergstrand ($182283 \text{ kJ m}^{-2} \text{ y}^{-1}$) are exceedingly high. When compared with energy budgets estimated for ecosystems in these regions (e.g. Newell *et al.*, 1982; Field and Griffiths, 1991) it would in fact appear that there is insufficient production to supply the amount of food calculated to have been consumed by the anemones. The reason for this is two-fold. Firstly, our study sites were positioned in areas of known high anemone abundance. If anemone abundance was averaged over a longer length of coastline, incorporating both suitable and unsuitable sites, estimated densities and hence consumption rates would be greatly reduced. Secondly, community energy budget studies calculate production figures per m^2 , whereas anemone beds may act as traps for migratory or wave-swept prey items which originate over a far wider area. In the case of mussels in particular, it is known that extensive mussel beds on the west coast of South Africa extend well into the sublittoral zone, sometimes to depths of over 40 m and hundreds of metres seaward of the low water mark (van Erkom Schurink and Griffiths, 1990). These sublittoral beds are likely to provide a major food source for the anemones—not only in the form of the mussels themselves, but also the many invertebrates that live in association with them.

From the above discussion it can be concluded that intertidal anemones in the south-western Cape have the potential to consume very large amounts of prey. Since they are opportunistic feeders and much of their prey is wave-tumbled and hence essentially lost to the parent population anyway, anemones are unlikely to feature in the structuring of sessile prey populations. However, anemone predation may be a major factor in the biology of those motile species which are frequently consumed.

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.

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