

**FEEDING BIOLOGY OF INTERTIDAL SEA ANEMONES
IN THE SOUTH-WESTERN CAPE**

by

Lisa Kruger

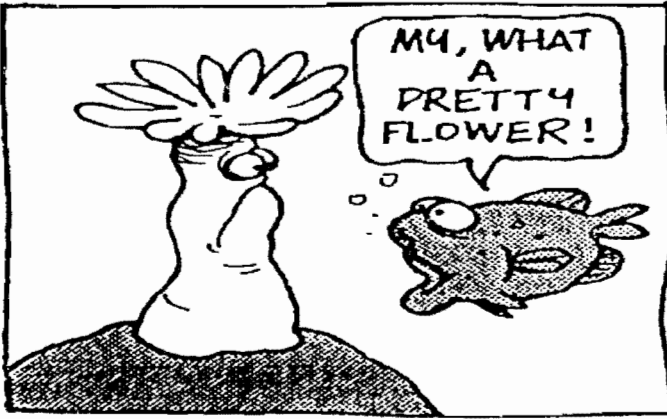
Thesis submitted for the degree of
Master of Science

Zoology Department and Marine Biology Research Institute,
University of Cape Town

May 1995

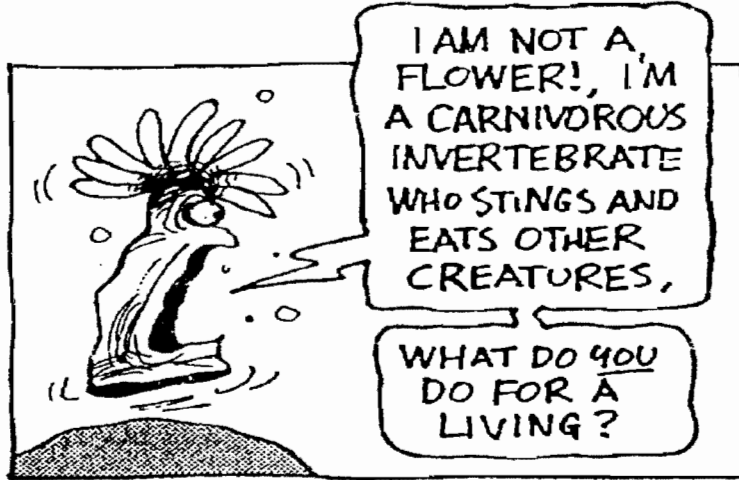
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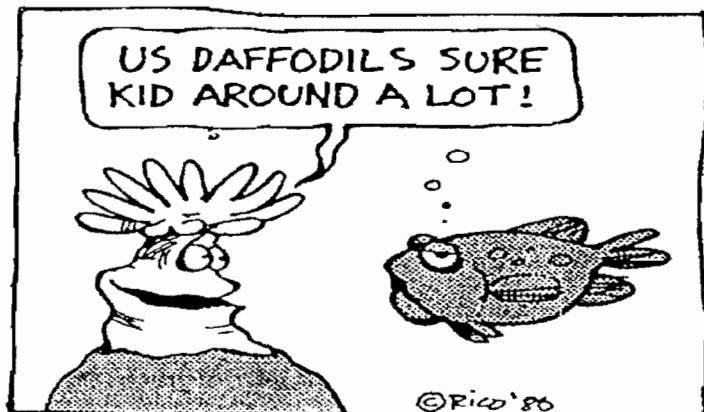


SEA PEOPLE

by Rico



I EAT SEA ANEMONES



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*For my best friends, Des - who helped the most and Dee - whose memory
accompanies me always*

DECLARATION

This thesis reports the results of original research which I have carried out in the Marine Biology Research Institute, University of Cape Town, between 1992 and 1995. Throughout this study I was involved in the gathering, assimilation and interpretation of data, as well as the writing up of the project. This work has not been submitted for a degree at any other university and any assistance I received is fully acknowledged.

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Lisa Kruger

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Date

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ABSTRACT. Kruger, L.M. 1995. *Feeding biology of intertidal sea anemones in the south-western Cape*. M.Sc thesis, University of Cape Town

The species composition, abundance and distribution of intertidal sea anemone assemblages were investigated by means of line-transects at two sites on the Cape Peninsula - Wooley's Pool in False Bay and Blouberg in Table Bay. A single species, *Bunodactis reynaudi* dominated at Blouberg (average density 901 running m^{-1}). Juveniles (<35mm basal diameter) were particularly abundant in mussel beds. Seven species exhibiting clear vertical zonation were found at Wooley's Pool (average density 658 m^{-1}). High-shore species were *Actinia equina* and *Anthothoe simpsoni*. *A. simpsoni* was the smallest (9.1mm mean basal diameter) and most abundant (maximum density = 1450. m^{-2}) anemone at Wooley's Pool. Three species were found at mid-shore: of these *Anthopleura michaelseni* and *Bunodosoma capensis* had the same vertical distribution and extended to higher tidal levels than *Bunodactis reynaudi*. Two species of *Pseudactinia* favoured the sheltered low-shore. *P. flagellifera* was confined to the subtidal zone and was the largest (60.2mm mean basal diameter) and least abundant of all the species (10. m^{-2}), while *P. varia* extended into the low intertidal. Although different anemone species exhibit distinct zonation on the shore, they show considerable overlap. Different morphological and behavioural characteristics facilitating this zonation are discussed.

Respiration rates of the seven species of intertidal sea anemones were measured with and without illumination to determine whether zooxanthellae contribute to their nutritional needs. Light had no significant effect on the oxygen consumption in any of the species, suggesting that they are all azooxanthellate. Gut content analysis showed that at Wooley's Pool 39.4% of anemones contained food while only 7.4% of those at Blouberg did so. A wide spectrum of prey types were consumed by the different species, although considerable dietary overlap occurred. All seven species ingested pelecypods, gastropods and isopods. Pelecypods dominated the diet of *Bunodactis reynaudi* at Blouberg (91%), but were recorded in only 42% of the same species at Wooley's Pool. Numerically gastropods were the main prey items eaten by *Anthopleura michaelseni* (67%), while isopods were the main constituent in the diet of *A. simpsoni* (62%) and *Bunodosoma capensis* (16%). *A. equina* was the only species where insects formed a large part of the diet (26%). Large quantities of algal material and indigestible debris were also ingested, indicating that sea anemones are unselective feeders. Cluster analysis and multi-dimensional scaling techniques revealed four distinct feeding groups among anemone assemblages viz., microphagous (*A. simpsoni*), 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).

Digestion rates of natural prey items eaten by the sea anemones were determined experimentally. Fresh prey fed to the anemones were removed from the coelenteron and examined at regular intervals post-feeding, to assess the degree of digestion as given on a predetermined scale. A weighted running mean was used to determine the course of digestion and average digestion time for various prey consumed. *Actinia equina* showed the fastest digestion times of all the anemone species (12 hours for amphipods, 15 hours for pelecypods and 23 hours for isopods). There was considerable variation in the time taken by different anemone species to digest the same prey types. This difference was significant for isopods and pelecypods. Amphipods were digested in the shortest time (12 hours), while

pelecypods remained in the coelenteron the longest (72 hours). Mean digestion times in *B. reynaudi*, the only species found at both sites were strongly temperature dependent. Digestion rates decreased from 72 to 60 hours for pelecypods and 43 to 30 hours for gastropods at 12°C and 17°C respectively.

Field surveys, stomach content analyses and digestion rate experiments were combined to estimate total annual consumption by natural populations of anemones. It was calculated that the anemones occupying one running metre of shore at Wooley's Pool consumed: 101 993 isopods, 9 120 amphipods, 20 721 cirripedes, 35 039 pelecypods and 28 537 gastropods per year. At Blouberg *B. reynaudi* consumed 38 437 polychaetes m⁻¹, 129 744 pelecypods m⁻¹ and 116 229 gastropods m⁻¹ annually. Comparisons with other major invertebrate predators revealed that *B. reynaudi* at Blouberg is capable of consuming five times as many mussels as the rock lobster *Jasus lalandii*. *B. reynaudi* at Wooley's Pool consumed twice the number of barnacles as the whelk *Nucella dubia*. However, most of the bivalve prey taken by anemones are dislodged individuals, hence the anemones are not likely to play a significant role in the structuring of their prey populations. By contrast, the consumption of motile prey, such as the isopod *Cirolana imposita*, may impact significantly on the prey population. Overall annual consumption by naturally occurring anemone assemblages at Blouberg were calculated to be 182 283 kJ m⁻² y⁻¹ which is six times higher than that at Wooley's Pool (30 851.1 kJ m⁻² y⁻¹). These very high rates suggest that anemones are highly significant secondary consumers in rocky shore intertidal communities in the south-western Cape.

ACKNOWLEDGMENTS

No endeavour is ever achieved alone and this one was no exception.

I gratefully acknowledge the financial support for this project from the Foundation For Research Development (FRD) and the Marine Biology Research Institute (MBRI), University of Cape Town.

My heartfelt appreciation goes to my supervisor Prof. Charles Griffiths who nurtured both this project and me throughout its course. Many thanks, Charlie for all your insight, immense patience and guidance en route and in particular for the many late nights and weekends spent reviewing various drafts.

Sincere thanks to Éva Plagányi for going beyond the bounds of friendship and providing me with continuous encouragement, advice (whether asked for or not) and unfailing support in this task and life in general.

David Glassom's sometimes cynical views of life and science have sustained me through out this time. For all your help and input Dave, thanks a million.

To Bruce Emanuel for all the numerous middle of the night anemone feeding sessions, thank you. Without your help I would have had far less sleep.

Numerous other people assisted me in many ways. Thanks to all those who braved the shores with me, in particular Peppi Gleesen and Tracey Phillips, who also gave willingly of her comments on earlier drafts.

Thanks to Jan Korrûbel for all the computer and printing help. You deserve a medal for putting up with me.

Jay Walmsley gave a whole new meaning to assistance from afar. For all your invaluable halva-induced help Jay, I thank you.

Muchas gracias to two very special friends, Sol Rojas-Lizana and Rodrigo Bustamante, who helped me in so many ways in the early stages before they left for "oceans bluer".

I would like to extend special thanks to Carlos Villacastin who was always there to help me (even when he was in Italy!!) with my numerous computer "hassles".

To my parents and sister, Clare, for continuing to believe in me and giving me continuous moral support, I thank you.

And finally, to my husband, Des. What can I say? - you are the best and make everything worthwhile.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Sea anemones have a ubiquitous global distribution, occurring from the high intertidal to depths of over 5 000m. They exhibit a wide range of different morphologies and vary in size from only a few millimeters to well over one metre in diameter. They are found in a variety of different locations and microhabitats, which may profoundly effect the food available to them, and consequently, because they are organisms with indeterminate growth, will determine their individual size and abundance. Sea anemones are long-lived and some species have been known to have a longevity of well over 50 years (Ottaway, 1980; Sebens, 1983), often surviving very extreme conditions. In temperate regions, they are often dominant members of intertidal and shallow subtidal ecosystems (Harris, 1991), where they sometimes form an integral part of complex food webs (Ayre, 1984). Observations at various sites around the coast of South Africa suggest that here too, sea anemones may be important members of these systems. In the south-western Cape the species composition and abundance of anemone assemblages varies enormously with the environmental conditions of the region.

Sea anemones have been a subject of research around the world for many years. Although they have attracted attention in European literature since at least the middle of the 18th century, the first reference to South African sea anemones was one by Lesson in 1830 (In Carlgren, 1938) who described *Actinia equina* and *Bunodosoma capensis*. The following species were added to the fauna list during the remainder of the 1800's and early 1900's (Carlgren, 1938): *Bunodactis reynaudi* - Milne-Edwards 1857, *Anthothoe stimpsoni* - Verrill 1868, *Pseudactinia flagellifera* - Hertwig 1882, *Anthopleura michaelseni* - Pax 1920 and *Pseudactinia varia* - Carlgren 1928. The most extensive investigation into South African Actiniaria this century was that by Carlgren (1938). Since then, remarkably little work has been done on South African sea anemones. Krijgsman and Talbot (1953) did experiments on the digestion of *Pseudactinia flagellifera*, Griffiths (1977a, b) looked at the ability of *Actinia equina* to tolerate the widely varying climatic conditions that it encounters in the intertidal, Bernheimer *et al* (1984) examined the hemolytic potency of five South African species and Ayre (1984) examined the gut contents of a very small sample of *A. equina* from the Cape Peninsula. All in all therefore, very little is known about the biology of South African sea anemones which remain one of the least studied major invertebrate groups in this region (Branch and Griffiths, 1988; Griffiths and Branch, 1991), despite the fact that they often dominate certain zones of shore (McQuaid and Branch, 1984; Field and

Griffiths, 1991). No quantitative data exists on the relative abundance, habitat preferences or feeding biology of anemones in South Africa. The ecological role of anemones in rocky shore communities where they are relatively abundant has also not been addressed. This thesis thus aims to examine these issues by focusing on two major objectives:

1. To examine the species composition, abundance and distribution patterns of sea anemone assemblages of rocky shores at two sites on the Cape Peninsula.
2. To investigate aspects of the feeding biology of these anemones.

To achieve these objectives key questions were formulated as follows:

1. What is the species composition of intertidal sea anemone assemblages at the two chosen study sites?
2. What is the abundance and size structure of the different species and how are they distributed on the shore in terms of tidal level and specific habitat preferences?
3. Do any of the anemone species harbour endosymbiotic zooxanthellae and if so, what is the contribution of the zooxanthellae to the metabolism of these species?
4. What are the diets of the different sea anemone species?
5. What is the effect of wave action on diet composition and feeding success and how can this be related to the habitat that each species occupies?
6. What are the digestion rates of the different species?
7. To what extent are the different species significant consumers of prey species in the habitats in which they occur and what implications does this have for other intertidal organisms?

OVERVIEW OF THE RESEARCH

The key questions outlined above are addressed in the four following chapters. A brief résumé of these chapters is given below:

1. The nature and distribution of intertidal sea anemone assemblages at two sites in the south-western Cape

The rocky intertidal sea anemone assemblages from the south-western Cape have not been documented previously. This chapter deals with the distribution of sea anemone species and their abundance at different shore heights at sites on the False Bay and Atlantic coasts of the Cape Peninsula (*viz.* Wooley's Pool and Blouberg respectively) in South Africa. A series of wide belt transects were run across the shore at each site. The number of each species and their individual sizes were recorded at different heights on the shore. Seven species of sympatric actiniarian anemones were found at Wooley's Pool. All are members of the family Actiniidae, except for *Anthothoe stimpsoni* which belongs to the family Sagartiidae. Distinct vertical zonation of individual species on the shore was apparent, but considerable overlap occurred. A single species, *Bunodactis reynaudi* dominated the shore at Blouberg, where clear size-partitioning of the shore was exhibited. The habitat preference of each species and morphological and behavioural adaptations that enhance their survival, are discussed.

2. The diets of seven species of sea anemones from the south-western Cape

Sea anemones have been noted previously as conspicuous members of rocky intertidal systems in the south-western Cape. No information exists however, on the energetic basis that supports this high anemone biomass. This chapter thus considers aspects of the feeding biology of intertidal sea anemones from the two study sites in this region and investigates their natural diets. Rates of prey capture were remarkably low and therefore anemone respiration was measured under light and dark conditions, to determine if the nutritional contribution from endosymbiotic algae was utilized by the anemones as an additional food source. Prey species that were consumed were quantified from gut content analyses from anemones in the field. A wide spectrum of prey types were consumed, but considerable overlap in the diets of the different species exists. This chapter examines how the different species partition the available food resources and the degree of similarity between the diets. Four distinct feeding groups were apparent among the anemone species, suggesting that while they are

opportunistic consumers, a certain degree of resource partitioning does occur, probably by virtue of morphological and behavioural differences and habitat preferences. Blouberg, an exposed site, is subject to greater wave action than the more sheltered Wooley's Pool. Sessile prey, particularly bivalves formed a much larger proportion of the diet of anemones at Blouberg. Prey capture was however less frequent, and was often limited to those anemones that occupied crevices or pools in which prey became stranded.

3. Consumption rates of intertidal sea anemones from the south-western Cape

Pseudactinia flagellifera is the only anemone examined in this study whose digestive processes have been previously investigated (Krijgsman & Talbot, 1953). In this chapter the digestion rates of natural prey items most frequently consumed by each anemone species were determined experimentally. High shore anemones subjected to longer periods of emersion digested prey more rapidly than those at lower tidal levels. As a group crustaceans were digested more rapidly than hard-shelled prey. Digestion time was controlled by the nature and behaviour of the prey. Amphipods were digested in less time than isopods, which are more heavily "armoured" and often curled up into a ball when ingested, thus making it more difficult for the digestive enzymes to come into contact with the more permeable regions of the chitinous exoskeleton. Turnover times were strongly temperature dependent - *B. reynaudi* at Blouberg on the colder Atlantic coast (12° C), took longer to digest the same prey item than the same species at Wooley's Pool in False Bay (17° C).

4. Sea anemones as secondary consumers on rocky shores in the south-western Cape

Anemones have previously been recorded as conspicuous members of intertidal systems in the south-western Cape (Field & Griffiths, 1991; Griffiths & Branch, 1991), yet no quantitative data regarding their ecological role in these systems exist. In this concluding chapter, the annual consumption of prey items consumed most often by the different anemone species (Chapter 2) was estimated using experimentally recorded digestion times (Chapter 3). These were then extrapolated to a population in the field, using the abundance data from Chapter 1. It was then possible to compare this estimated annual population consumption with the amount of prey known to be available to the anemones, in order to ascertain their importance as consumers in rocky shore systems and hence their impact on prey populations. The nature of the prey determines the effect that anemones will have as consumers. The population structure

of motile groups, where the individuals captured are frequently live and healthy, may be severely effected by anemone consumption. There is, however, no control of sessile prey populations, as these prey are usually wave-tumbled, having been dislodged previously, and would probably be lost to the population anyway.

Anemone consumption rates were compared with those of other intertidal consumers. Anemones, because they do not forage, do not actually compete with predators, such as the rock lobster *Jasus lalandii* and the whelk *Nucella dubia*. They are however capable of consuming more prey than these successful predators. *Bunodactis reynaudi* can ingest five times as many mussels as *J. lalandii* and twice the number of barnacles as *N. dubia*. It is therefore apparent that anemones are important secondary consumers in intertidal rocky shore ecosystems and while they may not necessarily impact on the structuring of all their prey populations, they form a significant pathway for energy flow through the system.

CHAPTER 1

THE NATURE AND DISTRIBUTION OF INTERTIDAL SEA ANEMONE ASSEMBLAGES AT TWO SITES IN THE SOUTHWESTERN CAPE

INTRODUCTION

Sea anemones are ubiquitous on rocky substrata world-wide and being effective space competitors are often dominant benthic organisms intertidally and subtidally (Hunter, 1984; Harris, 1986, 1991; Shick, 1991). Although the population ecology, community relationships and distribution of rocky shore anemones have been widely studied in other parts of the world (Hand, 1955; Sassaman & Mangum, 1970; Dayton, 1971; Ottaway & Thomas, 1971; Francis, 1973, 1979; Sebens, 1976, 1980, 1982a; Sebens & Paine, 1978; Stotz, 1979; Harris, 1986, 1991; Peterson & Black, 1986) information on the biology of sea anemones along the South African coast is scarce. Early research included a brief study on the general ecology of *Actinia equina* and *Pseudactinia flagellifera*, and the genera, *Bunodactis*, *Bunodosoma* and *Anthopleura* (Stephenson, 1935), as well as a listing of identifying characteristics of the common South African intertidal sea anemones (Carlgren, 1938). More recent studies include experiments on the digestion of *P. flagellifera* (Krijgsman & Talbot, 1953), temperature acclimation and thermal stress in *A. equina* (Griffiths, 1977a, b) and toxicity of five species of South African sea anemones (Bernheimer *et al.*, 1984). However, no quantitative information exists on the relative abundance, habitat preferences or population structure of anemones on South African shores.

Numerous physical and biological factors can affect the species composition, population size and structure of anemone assemblages. The physical conditions, in particular water movement and desiccation, are the most important factors influencing species distribution and size (Lewis, 1968; Denny, 1987). Strong currents and high wave action impose shear stresses on intertidal organisms (Denny, 1985; Denny *et al.*, 1985) that may result in their being dislodged (Koehl, 1982). Large, delicate anemones are therefore morphologically unsuited to areas of high wave action. The force of breaking waves may determine the optimal size to which anemones grow (Denny, 1987). Although faster flow may increase food availability, the stress imposed on the anemones may prevent them from retaining captured prey (Shick & Hoffman, 1980). The vertical range of many intertidal organisms is extended in areas exposed to high wave energy, because the height reached by the

waves and spray is increased (Lewis, 1968). Temperature and tidal level determine both stress due to desiccation and the feeding time available (Griffiths, 1977a, b). The distribution of anemones on the shore depends therefore on their morphological, physiological and behavioural adaptations to these stresses (Stotz, 1979). Sessile invertebrates frequently decrease in size with increasing shore height (Griffiths & Hockey, 1987; Griffiths & Branch, 1991; Harris, 1991). Two species of *Anthopleura* seem to follow this trend (Shick, 1991), although high-shore *A. elegantissima* (1.5m above mean low-water) may sometimes be as large as low-shore anemones. Probable explanations include more efficient prey capture and utilization by animals higher on the shore (Sebens, 1983; Zamer, 1986). However, only very small individuals are present at the upper distribution limits (Shick, 1991), where high temperatures and longer periods of emersion effectively preclude the less tolerant larger anemones.

Biological interactions may also have an influence on the distribution and abundance of anemone populations. Preferential predation on small *Metridium senile* by the nudibranch *Aeolidia papillosa* affects the size and spatial structure of the population (Harris, 1986). Intraspecific competition to maintain space between individuals has been demonstrated in the anemone *Haliplanella luciae* (Fukui, 1986), while interspecific competition is known to occur, not only between different anemone species, but also between anemones and other intertidal organisms. *Anthothoe chilensis* prevents *Phymactis clematis* from occupying low shore positions (Stotz, 1979). The shading effects of algae controls the lower distribution limits of the zooxanthellate anemone *Anthopleura elegantissima* (Sebens, 1983).

This study compares the distribution patterns, species composition and relative abundance of the dominant intertidal species of sea anemones found on rocky substrata in the south-western Cape, and relates these to the physical and biological characteristics of the rocky shores. This information is important if one is to accurately assess and interpret intertidal rocky shore community structure and biomass or assess the role of anemones as consumers in rocky shore systems.

METHODS

STUDY SITES

Two study sites with large sea anemone populations were selected on the Cape Peninsula, South Africa (Fig. 1.1). The entire region is subjected to a semi-diurnal

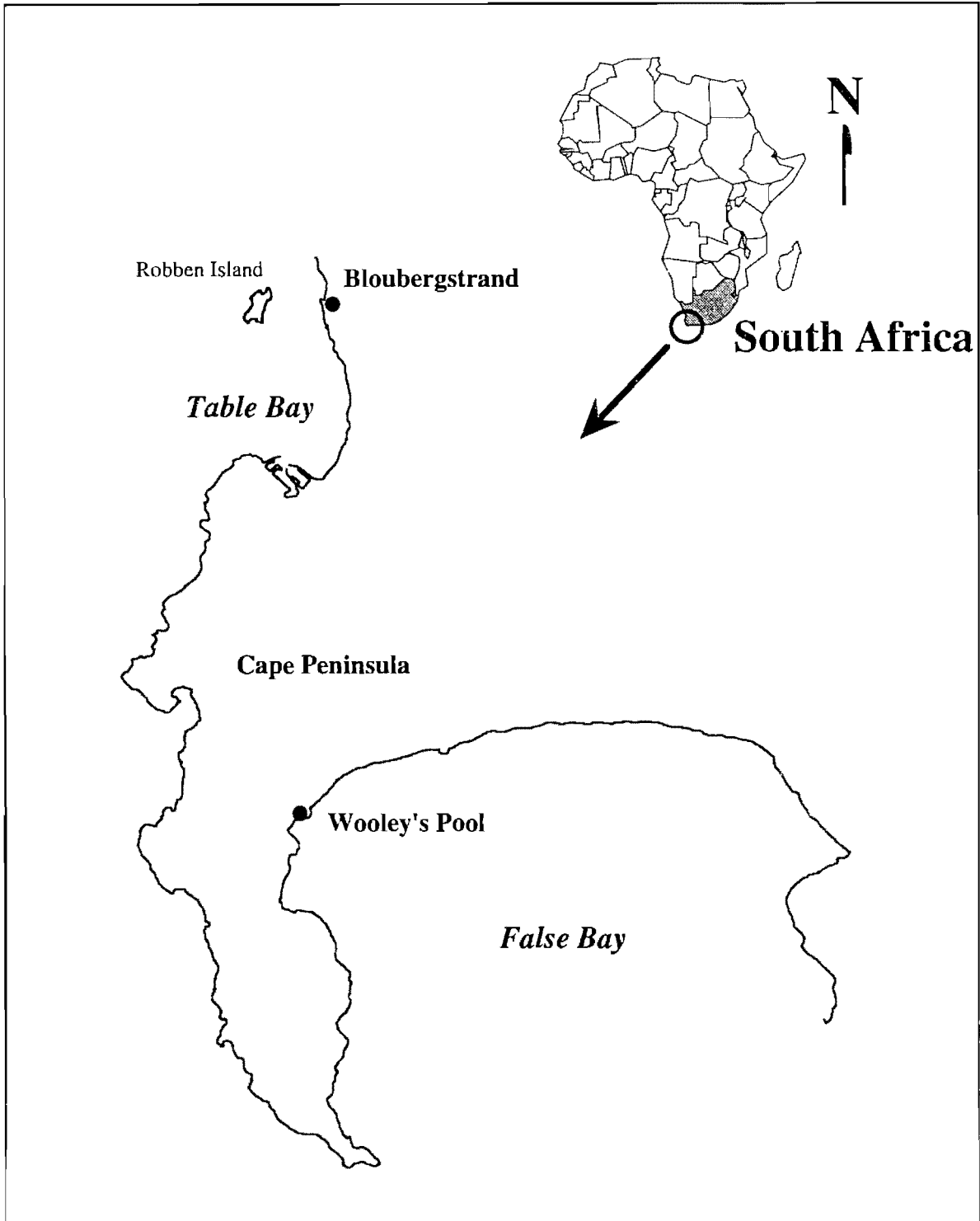


Figure 1.1: Map of the south- western Cape showing the study sites.

tidal régime with a spring-tide amplitude of 2-2.5m and a neap-tidal range of approximately 1m (Field & Griffiths, 1991). The exposed coastline is subjected to strong wave action with waves sometimes exceeding 6m in height, but normally between 1-2m. The Peninsula is a transition zone between the cold-temperate region of the west coast and the warm-temperate south coast (Brown & Jarman, 1978; Griffiths & Branch, 1991). The two study sites chosen included one on the south coast and one on the west coast.

1. Wooley's Pool

This site is situated on the False Bay coastline at 34° 12'S and 18° 43'E (Fig. 1.1). Mean monthly sea surface temperature ranges between 14-19°C (McQuaid & Branch, 1984). The area is partly protected by offshore reefs and rock outcrops close to the shore. The substratum consists of Table Mountain Sandstone, which forms hard, broad expanses of rock subtidally and large rounded boulders intertidally. Although present, mussel beds were confined to an offshore rocky outcrop separated from the site by a water-filled channel, and were not included in the transects.

2. Blouberg

This site is in Table Bay on the Cape west coast at 33° 47'S and 18° 29'E and has a mean monthly sea surface temperature of around 14°C. Winter temperatures are fairly constant (11-13°C), but summer upwelling can cause a short-term reduction in temperature from 18°C to as low as 8°C (McQuaid & Branch, 1984; Field & Griffiths, 1991). The coast in this region is very exposed and almost linear in extent (Field & Griffiths, 1991). Although the study site is somewhat sheltered by Table Bay and Robben Island, wave action is stronger than at Wooley's Pool and 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 was covered with mussels (*Mytilus galloprovincialis*, *Aulacomya alter* and *Choromytilus meridionalis*).

SAMPLING PROCEDURE

Transects were used to estimate the density of the various anemone species at each site and to determine their variation with tidal elevation. Three transects were censused at Wooley's Pool and four at Blouberg, each on a single occasion over the period April to August 1992. Due to variable topography, transects at both sites included surge channels that remained covered by water except at extreme low spring

tides, as well as minor headlands. The latter were far more exposed and consequently wave-beaten. Transects extended from 20 cm below Low Water of Spring Tides (LWS) to an elevation of 2m above LWS. The length and profile of each transect was recorded. Along each transect, three 0.1 m² quadrats were then thrown randomly within each 20cm height level. The anemones in each quadrat were identified according to Carlgren (1938). The total number of each species of anemone was recorded and the maximum basal disc diameter of at least 20 individuals of each species was measured to the nearest 1mm using calipers. If fewer than 20 individuals were present in the quadrats, additional anemones were measured outside the quadrats, if these could be located at the same tidal level. These measurements were always taken at low tide, when all the tentacles were retracted. Counts from all transects were pooled for each height at each site. To test the accuracy of the visual counts of anemones, a quadrat was cleared at three different shore heights at each site, and the anemones within these quadrats sorted and counted. Numbers of collected anemones were compared with the numbers estimated *in situ*. The microhabitats and zones occupied by each species were also noted. Microhabitats were defined as (a) exposed rock, (b) rock pools, (c) rock crevices and (d) mussel beds. The division of the shore into zones followed that of Day (1974) and Field & Griffiths (1991). The population data obtained from the individual quadrats were analysed to determine species assemblages and zonation patterns at the different shore heights at each site. Anemone abundances were expressed per running metre (m⁻¹), a standard measure that takes into account changes in shore profile (Field & Griffiths, 1991).

RESULTS

The mean horizontal distance measured from 20cm below LWS level, 2m vertically up the shore at the two sites was similar (Wooley's Pool: $\bar{x} = 17.9 \pm 3.02\text{m}$, Blouberg: $\bar{x} = 18.4 \pm 5.40\text{m}$). However, because the slope at Blouberg is more even, the waves swash higher up the shore than at the more irregular stepped shore at Wooley's Pool, and hence the biological zones on the shore are much wider at Blouberg. At Wooley's Pool the zones are condensed and the vertical range from the Cochlear to the Littorina zones is reduced, occurring within a 1m height elevation. At Blouberg the same vertical zonation occupies up to 2m height.

The counts of anemones obtained from the cleared quadrats indicated that approximately 3.8% of individuals were missed in visual counts (Table 1.1). Peterson

& Black (1986) considered an underestimate of 2-5% to be an acceptable estimate of counts.

Table 1.1: 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
Wooley's Pool	132	134	2
	24	24	0
	79	80	1
	85	89	5

Abundance and Distribution

The intertidal distribution and abundance of sea anemones at the two sites are depicted in Fig. 1.2. Species distribution and abundance varied considerably between the two sites. The overall abundance of anemones was 660 running metre (m⁻¹) at Wooley's Pool and 901 m⁻¹ at Blouberg. At Blouberg the diversity was low, with only *Bunodactis reynaudi* being present, while seven species were found at Wooley's Pool.

The vertical distribution of *B. reynaudi* was significantly different at the two sites ($\chi^2 = 18.3$, d.f. = 10, $p < 0.05$). At Blouberg samples were not taken subtidally, but *B. reynaudi* was distributed throughout the intertidal zone. The upper limit of distribution was 200cm above LWS at Blouberg and 80cm above LWS at Wooley's Pool. Abundance was consistently high across almost the entire shore at Blouberg, particularly from the Cochlear to the lower Balanoid zones (0-100cm above LWS), where the average density of anemones was 1380 m⁻². The high density of *B. reynaudi* at Blouberg is largely attributable to juveniles packed within the mussel beds, where the maximum density was 2310 m⁻², 60-80 cm above LWS. This declined to 37 m⁻² at the upper limit of the mussel beds (140cm above LWS). The maximum density of *B. reynaudi* on the rocks was 1583 m⁻², at 80-100cm above LWS level, and the minimum was 10 m⁻², 160-180cm above LWS. In the more exposed upper reaches, anemones were usually confined to rock pools or crevices.

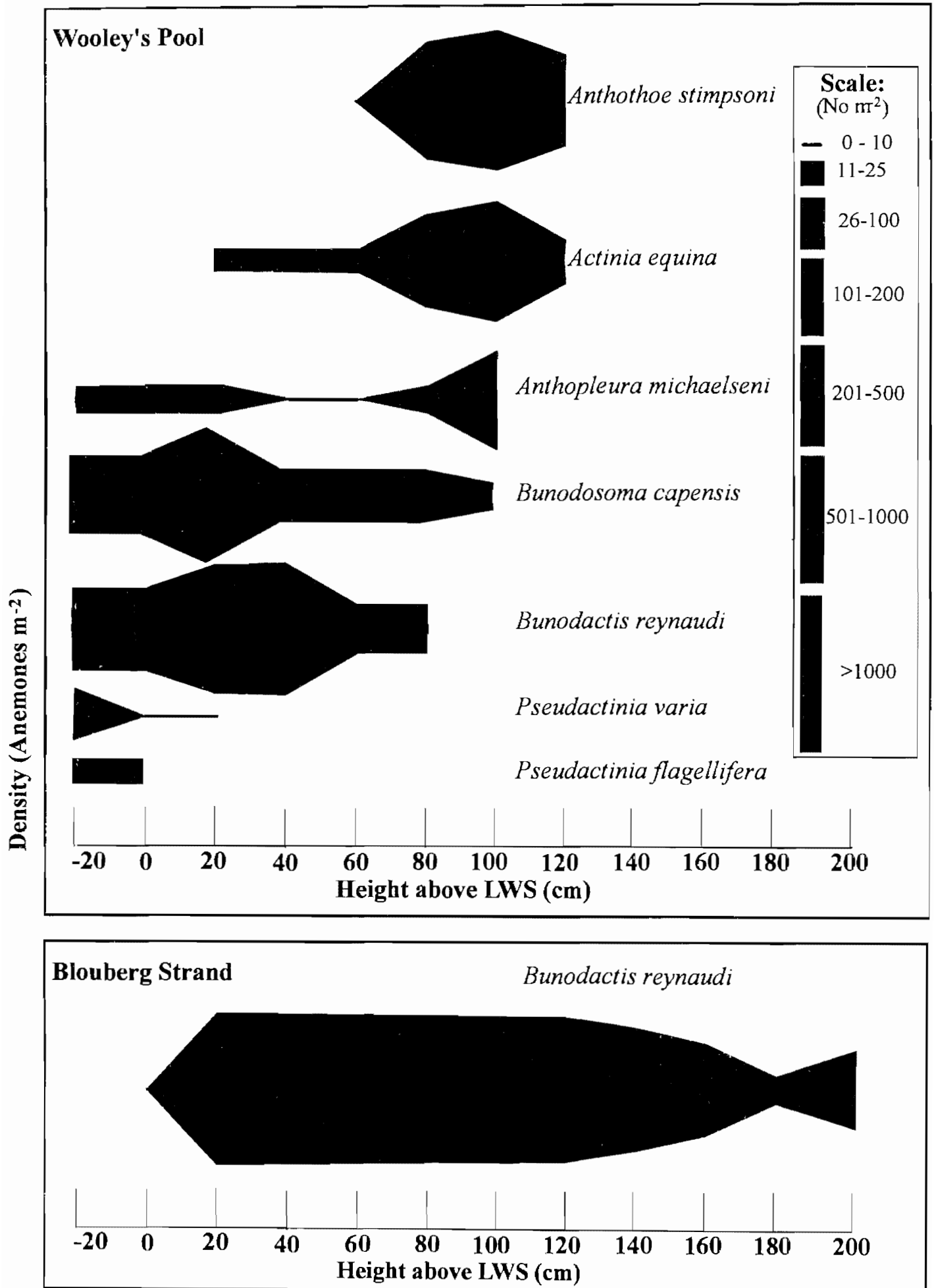


Figure 1.2: Vertical zonation and abundance of intertidal sea anemones at the two study sites in the Cape Peninsula.

At Wooley's Pool the species can be divided into three groups according to their zonation on the shore. The first group, *Actinia equina* and *Anthothoe stimpsoni*, were absent from the lowest levels and occurred from 20cm above LWS up shore and are referred to as high-shore species. The second group, consisting of *Anthopleura michaelseni*, *Bunodosoma capensis* and *B. reynaudi*, occupied the widest range in the intertidal zone, but did not extend above 100cm above LWS and are identified as mid-shore species. The two *Pseudactinia* species comprised a low-shore group. Both were common subtidally and in pools, but *P. varia*'s range also extended to 20cm above LWS.

A. equina extended further down shore than *A. stimpsoni*, into the lower Balanoid zone. Density increased from 7 m⁻² in this zone (20-60cm above LWS) to 243 m⁻², 80-100cm above LWS. The overall abundance of *A. equina* was 60 m⁻¹. *A. stimpsoni* had a narrower range than *A. equina*, occurring only in the upper Balanoid and Littorina zones (60-120cm above LWS). It was nonetheless the most abundant species (\bar{x} = 466 m⁻¹) at Wooley's Pool, reaching maximal densities of 1450 m⁻² in pools at 80-100cm above LWS, and a minimum of 80 m⁻² at its upper limit (120cm above LWS).

A. michaelseni, *B. capensis* and *B. reynaudi* had similar vertical distributions, extending from the shallow subtidal to the upper Balanoid zone (100cm above LWS). *A. michaelseni* had the lowest overall abundance of the mid-shore species (25 m⁻¹) and ranged from 97 m⁻² at the upper limit to 3 m⁻² in the lower Balanoid zone (20-60cm above LWS). There were 35 *B. capensis* m⁻¹ of shore. Densities varied from 150 m⁻² in the Cochlear zone (0-20cm above LWS) to 7 m⁻² in the upper Balanoid zone (80-100cm above LWS). *B. reynaudi* was the most abundant mid-shore species (49 m⁻¹) with a maximum density of 147 m⁻² in the lower Balanoid (20-40cm above LWS), while a minimum of 30 m⁻² occurred at their upper limit (60-80cm above LWS).

The two low-shore species had the narrowest ranges and occurred in the lowest densities. *P. flagellifera* was only found in the shallow subtidal where the density was 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 its densities varied from 43 m⁻² in the shallow subtidal to 3 m⁻² in the Cochlear zone (0-20cm above LWS).

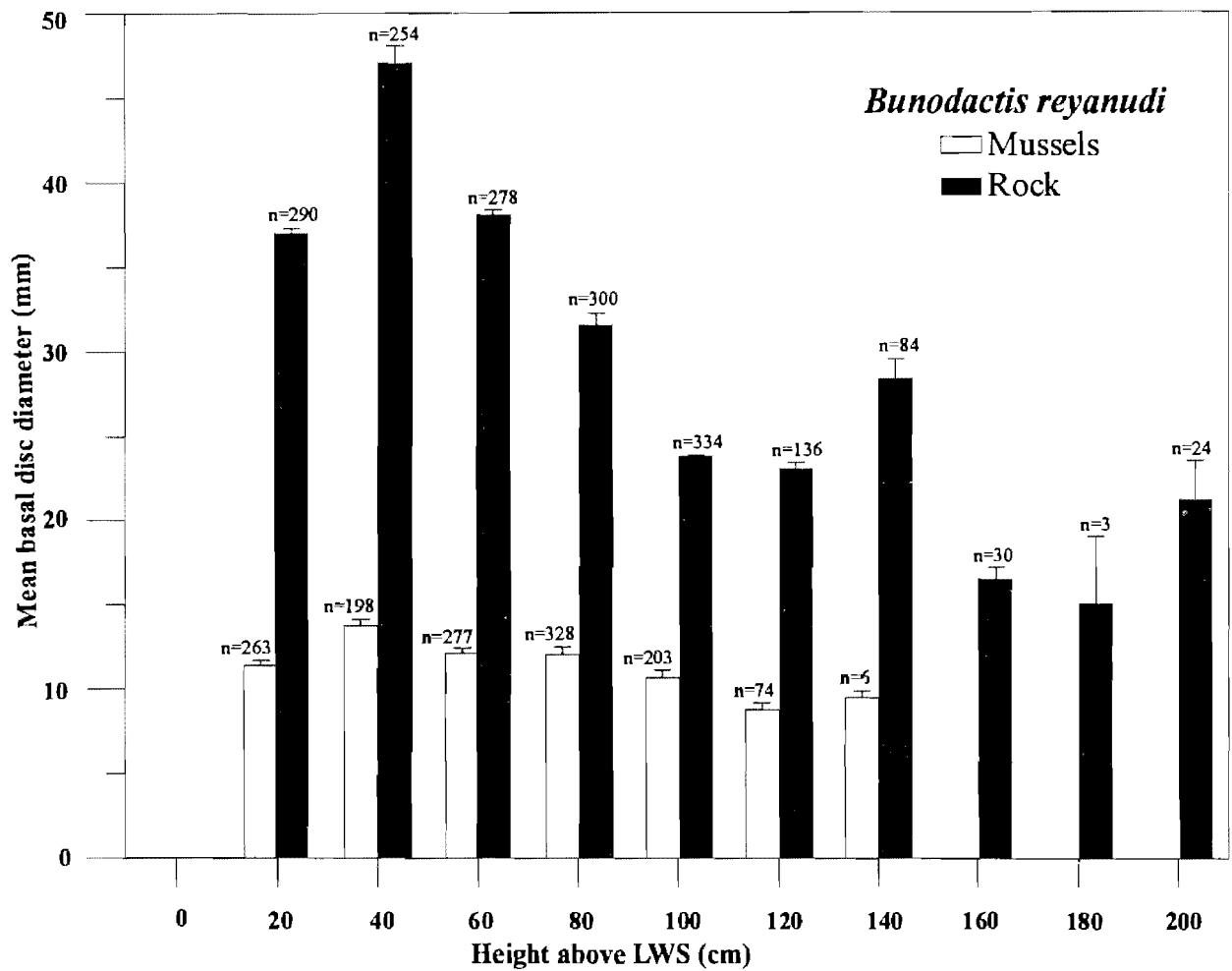


Figure 1.3: Size variations of *Bunodactis reynaudi* (mean diameter \pm standard deviation) inhabiting different habitats at Blouberg, plotted with intertidal height.

Size Distribution

Intraspecific differences in size distribution for the various species were superimposed on the zonation patterns described above. At Blouberg, small *B. reynaudi* (<15mm) were all found on mussels (Fig. 1.3), while the largest individuals (>30mm) all occurred on the rocks at the lower levels on the shore, from 0-80cm above LWS. Those of intermediate size (15-30mm) were found at the highest levels on the shore (from 100-200cm above LWS). The mean size of anemones on both substrata decreased as intertidal height increased. This trend was particularly pronounced for anemones occupying rocks ($r^2 = 0.7543$, $p < 0.01$). A few large individuals on the rocks were found at the highest levels on the shore (200cm above LWS), but these were confined to crevices or high-shore pools. The size gradient of anemones on mussels was less well defined ($r^2 = 0.6263$, $P < 0.05$) with smaller individuals being located higher on the shore.

There was no significant correlation between anemone size and height on the shore for any of the species at Wooley's Pool.

The relationship between size distribution and elevation for the different species at the two sites is presented in Figs 1.4-1.7. Measures of the maximum basal diameter represent the upper limit of each particular size class. The population structure and distribution of *B. reynaudi* in different habitats at Blouberg is given in Fig. 1.4. *B. reynaudi* had the widest size-range of all the species examined. Sizes ranged from 9-125mm on rocks ($\bar{x} = 28.2\text{mm}$) and from 2-63mm on mussels ($\bar{x} = 11.2\text{mm}$). The majority of individuals found on mussels measured less than 35mm. Except for the smallest individuals (<5mm), most size classes were present on the rocks just above the mussel beds. There was a general decrease in numbers with increase in size and very few anemones in the largest size classes (>110mm) were found. On the rocks *B. reynaudi* showed an increase in density up the shore, but density decreased again at the highest levels.

A. equina ($\bar{x} = 18.4\text{mm}$) ranged in size from 3-42mm. Anemones of different sizes were found at most vertical levels, but, large individuals were relatively scarce (Fig. 1.5). Most individuals measured fell in the size range 16-30mm. Density decreased down shore and only small individuals (<30mm) were found at the lowest shore levels. The largest individuals occurred only at the top of the range.

A. stimpsoni was the smallest species ($\bar{x} = 9.1\text{mm}$). It also had the narrowest size range (3-16mm) and occupied a very narrow zone on the shore (Fig. 1.5).

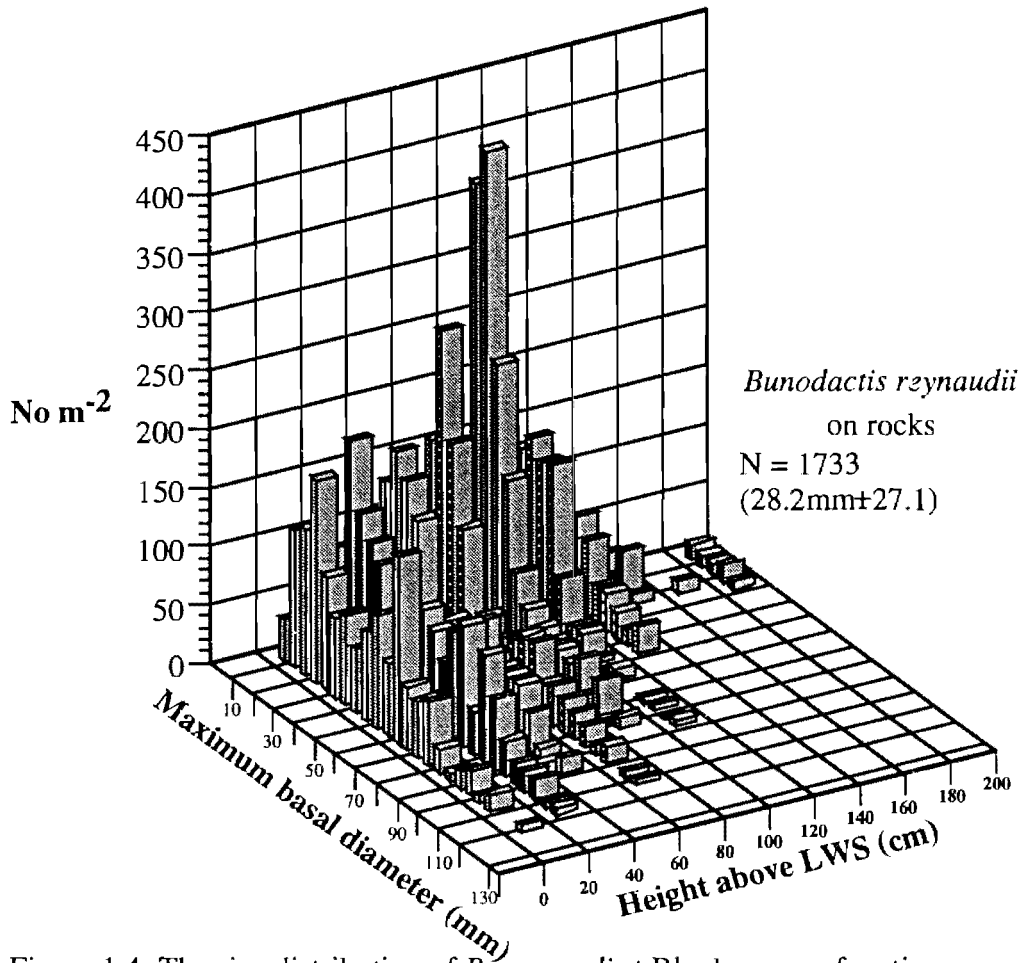
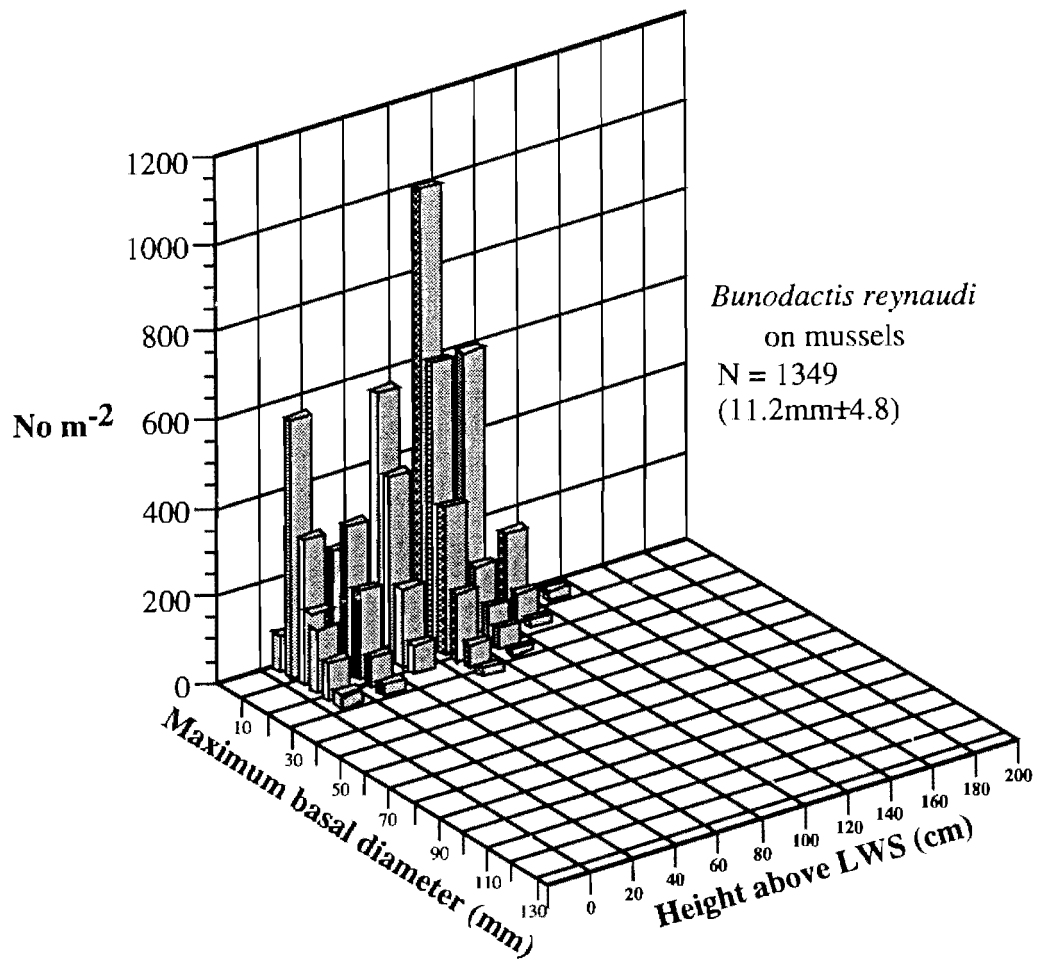


Figure 1.4: The size distribution of *B. reynaudi* at Blouberg as a function of tidal height. The density of each size is given for each level on the shore where it occurs. Samples were pooled for all transects. The maximum basal diameter represents the upper limit for each particular size class. The mean size with sd is given.

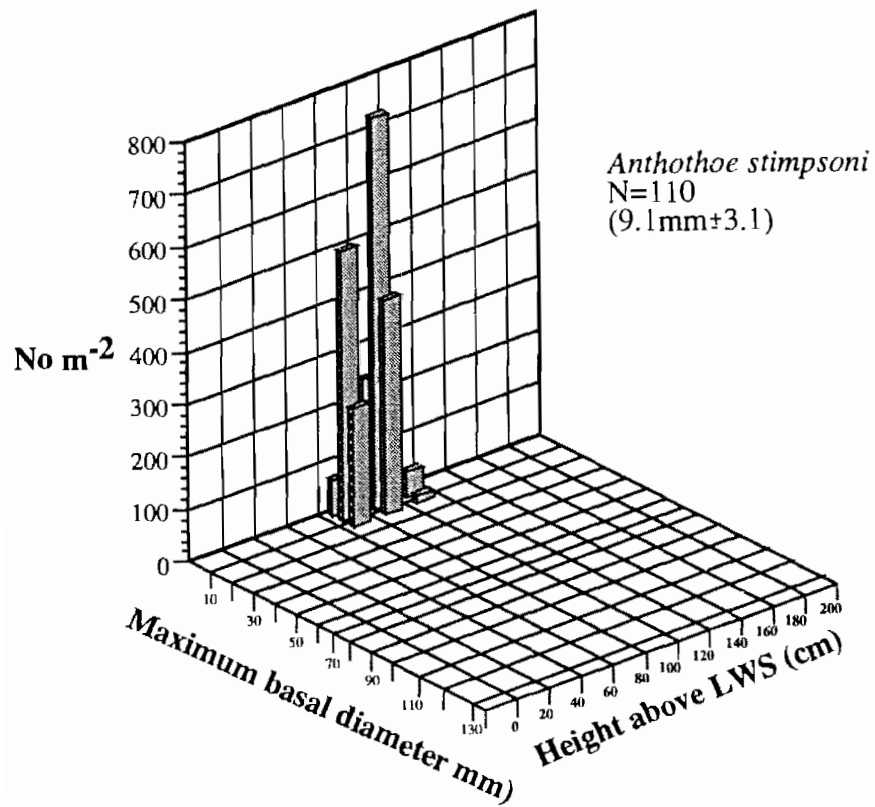
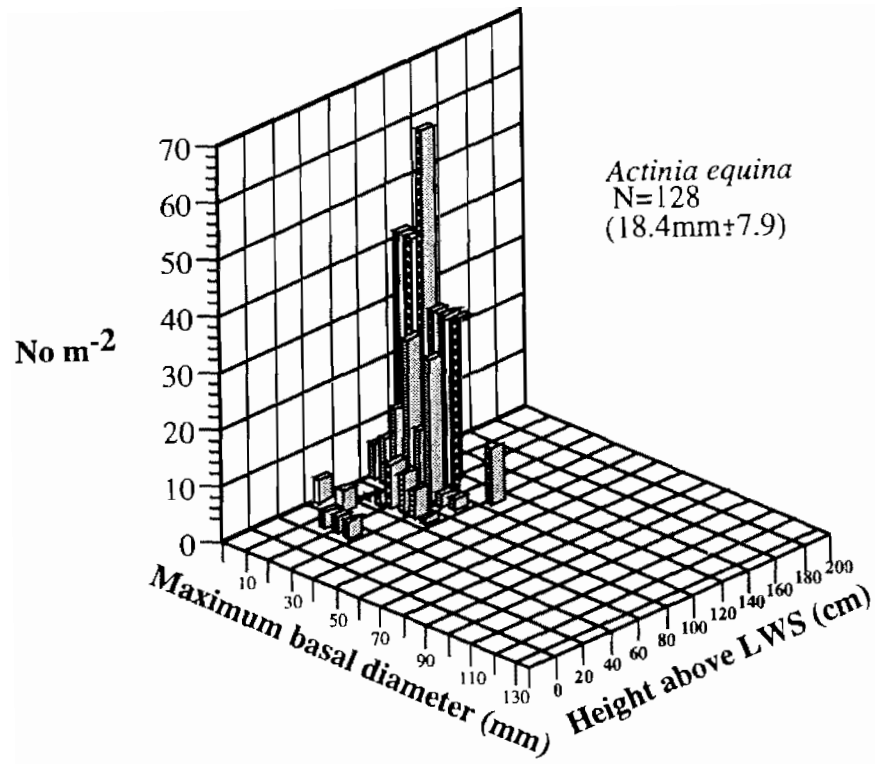
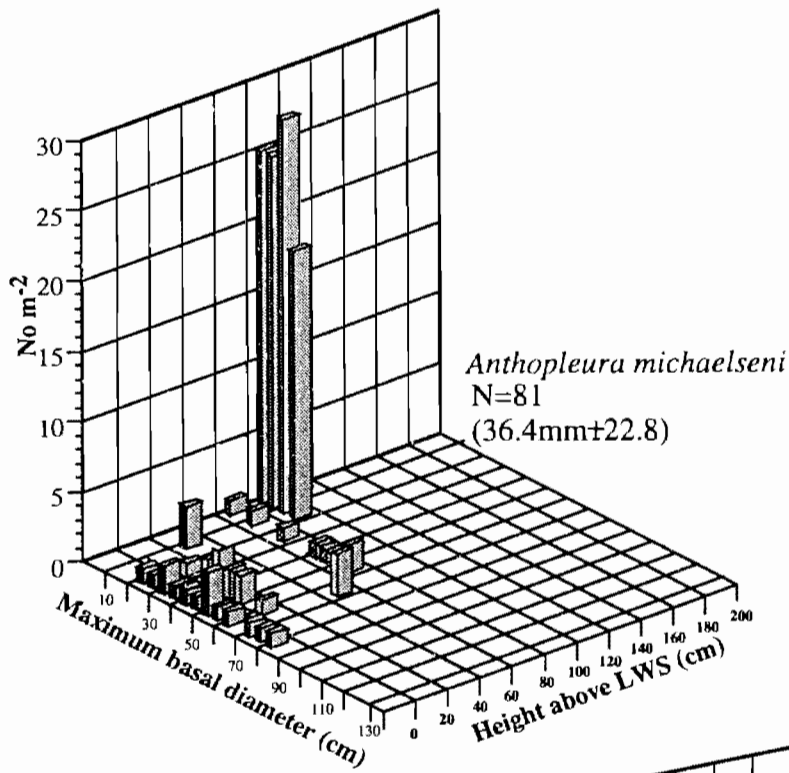


Figure: 1.5: Size distributions of the two high shore species at Wooley's Pool with respect to their position on the shore. The density of each size class is given for each height elevation from the LWS level to 2m above LWS. Sample size, mean size and sd are also shown.



Bunodosoma capensis
 N=270
 (33.2mm±8.3)

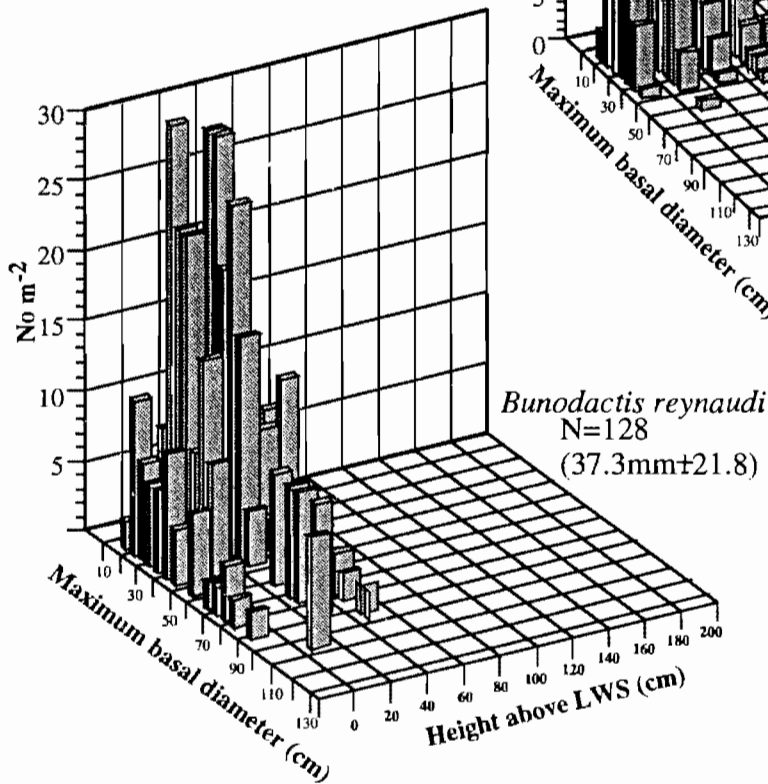
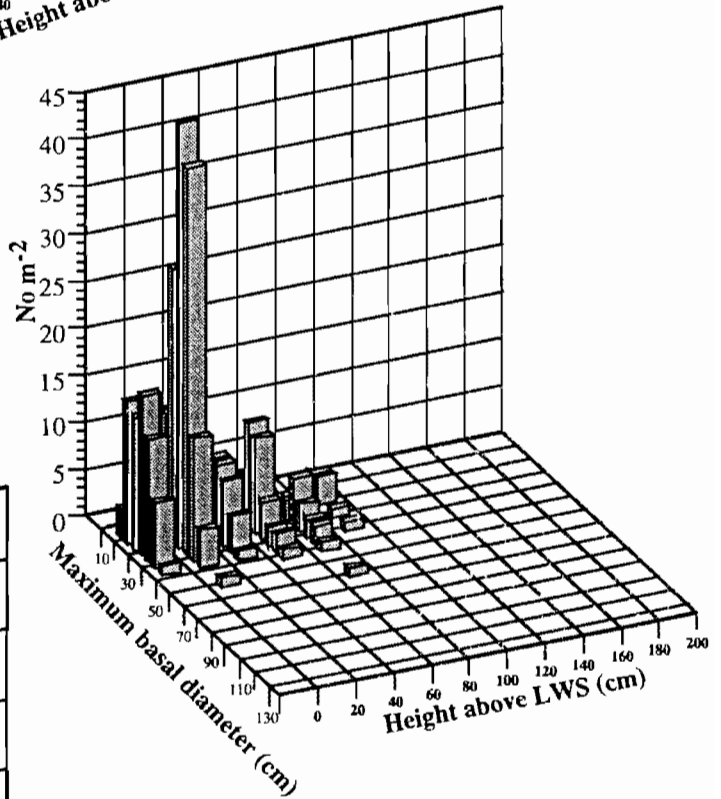


Figure 1.6: Size distributions of the mid shore anemone species at Wooley's Pool are represented as the No m⁻² at each level above the LWS. The mean size and sd are given, as is the sample size (N).

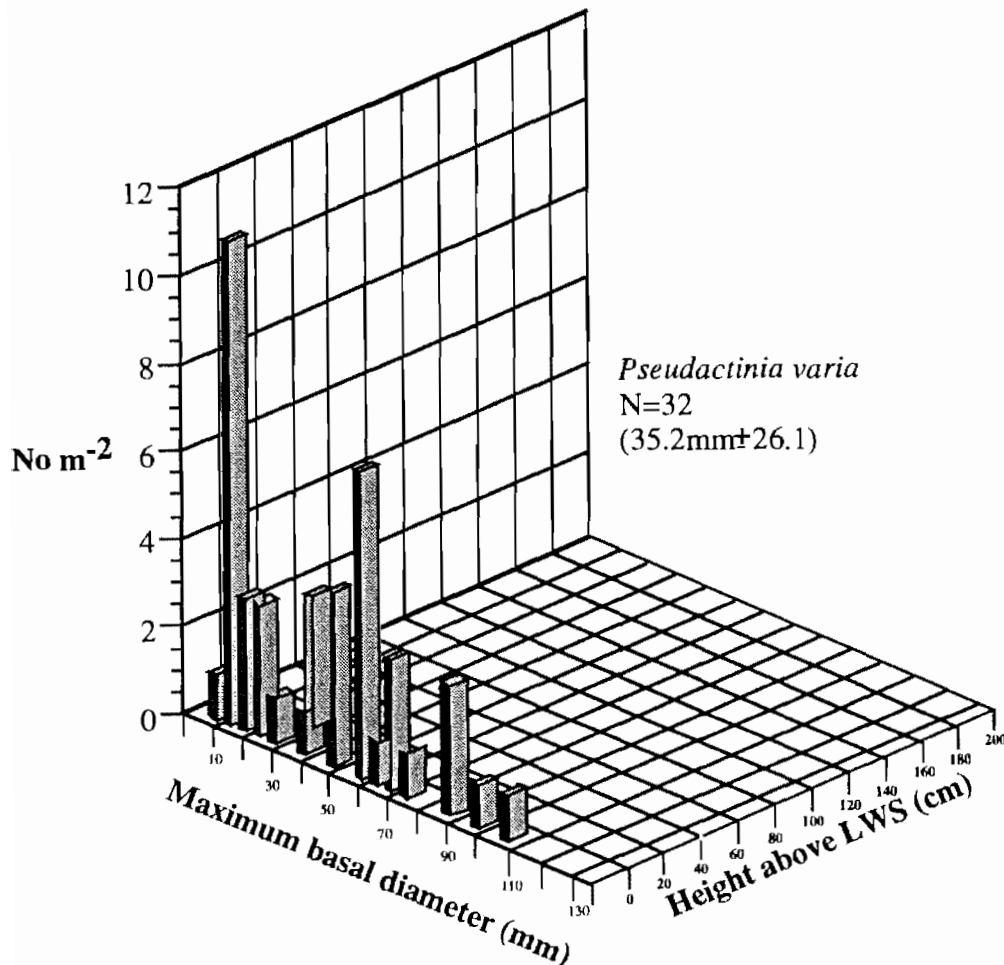
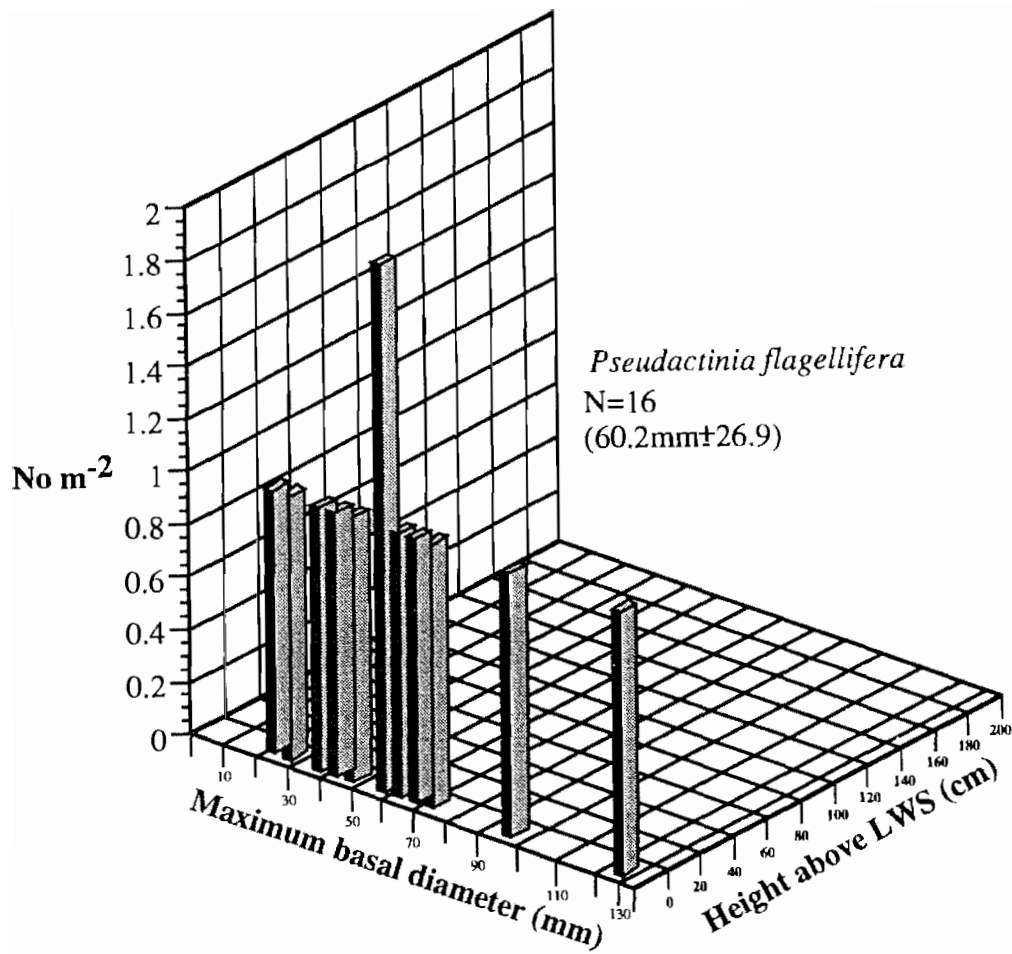


Figure 1.7: Population structure for the two low shore species at Wooley's Pool is shown as the No m⁻² for each height level on the shore. The mean size and sd is shown. Sample size (N) is also given.

Individuals in the smallest size class (1-5mm) were rare. Specimens in the mid-size range were well represented. Most individuals measured 6-10mm.

A. michaelseni ranged in size from 2 - 85mm ($\bar{x} = 36.4\text{mm}$). A degree of bimodality is evident in the size distribution of this species (Fig. 1.6). Small individuals (<20mm) occurred with the highest frequency, followed by anemones in the 50-70mm size class. *A. michaelseni* had a very patchy distribution. Small individuals were only common at the highest levels and were entirely absent from the lowest levels on the shore. The largest individuals were only found subtidally.

B. capensis ($\bar{x} = 33.2\text{mm}$) ranged in size from 15mm to 70mm. (Fig. 1.6). The intermediate sizes (21-40 mm) were the most abundant and numbers of very large *B. capensis* (>60mm) were low. *B. capensis* decreased in density up shore. Most occurred just above the LWS level. Only animals larger than 12mm were found at the highest levels.

The population structure and distribution of *B. reynaudi* at Wooley's Pool and on the rocks at Blouberg were similar. However, the mean size for *B. reynaudi* at Wooley's Pool (37.3mm) was larger than that of individuals found on the rocks at Blouberg (28.2mm), although the range in size of *B. reynaudi* at Wooley's Pool was smaller (15-110mm) compared with 9-125mm at Blouberg. At Wooley's Pool most of the anemones were in the 21-35mm size class, while at Blouberg the majority of individuals on the rocks were between 11mm and 30mm. There was an increase in density up shore at both sites. More small individuals were found on the rocks at Wooley's Pool than at Blouberg, but that may be due to the absence of mussels in the transects at this site. Density decreased with increasing size at both sites (Fig. 1.6).

The two-low-shore species exhibited very low densities (Fig. 1.7). *P. flagellifera* only occurred subtidally where it had a very even size distribution of 1 m⁻² in most size classes. *P. flagellifera* had the largest mean size (60.2mm) of all the species in this study and ranged in size from 22-135mm. No small individuals of less than 20mm were found. Most common sizes were between 50mm and 60mm. Large individuals had a patchy size-distribution. *P. varia* were smaller than *P. flagellifera* with a mean size of 35.2mm and ranging from 9-110mm, and exhibited a decrease in numbers with increased size. Their size frequency distribution was bimodal. Small individuals (11-20mm) occurred with the highest frequency with intermediate classes (45-70mm), contributing to the second peak.

DISCUSSION

The distribution and abundance of a species is determined by a complex interaction of both physical and biological factors encountered in its environment (Stotz, 1979; Ottaway, 1979; Francis, 1988). Factors influencing the distribution of sea anemones on the rocky shore, as with other intertidal invertebrates and algae, include, *inter alia*, exposure to wave action, topography of the shore, the nature of the substratum exposure to air (desiccation) and biological interactions, such as competition and predation (Newell, 1979).

Overall anemone density was highest at Blouberg, while the number of species present was lowest (Fig. 1.2). Seven species of intertidal sea anemones were found at Wooley's Pool and only one at Blouberg. Blouberg falls within the geographical range of all the Wooley's Pool species (South African Museum records; Carlgren, 1938; Day, 1974; Branch *et al.*, 1994), yet *B. reynaudi* was the only species common to both sites. This suggests that some local parameter prevents the other species from occurring here. Results obtained are consistent with Connell's (1978) "Intermediate Disturbance Hypothesis", which predicts that high levels of disturbance result in low species diversity. The presence of mussel beds is indicative of an exposed shore (Field & Griffiths, 1991) and exposure to wave action has been shown to affect the species composition of the community living in a particular area (McQuaid & Branch, 1985). Considerable sand dumping accompanies the wave action at Blouberg. It is possible that the continual disturbance caused by wave action, sand abrasion and deposition excludes all anemone species except *B. reynaudi* from this site. Species such as *A. equina* and *Pseudactinia* sp. are known to avoid sandy areas. On the other hand, Brown *et al.* (1991) noted that *B. reynaudi* appears to prefer positions of mixed rock and sand, protected from very heavy wave action, rather than bare rock. At both sites they were typically found in sandy crevices and cracks or on rocks inundated with sand. While sand inundation may not be unfavourable to all the other species (e.g. *A. michaelsoni*), *B. reynaudi*'s domination of the shore suggests that it gives this species a competitive advantage. The higher number of species in False Bay reflects the general trend in the diversity of intertidal species noted by Stephenson (1939, 1944, 1948) and more recently McQuaid & Branch (1984) and Bustamante (1994) on the two sides of the Cape Peninsula. Temperature differs markedly between the two sites. While this is known to influence species distribution (McQuaid & Branch, 1984), the geographic range of all the other species extends beyond Blouberg, and hence it seems unlikely that it is a determining factor here. McQuaid & Branch (1984) also concluded that the biota of

South Africa was more affected by exposure to wave action than by the temperature regime. The degree of exposure increases the biomass of species in a particular habitat (McQuaid & Branch, 1984; Bustamante, 1994). The higher density at Blouberg may be attributed to the strong wave action that increases the amount of prey available to the anemones.

Definite zonation was exhibited by the different anemone species at Wooley's Pool (Fig. 1.2). Dethier (1980) suggested that the upper limits and possibly geographical boundaries of organisms are determined by physical factors. The length of time for which the anemones are exposed to air appears to be the most important factor controlling the distributions of different species (Dayton, 1971; Sebens, 1983). The longer the period of exposure, the greater the probability of water loss due to evaporation. Anemones living higher up on the shore must therefore be adapted to cope with desiccation. Griffiths (1977a, b) demonstrated that *A. equina* compensates for the increased temperatures and reduced feeding time that it encounters by having a reduced metabolic rate, temperature independence and seasonal fluctuation. All the species whose ranges extended into the high-shore areas exhibited behavioural and morphological characteristics that enabled them to survive there. For example, *A. stimpsoni* was confined to permanent tidepools. The permanent covering of water will prevent dehydration of the anemones during this time. Their decrease in density up shore (Fig. 1.5) coincides with the paucity of suitable pools high on the shore.

Adult *A. equina* are extremely tolerant of desiccation (Griffiths, 1977a) but, juveniles are far more susceptible to dehydration (Ottaway & Thomas, 1971). Individuals of the genus *Actinia* often occupy positions where they are exposed during low tide (Ottaway, 1973) and this was found to be the case for *A. equina* during this study (Fig. 1.2). They were always found in damp, shady habitats and adopted a dome-shape to retain water in the coelenteron during emersion (Griffiths, 1977a). The effect of dehydration on juvenile stages determines the upper limits of distribution of *A. tenebrosa* in Australia and New Zealand (Ottaway & Thomas, 1971). Adults are confined to a zone, determined by their minimum requirement for exposure, but allowing settling juveniles the greatest chance of survival (Ottaway, 1973; Griffiths, 1977b). Viviparity in *A. equina* is advantageous as young are brooded until large enough to survive desiccation (Griffiths, 1977b). Ejected juveniles attach to the first solid substratum they encounter (Ottaway & Thomas, 1971). No information exists to suggest what selective forces may have led to the colonization of these inhospitable zones by either of these high-shore species.

A. michaelsoni and *B. reynaudi*, whose upper limits extended into the physiologically stressful high-shore areas (Fig. 1.2), attached sand and shell debris to their verrucae and were confined to cracks or crevices to reduce desiccation. This choice of habitat and behaviour has been shown by Hart & Crowe (1977) to significantly increase the survival of anemones and presumably enables these two species to survive higher on the shore. *B. reynaudi* was the most common species in the mid-shore. Harsher conditions and fewer suitable habitats up shore may have resulted in the reduction of numbers with tidal elevation (Fig. 1.2). *B. capensis* remained in damp and often shaded areas, hanging flaccidly from rocky overhangs. This quiescence during intertidal exposure not only reduces water loss, but also decreases metabolism (Shick *et al.*, 1988). A similar situation was found by Stotz (1979) in the anemone *Antholoba achates* in southern Chile. *B. capensis* possess columnar vesicles, that may be analogous to verrucae (Shick, 1991), and although somewhat weakly developed, may assist in regulating evaporation (Stotz, 1979). Various physiological adaptations for surviving in the intertidal have been proposed for species of *Bunodosoma* such as *B. cavernata* (Ellington, 1982). This species is able to survive prolonged periods of anoxia, by utilizing various efficient biochemical pathways and reducing energy consuming processes such as muscular activities. There is a paucity of information on *B. capensis* to assist in determining why this species is so successful in this zone. However, the flaccid posture adopted by this species during emersion, suggests that these processes may also be used by this species.

The two *Pseudactinia* species remained low on the shore where aerial exposure is minimised (Fig. 1.2). Their smooth columns, weak sphincter muscles and 'floppy' structure render them incapable of tolerating either desiccation or strong wave action.

Preferential predation on small individuals is known to greatly affect both the size and spatial structure of anemone populations (Harris & Howe, 1979; Harris, 1986). *A. equina* are the preferred prey of several subtidal predators such as sea stars and nudibranchs (e.g. *Aeolidia papillosa* (L)) in certain areas of its distribution (Hall *et al.*, 1984), which may account for their distribution in the often physiologically stressful intertidal areas. Predators are less tolerant to aerial exposure than the anemones. However, in South Africa, *A. equina* has no known predators (Griffiths, 1977b). The Aeolidacean nudibranch, *Aeolidiella indica* frequently feeds upon *A. stimpsoni* (Gosliner & Griffiths, 1981), but it is not known what effect it has on the distribution or structure of the population. Large size and a solitary lifestyle may have arisen either as a result of intraspecific competition, that reduces densities and

consequently increases growth rates and size (Sebens, 1983), or to reduce predation (Harris, 1991). In both *Pseudactinia* species, adults were always solitary, but small individuals were occasionally found in groups. Stotz (1979) suggested that the patchy distribution of intertidal sea anemones may be an indication of interspecific interactions, as they do not occupy all the suitable areas available to them. Because there is no information on the predators of either species, it is not, however, possible to draw conclusions concerning the effect of predation on their distribution. Both these species do, however, behave very aggressively towards conspecifics (Branch & Branch, 1981; Branch *et al.*, 1994). This method of maintaining space between neighbouring individuals is common (Francis, 1988), although these encounters are rarely fatal. (Fukui, 1986). *A. michaelsoni* and *B. reynaudi* occupied very similar habitats, however, *A. michaelsoni* reaches maximum density at the highest levels of their distribution where *B. capensis* is less numerous and *B. reynaudi* absent (Fig. 1.2). This could be a consequence of competitive interaction (Dayton, 1971). Except for this observation, however, no direct evidence for competition between these two species exists.

The large size attained by *Pseudactinia* spp. (Fig. 1.7) could be due to the increased amount of food and longer feeding time subtidally. *P. varia* are generally smaller than *P. flagellifera*, yet occurred in densities an order of magnitude higher (Fig. 1.7). Their success may be attributed to the fact that *P. varia* has the most powerful toxins of all the South African species (Bernheimer *et al.*, 1984). These assist them not only in prey capture, but also in defence against predators. Microhabitat selection may also provide some protection from certain predators (Harris, 1991). Only large specimens of *Pseudactinia* spp. were found on open rock surfaces, while small individuals were found grouped together under rock ledges. Possible explanations for this pattern include: reducing the risk of predation, providing protection from the direct force of the waves or increasing feeding efficiency as suggested by Buss (1981) and Harris (1991).

Population structure varies considerably with habitat (Shick *et al.*, 1979; Anthony & Svane, 1994) and many benthic marine invertebrates have been shown to have a habitat-dependent body size and indeterminate growth, which varies according to the energetic characteristics of a particular habitat (Sebens, 1981b). There was a tendency towards large size in the low intertidal at both sites (Figs 1.4, 1.6 & 1.7). Anemones attain their largest size in areas exposed to strong wave action, where prey are more abundant and they are less exposed to desiccation (Sebens & Paine, 1978). The largest anemones found were *P. flagellifera* at Wooley's Pool (Fig. 1.7)

and *B. reynaudi* at Blouberg (Fig. 1.4). *P. flagellifera* is a subtidal species, thus ensuring longer feeding time compared with the intertidal zone and resulting in increased growth. *P. varia* was the only species that was found both subtidally and intertidally. However, only a single individual was found in the intertidal and thus it is not possible to compare the size variation in these zones. At Blouberg, the largest *B. reynaudi* were found on the low-shore rocks, just above the mussel beds, while those of intermediate size were confined to the less favourable high-shore areas (Fig. 1.4). This increase in size down shore may be due to energetic considerations, as suggested by Sebens (1979), since strong wave action ensured that prey was dislodged and thus made available to *B. reynaudi*. At the other extreme, Zamer (1986) showed that high-shore anemones were undernourished, due to the shorter feeding time, compared with those found lower down on the shore. They did however, have an increased food absorption efficiency and increased prey capture and ingestion rates, and according to Shick *et al.* (1988) were more responsive to prey. Thus, although more prey was caught by low-shore individuals (due to longer immersion), those that live higher up on the shore were more efficient. This decrease in anemone size with increasing shore height has long been recognised. Smaller organisms are less susceptible to the brunt of wave-induced fluid-dynamic forces that are encountered higher on the shore (Denny, 1988). Harris (1991) suggested that large size would benefit anemones competing with other sessile organisms for space, which may account for the large size of *B. reynaudi* close to the mussel beds. Small *B. reynaudi* utilize mussel beds because this microhabitat is unavailable to the larger sized individuals and hence affords them the opportunity of the better feeding conditions in the low-shore. *A. elegantissima* size decreased with increasing temperature (Sebens, 1980), a situation associated with high tidal levels, and the same was true of *A. michaelseni* in this study. At the highest tidal limits of this species, only small individuals were found (Fig. 1.6). The bimodality in the size structure of *A. michaelseni* and *P. varia* (Figs 1.6 & 1.7) shows that the populations are composed mostly of small and medium-sized anemones. This may merely be indicative of juvenile settlement and growth. Alternatively, smaller individuals may be less susceptible to predation, because they are less visible or of low energetic value, as is the case in some limpet populations (Hockey & Branch, 1984). The patchy distribution resulting from intraspecific aggression may explain the low density of larger individuals of these species.

At Blouberg the very smallest individuals were found only low on the shore, in dense concentrations in mussel beds (Fig. 1.4) that act as a physically protected microhabitat and consequently serve as an important refuge and nursery area for

juvenile *B. reynaudi*. The rocks at Blouberg are subjected to inundation by sand, which prevents small anemones from attaching securely to the rocks. The mussels therefore offer a hard, relatively sand-free surface for attachment (Kaplan, 1984), in an area where competition for space is high. This situation is similar to that found by Sebens (1981a) in populations of *Anthopleura xanthogrammica*, which occupies a similar habitat on the west coast of North America. Large quantities of prey are available in the form of juvenile mussels and small invertebrates such as isopods, amphipods and gastropods. Microhabitats such as these are frequently occupied by various anemone species. Day (1974) noted that *B. capensis* is often found among red-bait and although the *Pyura* beds at Wooley's Pool were not included in the transects, they were frequently populated with *B. capensis* (pers. obs.). Fielding *et al.* (1994) also found that Actiniaria were an important component of the intertidal invertebrate community occupying this habitat in Natal.

The largest individuals of *A. equina*, *B. capensis* and *B. reynaudi* at Wooley's Pool were found only at the highest levels of the species distribution (Figs 1.5 & 1.6). Large anemones are able to retain more water than small individuals during exposure, as a result of a lower weight-specific metabolic rate (Johnson & Shick, 1977). However, Francis (1988), maintained that large size may be disadvantageous high on the shore, due to the increased turbulence and greater force of the waves. Anemones living in these areas were unable to stay erect and the tentacular crown was often deformed by these forces, decreasing the prey capture efficiency (Koehl, 1977). Although more prey may be encountered as current speed increases, captured prey may be dislodged before it can be ingested. For this reason the anemones that occurred in these regions, were usually in more sheltered positions (*A. equina*), away from the full force of the waves, or adopted methods such as shortening of the column to reduce the drag (*A. michaelseni*). Ottaway (1980) suggested that the very largest animals may be at a higher risk of detachment, although on stable rocks, the mortality of *Actinia tenebrosa* appears to be independent of size. When removing anemones from the rocks, it was noted that those species living in areas that are subjected to turbulence or wave action e.g. *B. reynaudi* appeared to adhere more strongly to the rocks than those found in calmer areas e.g. *Pseudactinia* spp.

Conclusion

Seven anemone species were recorded from below the LWS level to about 2m above it. The different species exhibited distinct zonation on the shore, although with some degree of overlap. The *Pseudactinia* species occupy mainly the subtidal and lower

intertidal zone. The mid-shore species include *A. michaelsoni*, *B. capensis* and *B. reynaudi*. *Actinia equina* and *A. stimpsoni* can be considered to be high-shore species. Different anemone species that occurred in the same areas, often occupied different microhabitats and displayed different methods of coping with the physiological stresses encountered there. It appeared that desiccation sets the upper limits of distribution. Various authors such as Stotz (1979) and Sebens (1983) have suggested that the lower limits of anemone populations in other parts of the world are controlled by competition and predation, but scant knowledge concerning these subjects with regard to South African species prevents any conclusion from being drawn here. Only the large, toxic *Pseudactinia* species are found exclusively subtidally, where predation is more likely to be a continuous danger. It may therefore be concluded that zonation of anemone species did occur at different levels on the shore, but distribution was patchy and often overlapped.

CHAPTER 2

THE DIETS OF SEVEN SPECIES OF SEA ANEMONES FROM THE SOUTH-WESTERN CAPE

INTRODUCTION

Sea anemones utilize various methods to meet their nutritional requirements. Many harbour endosymbiotic dinoflagellate algae (zooxanthellae) within their tissues (Kellogg & Patton, 1983). The photosynthetic products produced by the zooxanthellae provide an autotrophic input to the anemone's nutrition (Tytler & Spencer Davies, 1984). This autotrophic energy source is relied upon by the anemones because their limited hunting skills are often not sufficient to meet their total energy requirements. In nutrient-poor tropical environments zooxanthellae often supply 100% or more of the host's daily metabolic carbon requirements (CZAR = Contribution of Zooxanthellae to Animal Respiration) (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. Water flow encountered by sea anemones is determined by distance from the shore, depth and orientation to incoming waves. There is a specific relationship between flow speed and the efficiency of prey capture in anthozoans (Sebens & Johnson, 1991). At low flow prey capture is reduced, due to low encounter rates, while at high velocities, the force of the water may bend and deform the tentacles, preventing prey capture. Water flow is reduced in areas densely populated by anemones, and consequently the amount of prey encountered is decreased (Koehl, 1976, 1977). *Metridium senile* reaches a larger maximum size with increased water movements (Sebens, 1981b). However, where flow is very strong *M. senile* are smaller than in areas of lower flow (Shick & Hoffman, 1980). Where flow is very slow, however, animals are smallest, presumably due to decreased prey capture resulting from reduced water movement. Prey capture success is also determined by tentacle shape and size, polyp rigidity and morphology. Three main types of prey are available to sea anemones (Shick, 1991): planktonic prey carried in the water; sessile prey dislodged by foraging intertidal predators or wave action, and mobile prey.

Many sea anemones rely heavily on wave-tumbled prey in their diet (Branch & Griffiths, 1988). Cirripedes are frequently torn loose during high wave energy (Littler *et al.*, 1991) and the foraging behaviour of motile intertidal predators. Predators, such as the rock lobster *Jasus lalandii* or the starfish *Marthasterias glacialis*, wrenching loose a mussel or barnacle for their consumption may dislodge or loosen others. Once loosened, these are tumbled about by wave action and may be washed into surge channels or tide pools that are frequently the favoured habitats of sea anemones. The diet of the sea anemone *Anthopleura xanthogrammica* from the USA exhibited considerable overlap with the diets of the asteroids *Pisaster ochraceus* and *Pycnopodia helianthoides* (Dayton, 1973). Manipulation experiments illustrated that *A. xanthogrammica* derives much of its diet from the foraging behaviour of these asteroids. Since sea anemones are unable to procure sedentary prey items like mussels directly, the hypothesis that they acquire their prey as an indirect result of intertidal prey foraging and wave action seems highly probable.

Many of the sessile organisms that are prey to sea anemones, may also be loosened from the substratum by wave battering, or from damage caused by drifting logs or debris or by rolling rocks (Dayton, 1971). Fishermen collecting the mussel worm *Pseudonereis* sp. for bait, also dislodge numerous sedentary organisms from the mussel beds in the course of their activities (Van Herwerden, 1989) making them available to anemones.

Other factors influencing the quantity and type of prey captured by sea anemones include position on the shore, which affects the period of submergence and hence feeding time, and the water currents that will be encountered. Anemones living higher up the shore are exposed to the air for longer periods and consequently have a shorter feeding time than those in low-shore positions. To compensate for this, the high-shore anemone *Anthopleura elegantissima* in California have higher prey-capture rates and absorption efficiencies than those in the low-shore (Zamer, 1986).

The rate of prey capture also depends on biological characteristics such as the surface area available to intercept prey (Sebens, 1982a; Denny, 1988), prey mobility (Sebens, 1982a) and the behaviour and morphology of the sea anemones concerned (Sebens & Paine, 1978). Oral surfaces of almost all anemones point upwards to ensure that the greatest area is presented to intercept prey (Denny, 1988). The number, shape and length of tentacles and the elasticity of the mouth differ greatly between species and may affect the size of prey that can be caught and swallowed. Large size may confer a competitive advantage and allow the capture of large prey

(Sebens, 1982a). Furthermore, the degree of toxicity may determine the efficiency of prey capture. Prey size also affects capture success rate (Sebens, 1982a). Larger prey are more robust and consequently have a greater chance of escape.

Sea anemones form an important component of intertidal and shallow subtidal ecosystems, especially in temperate zones (Harris, 1991). Despite this relatively few studies have been done on the natural diets of sea anemones world-wide. The diets of large and small *Metridium senile* from the west coast of North America were investigated by Purcell (1977) and those of two species of the genus *Tealia*, from the same region, by Sebens & Laakso (1978). Rostron & Rostron (1978) looked at the diet of *Actinia equina* in the UK and Möller (1978) studied the Mediterranean sea anemone *Anemonia sulcata*. The diets of *Anthopleura xanthogrammica*, *Anthopleura elegantissima* and *Metridium senile* from the North American west coast were quantified by Sebens (1981b, 1982a). In addition Van-Praët (1983) worked on *A. equina* from the European coast. Ayre (1984) examined the diet of *Actinia tenebrosa* from Australia, and Herndl *et al.* (1985) analysed the prey composition of the giant sea anemone *Stoichactis giganteum* from Kenya. The diet of *Heteractis malu* from Australia was investigated by Peterson & Black (1986) and Littler *et al.* (1991) examined the gut contents of *A. elegantissima* in southern California.

In South Africa sea anemones are abundant in many regions although they achieve their greatest densities in the western and south-western Cape (McQuaid & Branch, 1984; Field & Griffiths, 1991; Griffiths & Branch, 1991). However, 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 *Bunodactis 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 composition of the diets of the 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 the available resources. This study aims to supply this knowledge by examining the coelenteron contents of the seven most common species of sea anemones in this area, as well as by testing each species for signs of autotrophic nutrition.

METHODS

Two study sites were chosen on opposite sides of the Cape Peninsula. These were Wooley's Pool in False Bay (34°12'S and 18°43'E) and Blouberg Strand in Table Bay (33°47'S and 18°29'E) (Fig. 1.1). Wooley's Pool is a fairly protected site. The force of the waves is broken by a gently sloping shore and offshore reefs. The anemones thus have rolling waves surging over them, rather than waves breaking directly onto them. Seven species of sea anemones occurred at this site (see Chapter 1). 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 here results in large quantities of sand accumulating in the rocky intertidal. *Bunodactis reynaudi*, the only species found at this site, were found in dense beds in water channels, pools and crevices. Juveniles were found mostly settled in mussel beds, usually on the shells of live mussels.

Tests for autotrophic nutrition via light and dark respiration rates

All the anemones used in this study were collected from Wooley's Pool (Fig. 1.1) during January and February 1995. A sample of each of the seven species was collected, 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 the platform in a closed perspex chamber. Small species such as *Anthothoe stimpsoni* and *Actinia equina* were placed in 0.25 liter chambers, while larger species occupied 1 liter chambers. Only expanded anemones were used in this study. An empty control chamber was run simultaneously with the three experimental chambers, to monitor the biological oxygen demand of the sea water. To ensure an even distribution of oxygen within the chamber, the water 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. The respirometer was immersed in a constant-temperature (19°C) water bath. Light was provided by a Thorn 500W quartz halogen lamp, positioned above the respirometer to give a light intensity equivalent to that recorded outside in natural sunlight at 12 noon. Respiration measurements were made for 10 to 15 minutes in the light and dark, following a 15 minute acclimation period.

Coelenteron contents : Field Sampling

The coelenteron contents of at least 50 individuals of each anemone species were examined to determine the natural prey consumed by the different species. Anemones were collected from March 1992 to December 1993 during low spring tides. To avoid sacrificing animals unnecessarily, larger anemones were finger-probed, following the method of Sebens (1981b), the numbers with empty coelenterons noted and only animals containing detectable food items collected. To ensure that the full size-range of anemones was examined, and to cater for small prey that may have been undetected, an additional sample of small individuals was collected at random and transferred to the laboratory. Samples of species, such as *Anthothoe stimpsoni* and *Actinia equina* that were too small to probe effectively, were also collected at random.

Animals containing prey were carefully prized off the rocks, any items attached to the column removed and each sea anemone placed into an individual collecting jar, filled with sea water. A 10% MgCl₂ solution was mixed 1:1 with the sea water in the collecting jar to narcotize and relax the freshly collected anemones. These were then 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 stored until ready for dissection.

Coelenteron Contents : laboratory dissection and analysis

The liquid from each collecting jar was poured through a 15µm mesh to retrieve any organisms egested during transportation or preservation. Mesh size was chosen to ensure that copepods and other similarly sized zooplankton and phytoplankton were retained. Preserved anemones, and items retrieved from the collecting jar were examined under a dissecting microscope using 35x magnification. Anemones were cut longitudinally to open the coelenteron. Large food items (usually covered in mucus) were removed, identified and wet weighed. Weights of hard-shelled prey included the shells. Mesenterial filaments were separated and scraped, or sprayed with water to free small prey items frequently held there. These items were transferred to a petri dish, which was then systematically searched under a dissecting microscope. Mucus aggregations containing fine sand grains were carefully examined for microscopic prey items. Recognizable prey were counted and their taxonomic group determined to species level wherever possible. Alternately prey were grouped into higher taxa, usually orders.

Inedible items such as empty shells, fragments of crustacean exoskeletons and other debris were frequently found in the coelenteron. These 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 was simply ingested as debris (Dayton, 1973). Similarly, some of the easily digestible, soft-bodied prey items may also have been overlooked. However, because Dayton (1973) suggested that such bias is small and would result in a reduced estimate of the percentage feeding, results are presented without correction. Unidentifiable detritus was also separated and excluded from further analysis.

The wet mass (to the nearest 0.01g) 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. Hyslop (1980) pointed out the errors involved when wet masses were recorded due to the varying water retention of different organisms, but since these measurements were for comparative purposes, they were considered acceptable. Samples were blotted with tissue paper to remove as much excess moisture as possible, before weighing on a top-loading balance.

The overall mass of each food type was expressed as a percentage of the total mass of prey consumed by each sea anemone species. Although such mass measures give a good estimate of the relative importance of a particular prey item in the diet, percentage mass gives no indication of how often that item was consumed. The frequency of occurrence of the different prey species or taxa was therefore also determined.

By considering both the percentage mass and percentage occurrence, a more realistic picture of the dietary importance of each food item is gained. An "index of relative importance" (IRI), a mathematical combination of both parameters, was calculated following the method of Pinkas *et al.* (1971) as given in Berg (1979):

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

where

%N = numerical percentage of a food item in each coelenteron combined;

%Mass = percentage by mass of the food item in the guts;

%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 a particular food category was found. This can be readily converted to the percentage of the total population using the data in Table 2.2.

In order to compare the diets of the various species, untransformed data (percentage occurrence) for each species were analysed using a cluster analysis technique. This was complemented with non-parametric multi-dimensional scaling techniques (MDS-ordination) (Field *et al.*, 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 2.1.

Table 2.1: Mean oxygen consumption of seven species of intertidal sea anemones from the south-western Cape, measured in light and dark conditions at 19°C. Light intensity was equivalent to natural sunlight recorded at 12 noon. The weight-specific respiration rate is expressed per unit wet weight. Each reading is the mean of nine 15 minute periods for nine animals.

Anemone species	Respiration rate in dark (mg O ₂ ·g ⁻¹ ·hr ⁻¹)	Respiration rate in light (mg O ₂ ·g ⁻¹ ·hr ⁻¹)
<i>Actinia equina</i>	0.02	0.02
<i>Anthothoe stimpsoni</i>	0.02	0.01
<i>Anthopleura michaelsoni</i>	0.03	0.04
<i>Bunodosoma capensis</i>	0.05	0.05
<i>Pseudactinia flagellifera</i>	0.07	0.08
<i>Pseudactinia varia</i>	0.07	0.09
<i>Bunodactis reynaudi</i>	0.03	0.06

To test for differences in oxygen consumption by the different anemone species, during light and dark conditions, a nonparametric Mann Whitney U test, appropriate for small sample sizes, was performed (Zar, 1984). The only species to show a significant difference in the respiration rate under the different light conditions was *B. reynaudi* (P < 0.05, Z=2.56, Mann-Whitney) but the respiration rate in this

species was higher in light than dark condition, possibly due to increased activity. *A. simpsoni* 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 much higher percentage (39.4%) of anemones (seven species) sampled at Wooley's Pool (n = 1334) contained food compared with the single species from Blouberg (7.4%, n = 918) ($\chi^2 = 257.010$; $p < 0.001$) (Table 2.2). Considering the one common species - *B. reynaudi*, the Wooley's Pool specimens also contained food more frequently (27.7%, n = 173) than the same species at Blouberg (7.4%, n = 918) ($\chi^2 = 39.194$; $p < 0.001$).

Table 2.2: Summary of the proportion of anemones that contained naturally captured prey items at the two study sites.

Species	Number sampled (n)	Number with food in gut	Percentage with food in gut
WOOLEY'S POOL			
<i>Actinia equina</i>	226	81	35.8
<i>Anthothoe simpsoni</i>	241	57	23.6
<i>Anthopleura michaelsoni</i>	103	48	46.6
<i>Bunodosoma capensis</i>	412	30	7.2
<i>Pseudactinia flagellifera</i>	68	53	77.9
<i>Pseudactinia varia</i>	111	63	56.7
<i>Bunodactis reynaudi</i>	173	48	27.7
Total	1334	380	39.4
BLOUBERG			
<i>Bunodactis reynaudi</i>	918	68	7.4

Coelenteron content analysis

The number of anemones of each species with food in the gut examined from the two sites, their size range (expressed as wet mass) and the composition of the coelenteron contents by percentage occurrence, percentage mass and Index of Relative Importance (IRI) are presented in Table 2.3. Algae and other plant matter were not included in the calculation of percentage frequency and mass of prey items as their nutritional benefit to sea anemones is uncertain (Shick, 1991). Inorganic material and unidentifiable parts of shells and carapaces were combined as an additional category and were also excluded from these calculations. It is apparent from Table 2.3 that

Table 2.3 : The diets of seven species of sea anemone in the south- western Cape (- indicates < 0.5% contribution to mass), IRI = (numerical percentage + percentage mass) x frequency of occurrence.

Species	Woolley's Pool							Blouberg
	<i>Actinia equina</i>	<i>Anthothoe stimpsoni</i>	<i>Anthopleura michaelseni</i>	<i>Bunodosoma capensis</i>	<i>Pseudactinia flagellifera</i>	<i>Pseudactinia varia</i>	<i>Bunodactis reynaudi</i>	
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	%Occ. %Mass IRI	%Occ. %Mass IRI	%Occ. %Mass IRI	%Occ. %Mass IRI	%Occ. %Mass IRI	%Occ. %Mass IRI	%Occ. %Mass IRI	%Occ. %Mass IRI
Edible								
Zooplankton	2 - -	2 - 4	5 - 20	5 - 20	2 - 2	6 - 18	2 - 2	1 - 1
Porifera	- -	2 - 2	2 - 2	2 - 2	2 - 2	- -	- -	- -
Hydrozoa	- -	- -	4 - 16	4 - 16	6 - 8	- -	- -	- -
Ostocorallia	- -	- -	- -	- -	4 - 8	- -	- -	- -
Actiniaria	- -	- -	4 1 12	11 - 132	- -	- -	- -	- -
Platyhelminthes	- -	- -	- -	- -	- -	- -	- -	- -
Nematoda	7 - 49	4 - 8	4 - 16	4 - 16	- -	- -	- -	- -
Polychaeta	4 1 12	8 81 696	2 - 2	5 11 75	4 1 12	4 - 8	4 - 28	4 - 28
Cirripedia	- -	- -	24 39 1752	5 10 70	8 - 32	6 - 18	10 - 90	10 - 90
Copepoda	- -	8 - 32	2 - 2	2 - 2	2 - 2	2 - 2	2 - 2	2 - 2
Ostracoda	- -	- -	- -	- -	2 - 2	2 - 2	2 - 2	2 - 2
Isopoda	24 5 456	62 19 1092	9 - 63	16 - 176	18 - 324	17 - 153	2 - 2	6 - 30
Amphipoda	13 1 117	2 - 2	2 - 2	11 - 121	8 - 32	6 - 24	3 - 6	3 - 6
Tanaidacea	- -	- -	- -	- -	2 - 8	2 - 2	- -	- -
Mascara	- -	- -	- -	- -	- -	- -	- -	- -
Anomura	2 1 4	6 - 18	5 - 15	9 5 90	2 2 6	8 2 48	2 - 2	3 2 12
Brachyura	2 - 2	6 - 18	9 1 54	5 - 90	8 3 56	6 4 42	10 2 70	4 10 52
Acantho	26 1 572	8 - 32	5 - 15	5 - 15	- -	4 - 8	2 - 2	- -
Insecta	6 - 18	- -	4 - 8	5 - 15	- -	- -	6 - 18	- -
Araneae	7 13 119	- -	4 - 8	5 - 15	- -	- -	- -	- -
Bryozoa	2 7 18	- -	4 - 8	5 - 15	- -	- -	- -	- -
Amphineura	28 1 1204	4 - 8	18 9 342	9 - 54	2 3 8	2 - 2	42 42 3612	91 88 15197
Pelecyopoda	4 70 288	6 - 18	67 43 7437	7 18 168	43 28 2236	42 25 2856	25 10 700	19 - 589
Gastropoda	- -	- -	5 1 20	7 18 168	2 - 2	2 - 2	2 - 2	- -
Asterioidea	- -	- -	5 6 45	2 6 14	12 51 684	12 56 756	2 1 4	- -
Ophiuroidea	- -	- -	2 - 2	4 41 172	2 - 2	2 - 2	2 - 2	- -
Echinoidea	- -	- -	2 - 2	4 41 172	6 3 36	2 5 12	2 1 4	- -
Holothuroidea	- -	- -	5 - 15	4 - 8	2 - 2	2 - 2	2 - 2	- -
Crinoidea	- -	- -	5 5 98	4 - 8	2 - 2	2 - 2	2 - 2	- -
Tunicata	- -	- -	53 5 2491	25 1 425	25 1 360	25 1 475	12 5 84	3 - 6
Pisces	- -	- -	67 16 4824	38 20 1900	49 22 2793	48 12 2112	52 24 1924	16 2 224
Eggs	7 - 98	2 - 2	5 - 15	4 - 8	2 - 2	2 - 2	2 - 2	- -
Inedible								
Algae	13 1 104	2 - 2	53 5 2491	25 1 425	25 1 360	25 1 475	12 5 84	3 - 6
Other	35 6 910	6 - 24	67 16 4824	38 20 1900	49 22 2793	48 12 2112	52 24 1924	16 2 224

the majority of species consumed prey from a wide spectrum of prey types but that only one or two types invariably dominated the diet. Isopods, pelecypods and gastropods were found in the coelenterons of all species and at both sites, although their occurrence in the diet varied considerably. Isopods occurred with the lowest frequency in *B. reynaudi*- Wooley's Pool (2%) and the highest in *A. stimpsoni* (62%). Pelecypods ranged from 4% (*A. stimpsoni*) to 91% (*B. reynaudi* - Blouberg), while the percentage occurrence of gastropods was lowest in *A. equina* (4%) and reached a maximum of 67% in *A. michaelsoni*. The percentage occurrence of individual prey species in the guts of each anemone species is shown in Table 2.4. The diets of each species of anemone analysed are discussed separately below.

Actinia equina:

Fifty-four specimens of mass 0.09g to 8.51g were found to contain recognizable food in their coelenterons. In terms of occurrence pelecypods (28%) were the most abundant food items, 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 infrequently. 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 2.4), but because they are very small 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%), the isopods *Exosphaeroma* spp (11%) and *Cirolana* sp. (4%) and the amphipod *Hyale* sp. (6%).

Anthothoe stimpsoni

Prey items were collected from the coelenterons of 52 *A. stimpsoni*, whose mass ranged from 0.03-0.37g. This species 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 -

Table 2.4: Percentage occurrence of the prey items most frequently consumed by sea anemones in the south western Cape (p = present in less than five percent of coelenterons; - = absent).

	WOOLEY'S POOL							BLOUBERG	
	<i>Actinia equina</i>	<i>Anthothoe stimpsoni</i>	<i>Anthopleura michaelsoni</i>	<i>Bunodosoma capensis</i>	<i>Pseudactinia flagellifera</i>	<i>Pseudactinia varia</i>	<i>Bunodactis reynaudi</i>	<i>Bunodactis reynaudi</i>	
Zooplankton									
Harpacticoidea	-	8	-	p	p	-	-	-	
Zoea larva	p	-	-	5	-	-	-	-	
Nematoda	13	-	-	-	-	-	-	-	
Polychaeta									
<i>Euclymene</i> sp.	-	6	-	-	-	-	-	-	
<i>Scolelepis squamata</i>	-	-	-	-	-	-	-	9	
Cirripedia									
<i>Tetraclita serrata</i>	-	-	51	-	p	p	60	-	
<i>Balanus algicola</i>	-	-	p	-	p	8	21	-	
<i>Octomeris angulosa</i>	-	-	15	-	-	-	12	-	
Isopoda									
<i>Cirolana</i> sp.	p	p	5	p	p	p	p	-	
<i>Exosphaeroma</i> spp	11	13	p	p	25	p	-	5	
<i>Jaeropsis stebbingi</i>	-	33	-	-	-	-	-	-	
Amphipoda									
<i>Hyale</i> sp.	6	-	-	p	-	-	-	-	
<i>Paramoera capensis</i>	-	-	-	9	-	p	-	-	
Anomura									
<i>Paguristes gamianus</i>	p	-	5	p	p	8	p	-	
Brachyura									
<i>Ovalipes trimaculatus</i>	-	-	p	p	8	p	p	5	
<i>Plagusia chabrus</i>	-	-	-	-	-	p	8	p	
Acanthozoa									
Acanthozoa	p	6	-	-	-	-	-	-	
Insecta									
<i>Anurida maritima</i>	7	-	-	p	-	-	-	-	
Coleoptera	6	-	-	-	-	-	p	-	
Diptera	7	-	-	-	-	-	-	-	
Formicidae	6	-	-	-	-	-	-	-	

continued...

Table 2.4: continued.

	WOOLEY'S POOL										BLOUBERG	
	<i>Actinia equina</i>	<i>Anithoe stimpsoni</i>	<i>Anithoe michaelsoni</i>	<i>Bunodosoma capensis</i>	<i>Pseudactinia flagellifera</i>	<i>Pseudactinia varia</i>	<i>Bunodactis reynaudi</i>	<i>Bunodactis reynaudi</i>				
Araneae												
<i>Desis formidabilis</i>	p	8	-	-	-	-	-	-	-	-	-	-
Amphineura												
<i>Acanthochiton garnoti</i>	p	-	-	6	p	p	-	-	-	-	-	-
Pelecypoda												
<i>Choromytilus meridionalis</i>	-	-	9	-	6	12	21	72				
<i>Mytilus galloprovincialis</i>	-	-	5	-	14	6	44	42				
<i>Nucula nucleus</i>	76	6	p	9	p	p	10	p				
Gastropoda												
<i>Assiminea globulus</i>	-	-	11	p	6	-	p	-				
<i>Burnupena</i> spp	-	-	53	p	16	31	15	p				
<i>Crepidula porcellana</i>	-	-	15	-	p	6	6	-				
<i>Gibbula</i> spp	-	-	5	-	p	8	p	-				
<i>Helcion dunkeri</i>	-	-	p	-	6	p	-	-				
<i>Nucella</i> spp	-	-	5	-	-	-	-	-				
<i>Oxystele</i> spp	-	-	5	-	-	8	-	-				
<i>Patella</i> spp	p	-	16	p	-	p	p	p				
<i>Tricolia capensis</i>	-	6	5	-	12	33	-	43				
Asteroidea												
<i>Patriella exigua</i>	-	-	5	-	p	p	p	-				
Echinoidea												
<i>Parechinus angulosus</i>	-	-	5	p	12	13	p	-				

polychaetes (81%) and isopods (19%) formed a significant proportion of the diet by mass. The index of 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.

Anthopleura michaelsoni

The coelenteron contents of 55 *A. michaelsoni*, with wet mass ranging from 15.01-105.14g were analysed. The most common items in the diet were hard-shelled prey, with gastropods occurring most frequently (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 was consumed more frequently (53% occurrence) by 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 algalicola* (4%) and *Octomeris angulosa* (15%) were also found.

Bunodosoma capensis

A sample of 55 *B. capensis*, ranging from 4.06-70.37g contained food in the coelenteron. Nineteen prey categories occurred in more than 5% of the anemones examined (Table 2.3) 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 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 2.4).

Pseudactinia flagellifera

Fifty-one specimens, with wet mass varying from 3.16 to 188.37g, contained food items. Gastropods (43%) occurred most frequently, 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 were 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

A total of 52 anemones were found to contain food items. Anemones ranged in mass from 0.55 to 135.28g. As with *P. flagellifera*, gastropods (42%) occurred with the highest frequency, 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% percentage occurrence) and *Tricolia capensis* (33%). Of the pelecypods consumed, *Choromytilus meridionalis* occurred in 12% of the guts examined and the most important echinoderm in the diet was *Parechinus angulosus* (13%).

Bunodactis reynaudi

a). Wooley's Pool

The gut contents of 52 *B. reynaudi* from Wooley's Pool were examined. Anemone mass ranged from 9.01-178.63g. The most frequently occurring food categories 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 the ranking of importance in terms of the IRI calculations as cirripedes, 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 found feeding on holothurians.

b). Blouberg

Sixty-seven *B. reynaudi* containing prey were examined from Blouberg. Anemone mass varied from 0.37-138.81g. Relative to all the species at Wooley's Pool, this species had a very restricted diet. Coelenteron contents comprised only ten 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 analysed are shown in Figs 2.1 and 2.2. Four main groups were distinguished in the dendrogram (Fig. 2.1) at an arbitrary similarity level of 55%. *A. stimpsoni* clustered separately as it ate only small prey items, including more mites and spiders than any other species. The diet of *B. capensis* and *A. equina* were sufficiently distinct to form a separate group. These species are both generalists, with no particular prey category dominating their diets. They also appear to be opportunistic feeders. *B. capensis* was the only species that consumed platyhelminths, and *A. equina* was the only species where insects formed a large proportion of the prey captured. The two *Pseudactinia* species grouped together with *A. michaelsoni* and *B. reynaudi* at Wooley's Pool formed 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 dominated the diet far more than in any other species. 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 under light and dark conditions it is apparent that none of the anemone species examined show any detectable autotrophic activity. *B. reynaudi* was the only species in which there was a significant difference in the oxygen concentration of the chambers under the different light intensities. However, the rate of oxygen consumption was higher in the light than in the dark, possibly as a result of differing activity levels during illumination. Very few studies by other authors have measured respiration rates in any of the species from this study. My results are however consistent with those of Sebens & DeReimer (1977) who found that *Bunodactis* sp. did not possess any zooxanthellae and Griffiths (1977a) and Shick *et al.* (1988) who ascertained that *A. equina* does not contain endosymbiotic algae.

Under similar climatic and tidal conditions, there were a higher proportion of anemones at Wooley's Pool containing food items, than at Blouberg (Table 2.2). This result is surprising. Blouberg is an exposed site and subject to much stronger wave action than Wooley's Pool (Chapter 1). Strong wave action is often associated with increased amounts of food (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 would therefore be expected to be higher at Blouberg, than at Wooley's Pool. This 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 a potential food source for them. Larger or optimally positioned individuals may shield those situated further up the shore and reduce the 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 the higher prey capture efficiency at this site. Low flow reduces the amount of prey swept along helplessly in strong currents, and consequently more motile prey may become available to the anemones (Sebens & Koehl, 1984).

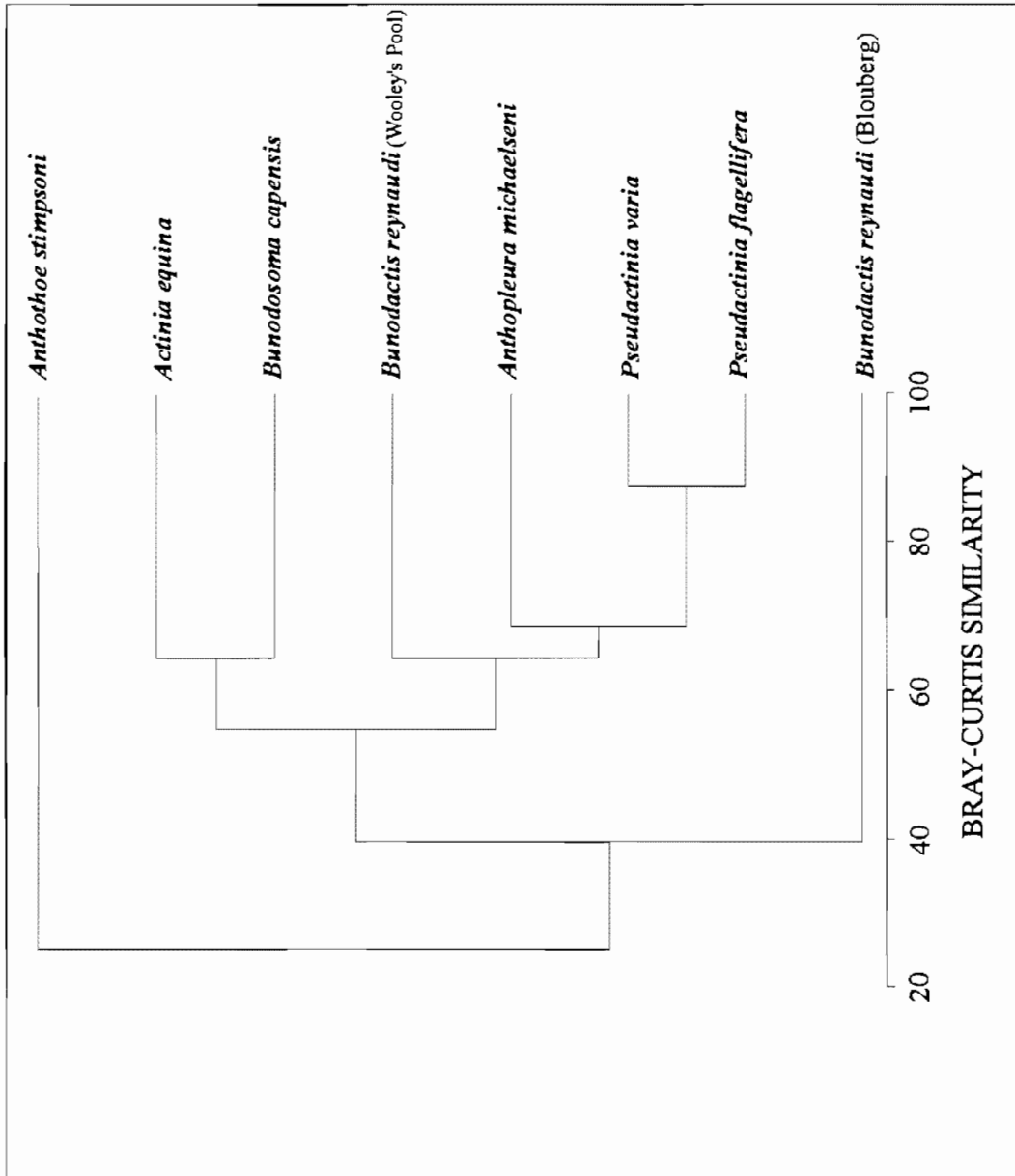


Figure 2.1. Dendrogram showing the degree of similarity between the diets of seven species of sea anemones in the south-western Cape based on the frequency of occurrence of the prey items consumed.

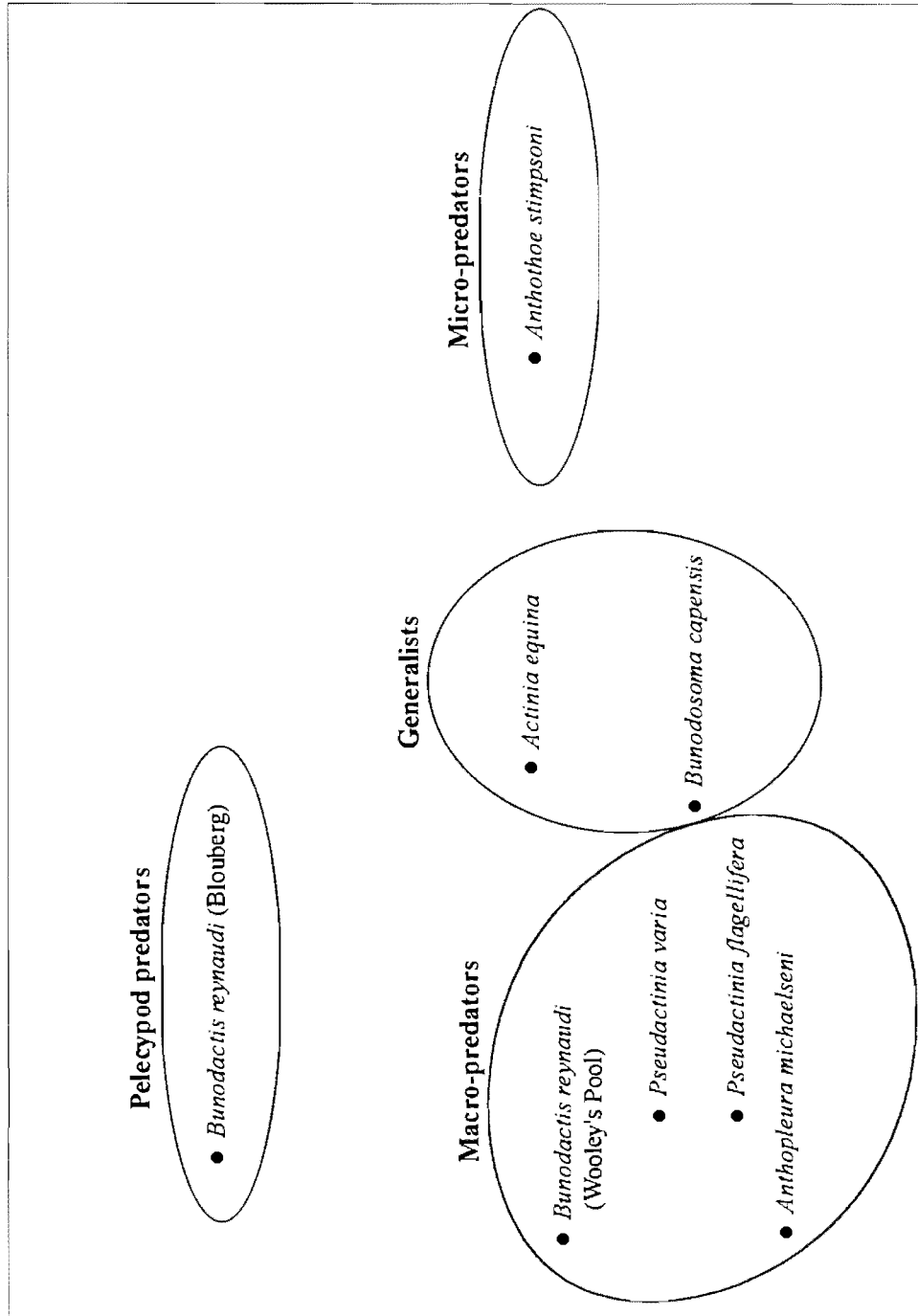


Figure 2.2: The relationship between the diets of the different anemone species at the two study sites. The ordination was obtained using multi-dimensional scaling on the same similarity matrix as Fig 2.1. *Bunodactis reynaudi* (Blouberg) was the only species that occurred at Blouberg, the remaining species were all found at Wooley's Pool. (Stress = 0.02).

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 michaelsoni*, *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 can be attributed to mass of the 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 & Griffiths, 1988) and diversity within them is low (Dethier, 1980; Huggett & Griffiths, 1986). It is not surprising therefore, that *A. stimpsoni*, which inhabits these pools (Chapter 1), 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 *A. michaelsoni* and the two *Pseudactinia* species, may be explained in terms of their morphology and the habitats that they occupy. *A. michaelsoni* 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 *et al.*, 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 *et al.*, 1985) such as cirripedes (*A. michaelsoni*) and pelecypods (*A. michaelsoni* and *Pseudactinia* spp.).

The components of the diets of the two *Pseudactinia* spp were remarkably similar (Table 2.3). Gut contents were represented by 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 very alike. There is a

predominance of motile prey in the diet (Table 2.3). This is to be expected because of the sheltered environment that these anemones inhabit (Chapter 1; Branch & Griffiths, 1988). In calm conditions prey capture may increase because prey can move about randomly, without being washed away by the current (Sebens & Koehl, 1984; Denny, 1987). Larger prey can also be held without them being "wrenched" from the tentacles by water movements. The low-shore position occupied by the two *Pseudactinia* species (Chapter 1) was close to the 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 the *B. reynaudi* populations at the two sites were the same, but a preponderance of pelecypods were consumed by the Blouberg population (Table 2.3). *Choromytilus meridionalis* and *Mytilus galloprovincialis* were the most common species eaten at both sites (Table 2.4). Wave tumbled mussels are frequently washed into the cracks and crevices occupied by *B. reynaudi* and the more than 300 short tentacles and highly contractile sphincter muscle possessed by this species, ensures 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 *et al.*, 1992). Mussel densities at Wooley's Pool were found to be 104 *M. galloprovincialis* per square meter and 0.1 *Aulacomya ater* per square metre (*C. meridionalis* are present in False Bay but were not found in the transects). By contrast Blaine (1988) estimated mussel densities at Blouberg to be: *M. galloprovincialis* (1074 m⁻²), *A. ater* (387 m⁻²) and *C. meridionalis* (298 m⁻²). It is not surprising therefore that pelecypods dominated the diet at the latter site. It is interesting to note that very few *A. ater* were found in the anemone coelenterons. *A. ater* is a much slower growing and longer lived species than *C. meridionalis* (Van Erkom Schurink & Griffiths, 1992) and also attaches much more firmly to the substratum than *C. meridionalis* (Griffiths & Seiderer, 1980) and is therefore much more difficult to dislodge. Competition for food limits anemone growth in high density areas, but not in populations of average density (Batchelder & Gonor, 1981). Anemone densities at Blouberg were very high (901 m⁻¹) and consequently food may have been a limiting factor at this site. This is supported by the fact that *B. reynaudi* at Blouberg were on average smaller than the same species at Wooley's Pool (Table 2.3).

Four feeding groups were revealed by the cluster analysis and MDS-ordination (Figs 2.1, 2.2). *A. stimpsoni* are small and consume only small prey items and are

therefore regarded as micro-predators. *A. equina* and *B. capensis* are generalists as neither appeared to favour any particular prey category. Both species are of intermediate size (Table 2.3) and consume prey covering a wide size range. The macro-predator group consists of the largest anemone species at Wooley's Pool viz., *B. reynaudi*, *A. michaelsoni*, *P. flagellifera* and *P. 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 2.4). Prey capture and its absorption are related to anemone size (Shick, 1991). These macro-predators are therefore probably the only anemones in this study 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 studied (Sebens & Koehl, 1984; Shepherd & Gray, 1985). Prey items from the *A. equina* population at Wooley's Pool correspond well with those from the U.K. (Rostron & Rostron, 1978) and from Europe (Van-Praët, 1985). In each case, small crustaceans formed the bulk of the diet. It is interesting to note that insects form a substantial part of the diet (Table 2.3) in both the present study and that of Van-Praët. Insects were also found to be important constituents in the diet of *Actinia tenebrosa* in Australia (Ayre, 1984). Because insects are only present during certain periods of the year, Ayre (1984) concluded that sea anemones are opportunistic predators. My results confirm this. Most of the anemones that contained insects were from samples collected in late spring (October and November, 1993), which coincides with the time that 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 2.3), they were almost all *Nucula nucleus* (Table 2.4). Mussels were completely absent from the gut contents of *A. equina* in this study.

There is no previous information on the diets of any of the other species examined during this study. However, *B. reynaudi* at Blouberg and *Anthopleura xanthogrammica* in the USA are morphologically and behaviourally very alike. Both occupy a very similar habitat and results indicate that they follow the same feeding régime. The very low proportion of *B. reynaudi* found to be feeding in the field at Blouberg (7.4%) corresponds well with the findings of Sebens (1982b) in his work

on *A. xanthogrammica* in the USA (<10%). Pelecypods were ranked as the most important constituent in the diet of both *B. reynaudi* (this study) and *A. xanthogrammica* (Dayton, 1973; Sebens, 1981b). Mussels constituted 88% of the diet of *B. reynaudi* by mass (Table 2.3) and 78% of *A. xanthogrammica* (Sebens, 1982a). Large size allows for more efficient food capture (Sebens, 1980). Thus to maximize growth and achieve a competitively successful size, *A. xanthogrammica* selects against asexual fission (Sebens, 1983). It is suggested that the same situation applies to the *B. reynaudi* population at Blouberg. Fission was frequently observed among small individuals in the mussel beds, but never in large specimens.

Sea anemones are passive suspension 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 (Chapter 1), sessile organisms, particularly the mussels *Choromytilus meridionalis* and *Mytilus galloprovincialis*, formed the bulk of the prey (Table 2.4). Wooley's Pool is a more sheltered site and here more mobile forms, such as gastropods and crustaceans, were more prevalent (Table 2.3). The density of mussels was considerably higher at Blouberg than at Wooley's Pool (see above). It is not surprising, therefore that large numbers of mussels were captured by the anemones at Blouberg. The density of gastropods was however similar at the two sites e.g. *Nucella* spp. - 37 m⁻² at Blouberg (Blaine, 1988) and 26 m⁻² at Wooley's Pool (Van Herwerden, 1989).

Macroalgal fragments were present in the gut contents of all the species and were consumed particularly frequently by *A. michaelseni* (Table 2.3). It is, however not known whether sea anemones derive any nutritional benefit from this plant material. Gastric juices of *A. 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 possess 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 *et al.*, 1987). Other species of *Anthopleura* such as *A. elegantissima* (Sebens, 1981b) and *A. ballii* (Cocks) (Minchen, 1983) also consumed large proportions of plant material. Some authors (Van-Praët, 1982) have considered phytoplankton to be an important constituent in the diet of *A. equina*. The consumption of plant material by other presumed carnivores, including littoral fish (Bennett *et al.*, 1983) and crabs (Le Roux *et al.*, 1990), has been reported in South Africa. As with the

anemone species examined however, the nutritional benefit to these predators has not been demonstrated.

The vast quantities of totally indigestible items found in coelenteron contents (Table 2.3) 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 & Guancia (1977) noted that *Condylactis gigantea* continues to accept prey after ingestion has already taken place, as does *P. flagellifera* (Krijgsman & Talbot, 1953).

Sea anemones appear to be less efficient predators than more mobile intertidal organisms. The number of anemones feeding at any time was very low (Table 2.2). By contrast in a sample of horseshoe crabs (*Limulus polyphemus*) studied by Botton (1984) in the USA, only one did not contain any food items. Locally, Zoutendyk (1988) found that 97% of rock lobsters (*Jasus lalandii*) sampled from a population at Robben Island contained food in their stomachs. In a sample of intertidal fish from Miller's Point in False Bay 95% of the fish were found to have been feeding (unpublished data from K. Prochazka).

The diet of sea anemones is less restricted than that of more motile predators (Van-Praët, 1985). The sea anemones examined in this study each consumed prey from between 11 and 19 prey categories (Table 2.3). Motile predators, however tend to have a narrower prey width. The crab *Carcinus maenas* from the same region consumed nine different prey types (Le Roux *et al.*, 1990). These more motile organisms are able to move around and search for prey and are often able to select specific food items. Anemones however, due to their sessile nature, depend entirely on water movements or the motility of the prey themselves. They consequently engulf everything that their tentacles encounter and can be regarded as unselective, opportunistic feeders.

Sea anemones rarely have an over-abundance of food (Shick, 1991). Despite this, their ability to utilize various methods to obtain their nutritional requirements lead Janssen & Möller (1981) to suggest that it is impossible for *Anemonia sulcata* to starve to death in nature. The opportunistic feeding behaviour of anemones (Ayre, 1984) suggests that they are capable of having a significant impact on the invertebrate populations that

they exploit (MacKenzie, 1977; Minchin, 1983, Mathieson *et al.*, 1991). This aspect will be dealt with in the following chapters.

CHAPTER 3

CONSUMPTION RATES OF INTERTIDAL SEA ANEMONES FROM THE SOUTH-WESTERN CAPE

INTRODUCTION

Several studies have been undertaken to determine trophic relationships and patterns of energy flow in rocky intertidal ecosystems in the south-western Cape (McQuaid & Branch, 1984, 1985; Field & Griffiths, 1991; Griffiths & Branch, 1991). Although sea anemones are recognized as an important and conspicuous predatory group in such systems (Griffiths & Branch, 1991), no work has yet been undertaken to determine their importance or potential impact as predators on intertidal assemblages.

Seven species of sea anemones are common in the intertidal and shallow subtidal zones in the south-western Cape (Chapter 1). Sea anemones are opportunistic feeders (Ayre, 1984; see chapter 2) and as such are potentially capable of exerting a strong influence as sedentary consumers in such systems. To determine their importance as consumers requires knowledge of their ingestion and prey turnover rates. One approach to this is to quantify the gut contents of anemones in their natural environment and to divide this by the time required for digestion (Peterson & Bradley, 1978; Sullivan & Reeve, 1982; Purcell, 1983). The dietary compositions of anemones have been studied previously (see chapter 2). Calculating the amount of prey consumed by a predator per unit time is difficult and subject to error, particularly when the feeding pattern is erratic (opportunistic) and a wide spectrum of prey types are consumed. However anemones make good subjects for digestion rate estimates, because prey can be ingested whole and are contained within the coelenteron, until egestion, which is easily observable.

In the present study turnover times of various prey items consumed by seven intertidal anemone species from the south-western Cape were determined in order to estimate consumption rates. These provide a preliminary means of quantifying the impact of sea anemones as predators in this region.

METHODS

Samples of the seven species of sea anemones (covering the range of sizes) were collected from two study sites: Wooley's Pool in False Bay and Blouberg on the Cape west coast (Chapter 1) during February 1993 and December 1994. Anemones were carefully removed from the rock surface with a blunt instrument or, where possible, collected together with the substratum to which they were attached. Undamaged animals were submerged in sea water in individual collecting jars and conveyed to the laboratory, where they were transferred to aquaria equipped with a circulating sea water system. Tanks were compartmentalized with plastic mesh to separate aggressive conspecifics without interfering with the water circulation. Anemones were placed singly in each compartment and left to reattach to either the glass walls of the tanks or to rocks placed on the bottom. A layer of sand was provided on the bottom of the tank for those species (e.g. *Anthopleura michaelseni* and *Bunodactis reynaudi*) that prefer this habitat. Anemones were maintained at the mean sea water temperature of the site from which they were collected, this being 12°C for Blouberg and 17°C for Wooley's Pool.

Actinia equina has a tide-related respiratory rhythm (Griffiths, 1977a, b; Jones *et al.*, 1977). To maintain healthy and responsive anemones, tanks were thus slowly drained, using a narrow-bore siphon hose and then refilled twice daily to simulate tidal action. Anemones were 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 to ensure that no food remained in their coelenterons.

The rate at which specific prey items were digested by the different anemones was determined by feeding a number of each species with an individual food item, and then assessing its digestion state, by removing the food bolus from the coelenteron of individuals within a group at regular time intervals. The state of digestion was evaluated according to a predetermined scale (Table 3.1). In most cases three of the most common prey items found in the gut content of each species (Table 2.3) were used as prey. However, for *Anthothoe simpsoni* and *Bunodosoma capensis*) only two prey types were utilized. Food items selected for use in the experiments were limited to marine species and their abundance in the field and ease of capture and handling were also taken into account. Live, undamaged prey were used to ensure that no deterioration of the tissues occurred prior to ingestion. The mass of each prey item was recorded (to the nearest 0.01g) and smaller-sized prey fed to smaller-sized

anemones to simulate natural feeding behaviour (Purcell, 1977; Sebens & Koehl, 1984). Prey were held with forceps and dropped onto the tentacles or oral disc of expanded anemones. The tentacles usually reacted rapidly and secured the prey, but in some instances the prey managed to escape or the anemones did not respond. Anemones were therefore inspected 10-15 minutes after feeding to ensure that ingestion had occurred, failing which a new prey item was offered.

At regular intervals thereafter three anemones from each group were sacrificed, their food bolus removed and its state of digestion determined. The time period between examinations depended upon the rate of digestion of the prey. Thus items that were digested rapidly were examined more frequently than less digestible ones. For each sample, randomly selected individual anemones were placed in a plastic collecting jar containing 10% MgCl₂ mixed 1:1 with sea water. They were then frozen rapidly at -80°C to prevent further digestion from occurring, and left for a minimum of two hours. The basal diameters of thawed anemones were measured (to the nearest 1mm), wet weighed using a top-loading balance (to the nearest 0.01g) and dissected to reveal the ingested food. The degree of digestion of each prey item was recorded according to the predetermined scale shown in Table 3.1. Anemone gut contents continued to be examined until egestion had taken place in the majority of individuals.

Table 3.1: Key used to determine the digestion rates of the different prey categories consumed by seven species of sea anemones. The digestion state index represents a change 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

There was considerable variation in the digestion states of the prey items removed from the three anemones sacrificed in each sample. In order to smooth this variability, a weighted running mean of the digestion states at three time intervals was used. The data were calculated by the equation $\frac{a+2b+c}{4}$, where "a", "b" and "c" represent the mean degree of digestion of prey items collected from three sequential samples.

RESULTS

Specific prey items used in the digestion rate experiments are listed in Table 3.2. These were not necessarily always those that occurred with the highest frequency in natural gut contents (Chapter 2). Three prey items 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 categories in these two species.

The change in the digestive state of prey items over time are shown in Figs 3.1 - 3.8. Comparison of these results indicate that the rate at which a species digested different prey items varied, as did the rate at which different species digested the same prey item. *A. equina* appeared to digest prey faster than any of the other species. It was the only species that produced egesta of all the items eaten within 24 hours following ingestion (Fig. 3.1). The amphipod *Paramoera capensis* (Table 3.2) was the most rapidly digested prey and was egested within 12 hours. Pelecypods (*Nucula nucleus* - Table 3.2) took 15 hours to be digested, while isopods (*Cirolana* sp.) were egested after 23 hours. A one-way ANOVA (Sokal & Rohlf, 1969) comparing the time from ingestion to egestion, indicated that the variation in the rate at which *A. equina* and other anemone species digested isopods and pelecypods, was significant ($P < 0.05$). Pairwise comparisons showed that while *A. equina* digested pelecypods most rapidly, there was some degree of similarity in the rate at which they were digested by *A. michaelsoni* and *P. flagellifera* (Table 3.3). *B. reynaudi* however, took significantly (Tukey test, $P < 0.05$) longer than *A. equina* and *A. michaelsoni* to digest pelecypods. These results were similar to those recorded for the rate at which anemones digested isopods (Table 3.4).

Table 3.2: Prey species fed to seven anemone species in the digestion rate experiments.

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

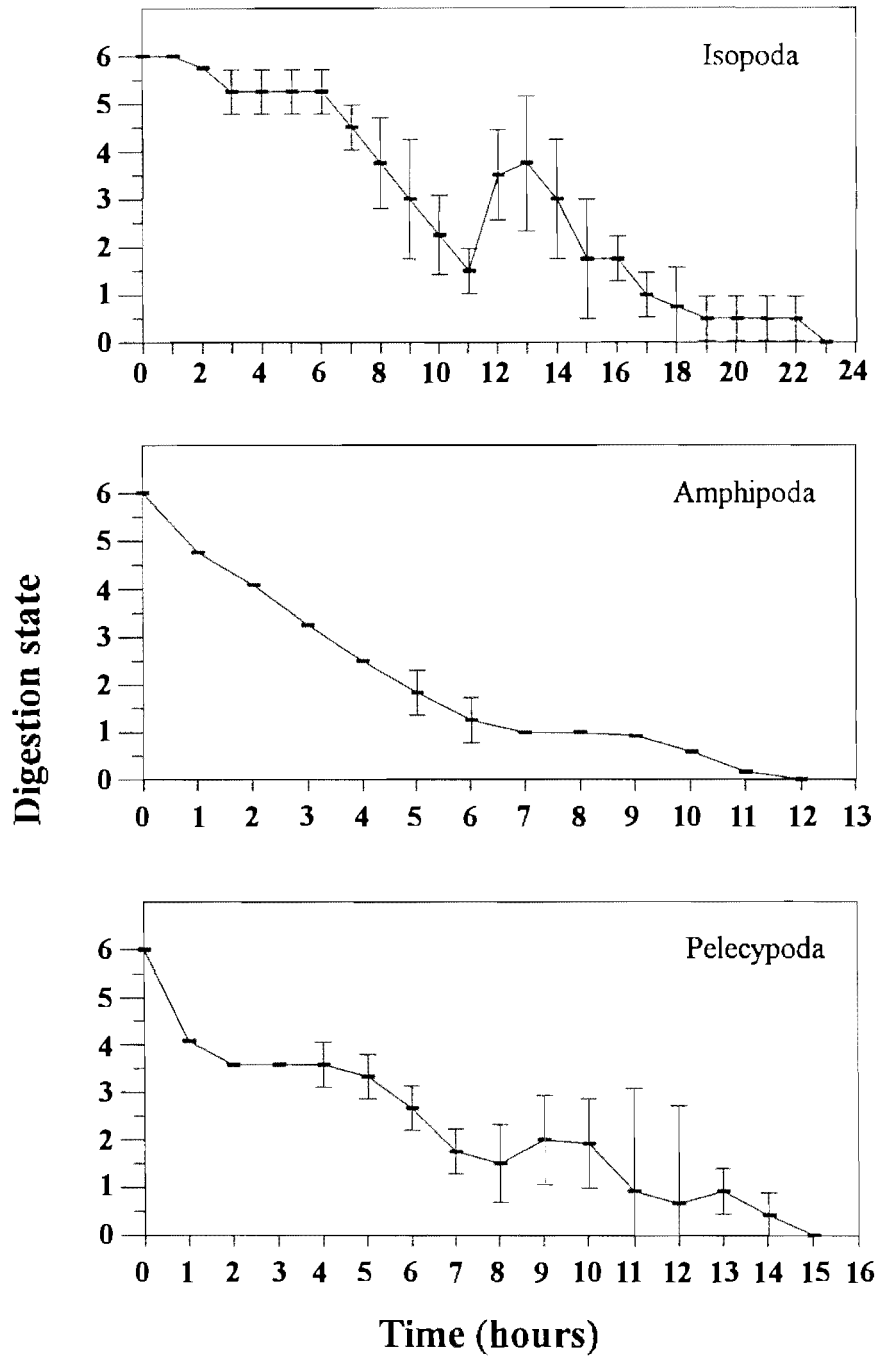


Fig. 3.1: Digestion times of the three most commonly consumed marine prey items of *Actinia equina* at Wooley's Pool. Points represent the running mean (\pm S.D.) of the digestion state of three anemones assessed at the time intervals as shown. The digestion state index refers to the condition of the food item as described in Table 3.1. The time interval scale of the three graphs is different due to the differences in the digestibility of the various prey items.

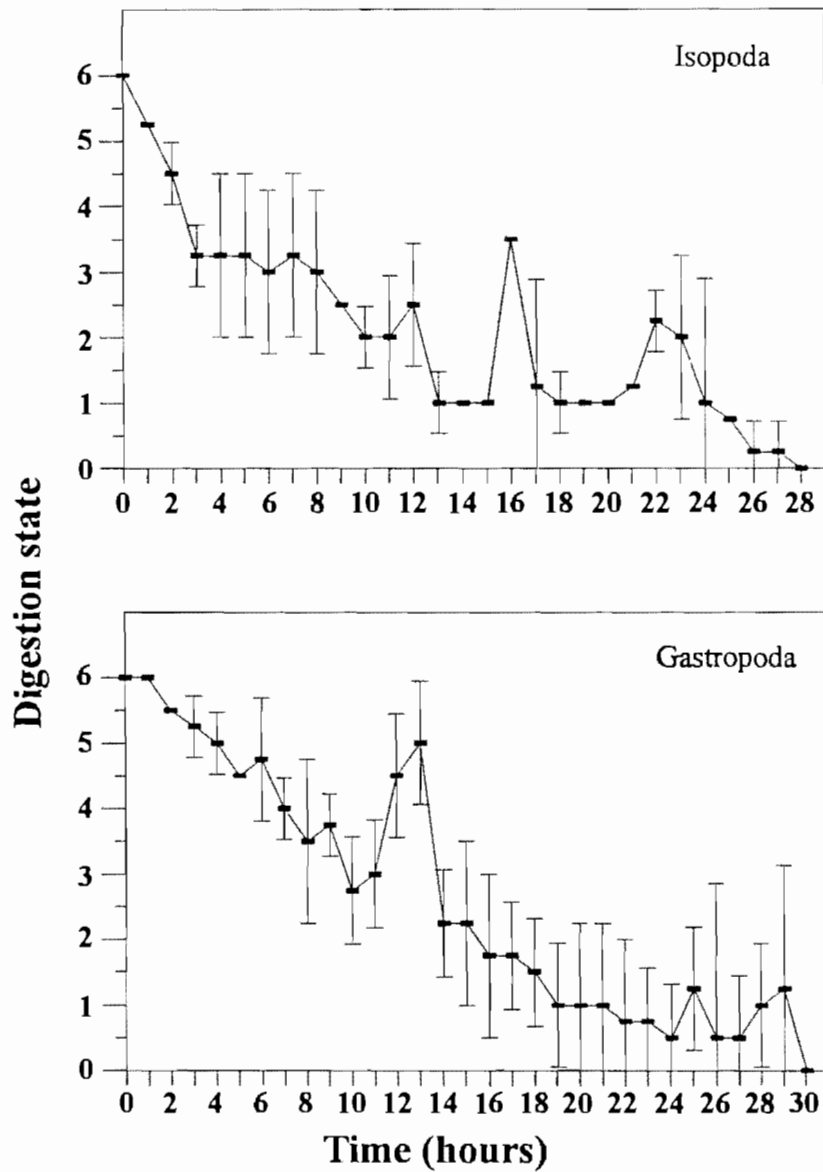


Fig. 3.2: Graphs showing the weighted running mean of the digestion rates of two prey items commonly consumed by *Anthothoe stimpsoni* from Wooley's Pool. S.D. is also shown. The digestion state refers to the condition of the food items as given in Table 3.1.

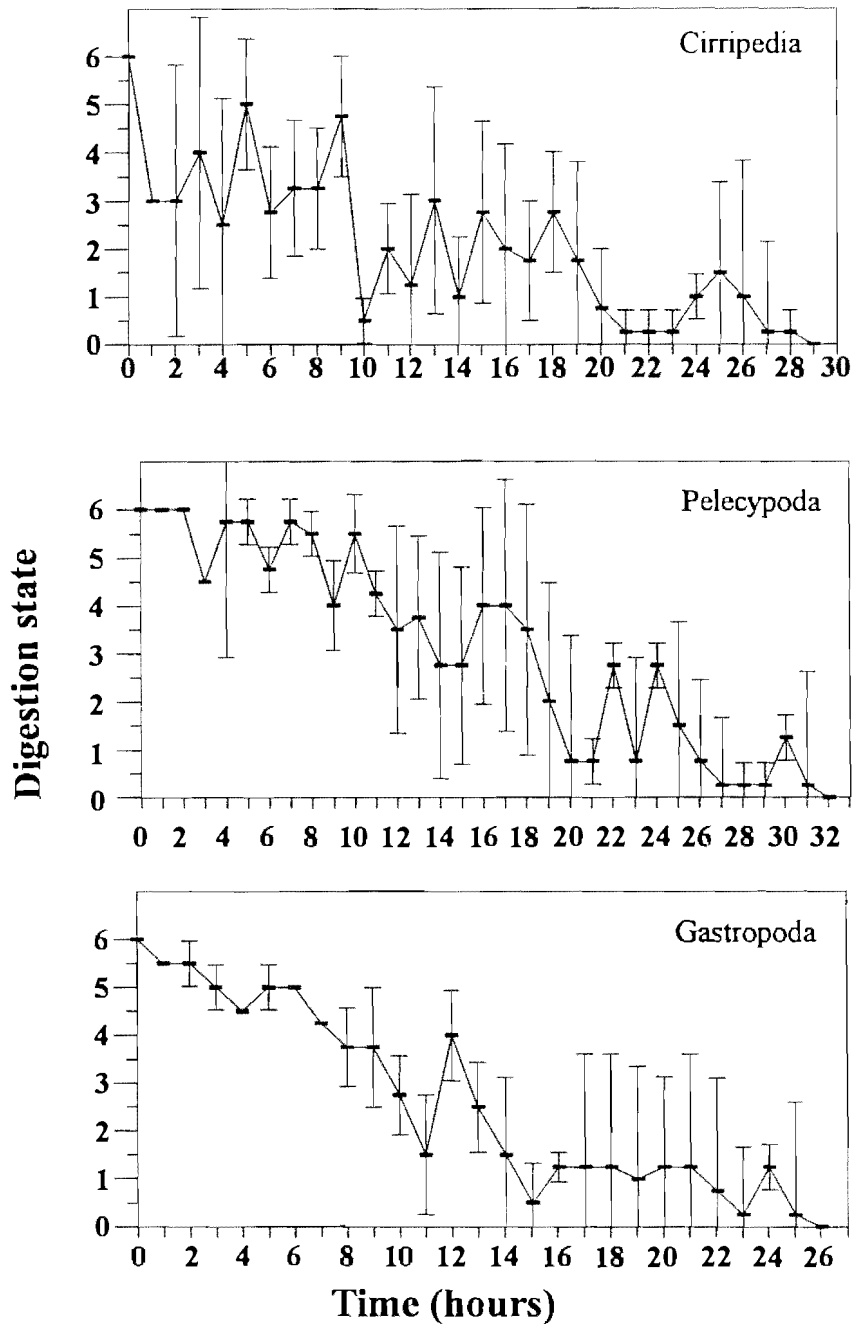


Fig. 3.3: Time taken for *Anthopleura michaelseni* from Wooley's Pool to digest the three most frequently consumed prey items. The weighted running mean (\pm S.D.) of the digestion states of the food consumed by three anemones is shown. The key of the digestion states is given in Table 3.1.

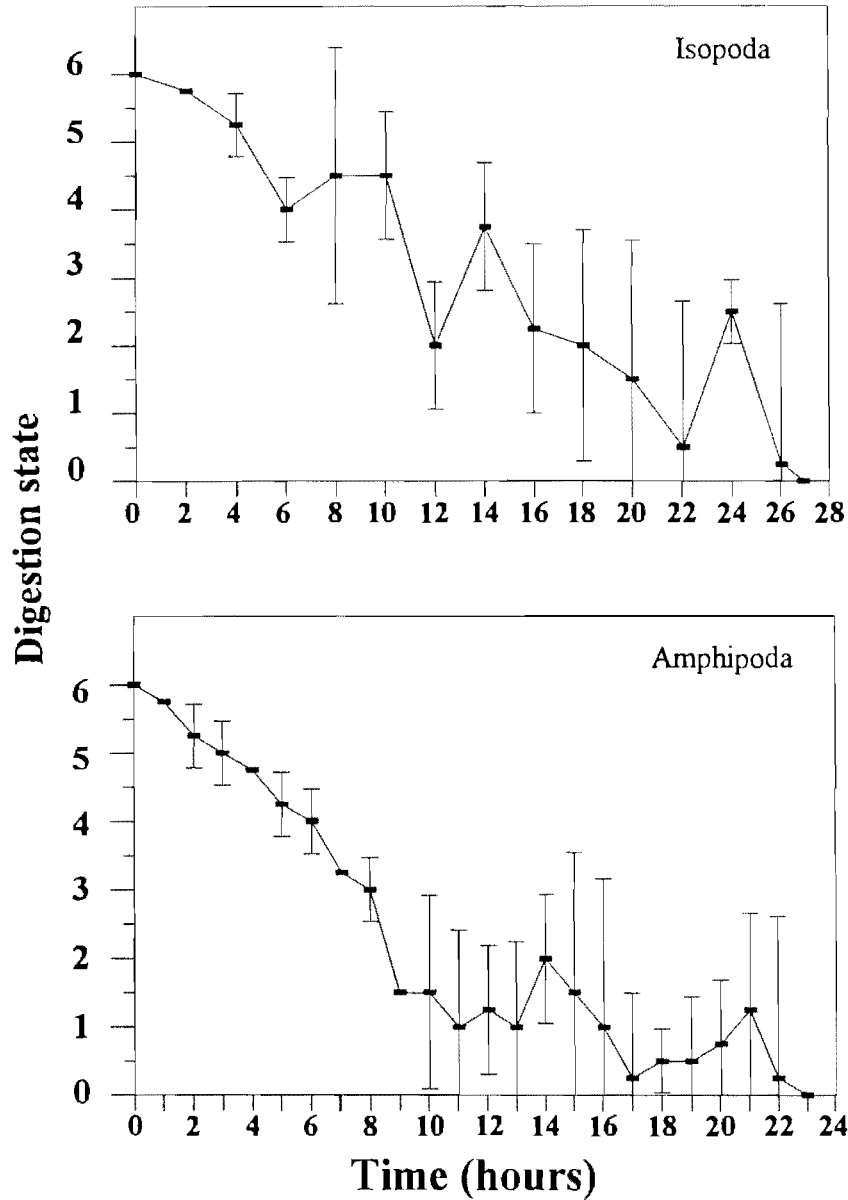


Fig. 3.4: Graphs showing the time taken for *Bunodosoma capensis* from Wooley's Pool to digest two prey items that are frequently consumed in their natural habitat. Points represent a weighted running mean and the S.D. is also given. The digestion states are described in Table 3.1.

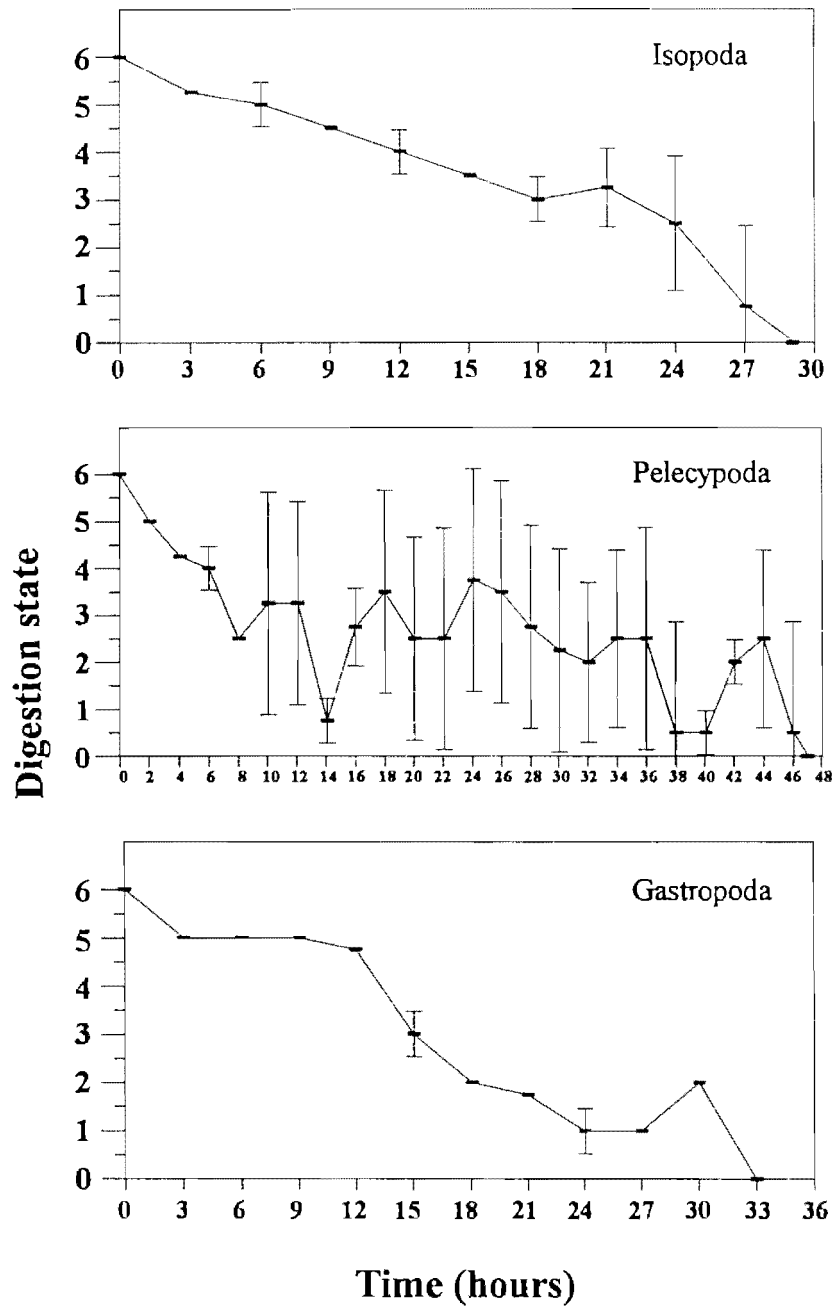


Fig. 3.5: Rate of digestion of the three food items most commonly consumed by *Pseudactinia flagellifera* from Wooley's Pool. Digestion state was determined using a weighted running mean. S.D. is also given.

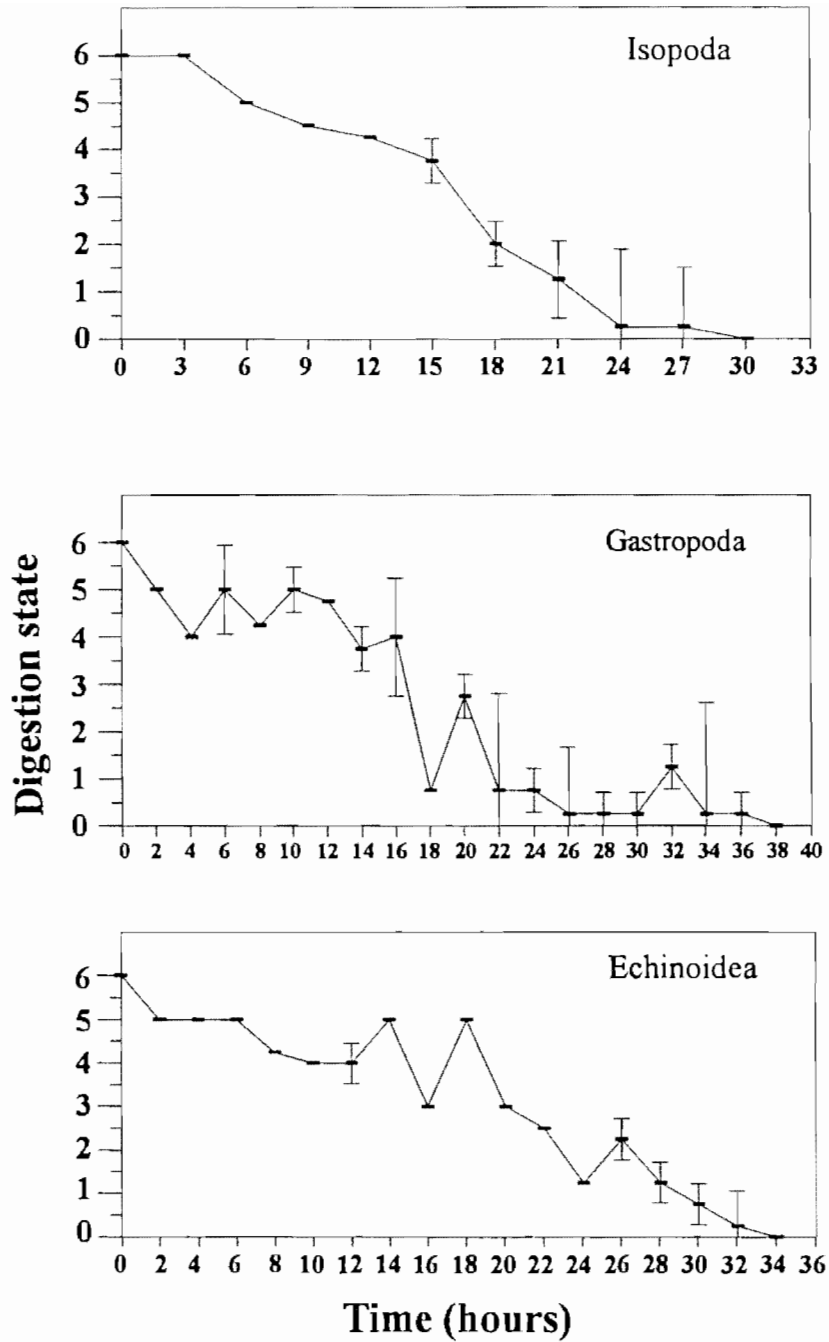


Fig. 3.6: Time taken for *Pseudactinia varia* from Wooley's Pool to digest three food items commonly found in their diets. Results were obtained from a weighted running mean of the three replicates. S.D. is also given. The digestion states are described in Table 3.1.

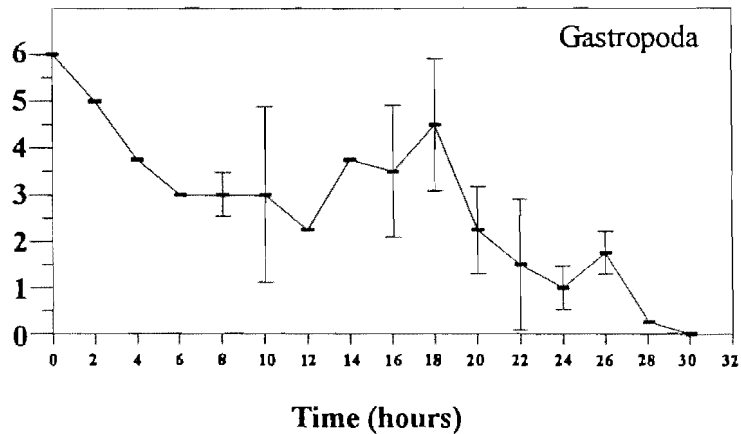
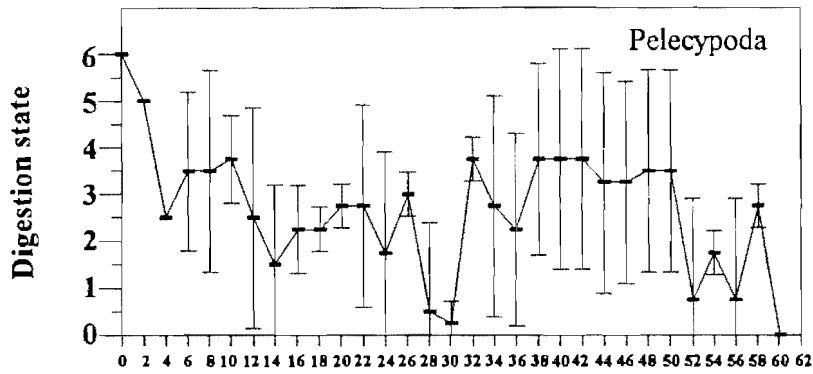
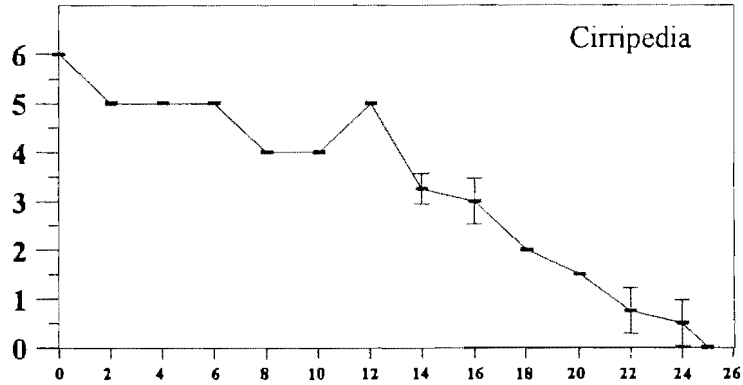


Fig. 3.7: Digestion rates of the three prey items most frequently consumed by *Bunodactis reynaudi* at Wooley's Pool. The points represent the weighted running mean of the digestion state of the prey items of three anemones at each time interval. S.D. is also shown. The key of the digestion states is given in Table 3.1.

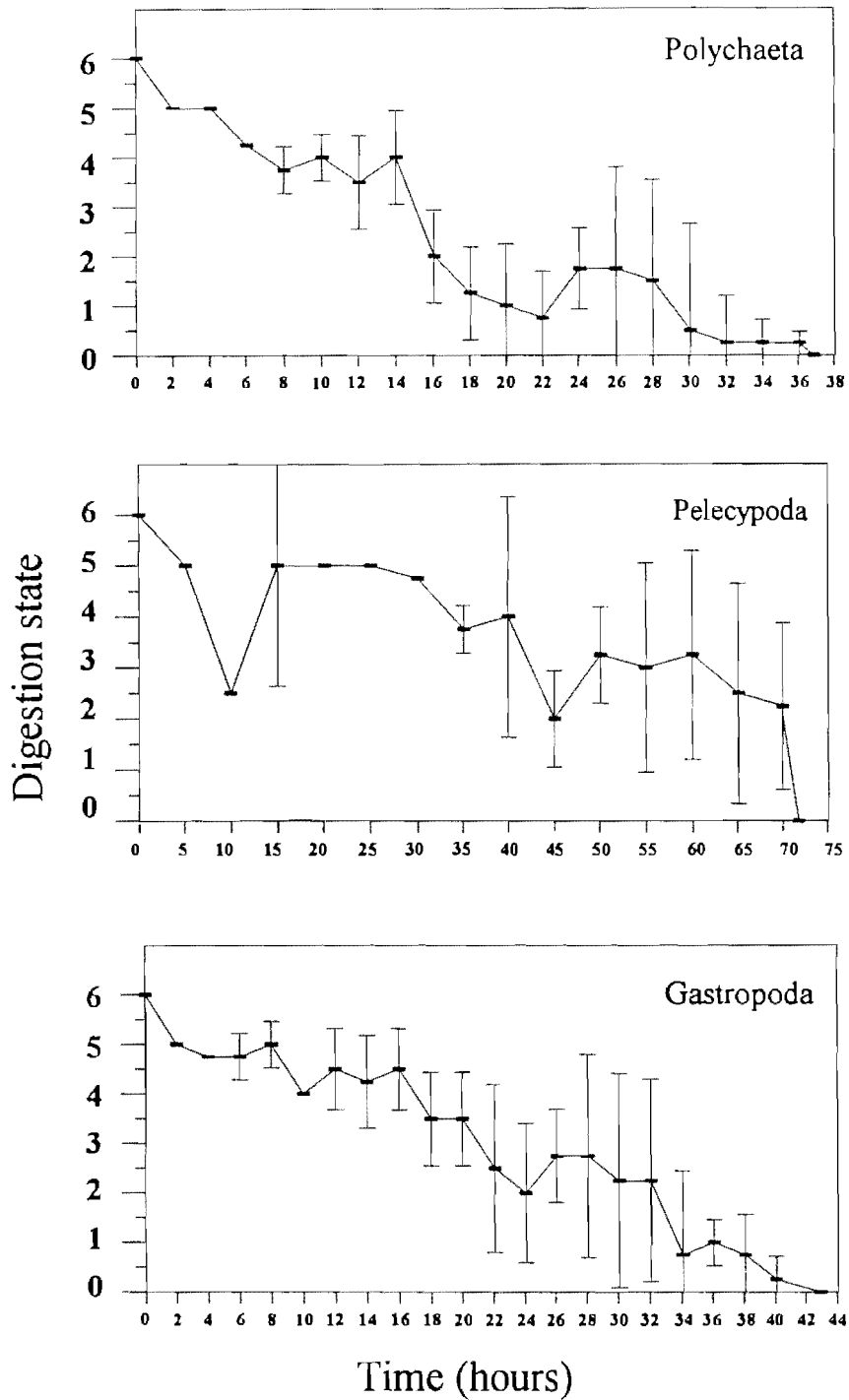


Fig. 3.8: The rate of digestion of the three most commonly consumed prey categories of *Bunodactis reynaudi* from Blouberg. The index of digestion state of the prey is given in Table 3.1. Points represent the weighted running mean of the digestion state of the prey consumed by three anemones at each time interval. S.D. is also given.

Table 3.3: Multiple comparison analysis (Tukey test) of the digestion rate of pelecypods consumed by anemones maintained at 17°C. A significant difference, at the 5% level, is apparent between *Actinia equina* and *Bunodactis reynaudi*. The homogeneous group (*) represents the level of similarity between the different species. Overlap between these groups represents a degree of similarity between the digestion rates of the different species.

Anemone species	Average digestion time	Homogeneous group
<i>Actinia equina</i>	11.67	*
<i>Anthopleura michaelseni</i>	23.67	* *
<i>Pseudactinia flagellifera</i>	37.00	* * *
<i>Bunodactis reynaudi</i>	42.33	*

Table 3.4: Multiple pairwise comparisons (Tukey test) of the time taken by anemone species from Wooley's Pool (17°C) to digest isopods. There is a significant difference in the digestion times of *Actinia equina* and *Bunodactis reynaudi* ($P < 0.05$)

Anemone species	Average digestion time	Homogeneous group
<i>Actinia equina</i>	19.67	*
<i>Pseudactinia flagellifera</i>	23.00	* *
<i>Bunodactis reynaudi</i> (Wooley's Pool)	24.00	* *
<i>Anthopleura michaelseni</i>	27.33	* *
<i>Bunodactis reynaudi</i>	33.33	*

There was no significant difference in the digestion rates of the other species from Wooley's Pool. *A. stimpsoni* took an average of 28 hours to digest isopods (*Cirolana* sp.) and 30 hours for gastropods (*Tricolia capensis*) (Fig. 3.2). The time taken for *Anthopleura michaelseni* to digest prey items varied from 26 hours for the gastropod *Burnupena cincta*, to 29 hours for the cirriped *Tetraclita serrata* and 32 hours for the pelecypod *Mytilus galloprovincialis* (Fig. 3.3). *B. capensis* took an average of 23 hours to completely digest the amphipod *P. capensis* and 27 hours for the isopod *Cirolana* sp. (Fig. 3.4). The gastropod *B. cincta* was voided 33 hours after ingestion by *P. flagellifera*, the isopod *Cirolana* sp. after 29 hours, and the pelecypod *M. galloprovincialis* after 47 hours (Fig. 3.5). Digestion rates for *P. varia*

were: 38 hours for *B. cincta*, 30 hours for *Cirolana* sp. and 34 hours for the echinoderm *Parechinus angulosus* (Fig. 3.6). The average time taken for *B. reynaudi* from Wooley's Pool, held at 17°C, to digest the cirriped *Tetraclita serrata* was 25 hours, while *B. cincta* (isopod) and *M. galloprovincialis* (pelecypod) took longer, at 30 and 60 hours respectively (Fig. 3.7).

The sample of *B. reynaudi* from Blouberg, held at 12°C, digested prey more slowly than any of the Wooley's Pool species. The rate of digestion by *B. reynaudi* of both pelecypods and gastropods at the two different sites was significantly different ($P < 0.001$, Mann-Whitney, Zar, 1984). The remains of the polychaete *Pseudonereis variegata* were voided after an average of 37 hours (Fig. 3.8). *B. cincta* and *M. galloprovincialis* took longer to be digested (43 and 72 hours respectively) than those eaten by the same anemone species at 17°C. The soft-bodied polychaetes consumed by *B. reynaudi* had a more rapid rate of deterioration than the hard-shell prey (Fig. 3.8). Twenty-two hours after ingestion, only the hard indigestible parts of the polychaetes remained, while the molluscs were still virtually intact.

DISCUSSION

Many anemones fed with common prey items during the digestion rate experiments rejected the food presented to them. Feeding rates of invertebrate predators are frequently depressed by laboratory conditions (Sullivan & Reeve, 1982; Purcell & Nemazie, 1992). While some food items were grabbed with alacrity and quickly ingested, others that were found in large quantities amongst the coelenteron contents of anemones in the field, were relinquished soon after feeding. *Bunodactis reynaudi* from both Blouberg and Wooley's Pool, whose diets are dominated by black mussels (Table 2.2) had to be coaxed into accepting them. The gastropod *Burnupena papyracea*, whose shell is covered with the bryozoan *Alcyonidium nodosum*, is a common prey item of *B. reynaudi* (Wooley's Pool), *Anthopleura michaelsoni*, *Pseudactinia flagellifera* and *P. varia*, yet hand-fed individuals were very sluggish in securing this prey and always released it shortly afterwards. This behaviour suggests a distinct dislike for the bryozoan on the shell, yet the fact that they formed part of the natural diet of these anemones is perplexing. Other *Burnupena* species, not covered with the bryozoan, were eagerly accepted, but there too were often subsequently discarded.

A wide variation in both intra- and interspecific prey digestion times was evident. *A. equina* had the fastest throughput times of the seven species examined in this study, while *B. reynaudi* at Blouberg digested prey most slowly.

INTERSPECIFIC DIFFERENCES

The rapid digestion of prey by *A. equina* is most likely attributed to their position on the shore. This anemone lives high in the intertidal zone (Chapter 1) and is therefore frequently subjected to aerial exposure. Because of the periodic emersion and reduced feeding time in the upper intertidal, it is necessary for the anemones that live there to conserve energy (Branch & Newell, 1978; Shick, 1981). When emersed, *A. equina* therefore always contract (Robbins & Shick, 1980; Navarro *et al.*, 1981; Shick *et al.*, 1988) and become quiescent (Griffiths, 1977a; Shick, 1981) in order to reduce their metabolic costs when the chance of catching food is low. Furthermore, their metabolism remains aerobic, thus ensuring a more efficient utilization of food during exposure (Shick, 1981). Digestion continues during exposure (Shick *et al.*, 1988) and it is suggested that the higher temperatures encountered may result in a faster rate of digestive enzyme activity. Higher temperatures were found to reduce the throughput time in colonial hydroids (Kinne & Paffenhöfer, in Zamer, 1986). Scope for growth is larger in high shore anemones (Shick *et al.*, 1988), which suggests that it may be beneficial for *A. equina* to have a higher rate of energy turnover in order to attain a large size as quickly as possible.

A. equina is the only species in this study that broods its young. Sufficient food must therefore be assimilated, not only to sustain the adults, but also to meet the requirements of their broods. Brooded young may induce oxygen depletion within the coelenteron of the adult (Griffiths, 1977a). Because oxygen consumption decreases with increasing size (Shick, 1991) and 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.

The two *Pseudactinia* species had the slowest digestion rates of all the Wooley's Pool species. They live at the lowest levels on the shore (see chapter 1), where food is more plentiful and they are not subjected to long periods of emersion. Feeding time is thus longer and they are rarely subjected to the high temperatures experienced by the other species higher on the shore. Digestion rates are reduced at lower temperatures (Sebens, 1980; Purcell & Nemazie, 1992). It is, therefore, suggested that the digestion rates of two *Pseudactinia* species are slower because of their position on the shore.

TEMPERATURE-RELATED DIFFERENCES

Digestion times of prey consumed by *B. reynaudi* maintained at 12°C (Fig. 3.8) were consistently longer than those kept at 17°C (Fig. 3.7). Sebens (1980) noted that there is a significant relationship between temperature and feeding régime. Prey capture, as well as digestion and assimilation rates are maximized at certain optimal temperatures (Sebens, 1982b) and any change in these may significantly affect these rates. Purcell & Nemazie (1992) have shown a similar situation in the digestion rates of the hydromedusan *Nemopsis bachei*. Digestion rate is reduced at lower temperatures, due 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, 1982b). Absorption is also temperature dependent. Anemones at lower temperatures gain less weight than those in warmer conditions (Sebens, 1980).

The digestibility of prey also determines the time for which it is retained within the coelenteron (Shick, 1991). Soft-bodied prey are digested fairly rapidly (Sebens & Koehl, 1984). Polychaetes were egested far sooner than any of the shelled prey items consumed by *B. reynaudi* at Blouberg (Fig. 3.8). The rate of deterioration was also faster. The shorter throughput time for amphipods compared with isopods (Fig. 3.1) can be explained in the same way. *Paramoera capensis* is a fairly delicate amphipod (Branch *et al.*, 1994) compared to the more heavily chitinized isopod, *Cirolana* sp. The isopods also roll up into a ball when disturbed. This frequently occurred when the isopods were ingested and may have assisted in protecting the delicate ventral surface and also in reducing the surface area of the prey exposed to the "chitinase activity" (Shick, 1991), retarding digestion. Moreover the isopods fed to the anemones were larger (mean wet weight 0.04g) than the amphipods (mean wet weight 0.01g) and would therefore be expected to take longer to digest.

Crustaceans were generally digested more rapidly than hard-shelled prey. 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 cirripeds eaten by *A. michaelseni* and *B. reynaudi* from Wooley's Pool, took less time to digest than similarly sized mussels eaten by the same species (Figs 3.3 & 3.7). Pelecypods eaten by *A. equina* were the small, thin-shelled bivalve *Nucula nucleus*. These were digested far quicker than the larger, more heavy-shelled black mussel *Mytilus galloprovincialis*, fed to the other species. When fed with *M. edulis*, *A. equina* retained the prey within the coelenteron for 40-60 hours

(Dicquemare, 1773 in Shick, 1991), which concurs well with the results obtained for mussels eaten by the same anemone in this study. Anemone size does not affect the time taken to digest prey (Sebens, 1981b).

Throughput times determined for the anemones in this study were generally longer than those obtained by other authors. *Artemia* sp. consumed by *Anthopleura elegantissima* were digested within 4 hours (Zamer, 1986). Purcell (1977) found that zooplankton remains were egested by *Metridium senile* in 24-48 hours, while Sebens & Koehl (1984) noted that it took only 2-6 hours. The medusivorous anemone *Entacmaea medusivora* digested its prey in 2-24 hours (Fautin & Fitt, 1991). Scallops were egested 7-15 hours after ingestion by *Anthopleura ballii* (Minchin, 1983), and the remains of crustaceans and echinoderms in less than 24 hours after ingestion by *Stoichactis giganteum* (Herndl *et al.*, 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 that of species in the present study. The only study reporting longer retention times than those recorded 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 the 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.

Ottaway (1974) suggested that the digestive efficiency of anemones is high and that they are able to break down and absorb food rapidly. However, with very few exceptions the results obtained in this study suggested that anemones have longer retention times than most other coelenterate predators. For example copepods took between 1.6 and 9.6 hours to be digested by siphonophores (Purcell, 1983), between 1.7 and 2.2 hours by ctenophores (Sullivan & Reeve, 1982) and about 3.6 hours by the hydromedusan *Nemopsis bachei* (Purcell & Nemazie, 1992).

CHAPTER 4

SEA ANEMONES AS SECONDARY CONSUMERS ON ROCKY SHORES IN THE SOUTH-WESTERN CAPE

INTRODUCTION

Intertidal sea anemones are abundant on rocky shores around the world, and yet very few studies have addressed their ecological role as consumers within these communities. Particular aspects of the energetics of sea anemones have been examined by various authors - for example oxygen uptake rates were measured in *Actinia equina* by Griffiths (1977 a, b) and in *Metridium senile* and *Anthopleura elegantissima* by Shick *et al.* (1979). Sebens (1981b) noted that prey capture in *A. xanthogrammica* depends on the feeding surface area. 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 Praët (1983), Ayre (1984) and Littler *et al.* (1991) have examined the diets of various anemone species. *A. elegantissima* is, however, the only anemone where several components of the energy budget have been quantified (Shick *et al.*, 1988). Integrated energy budgets have only been measured for *Aiptasia pulchella* (Hunter, 1984) and *A. elegantissima* (Zamer & Shick, 1987).

Several studies have attempted to determine energy flow through rocky shore ecosystems in the south-western Cape (Branch & Griffiths, 1988; Field & Griffiths, 1991; Griffiths & Branch, 1991). Sea anemones have frequently featured in these reports, but to date little is known of their feeding biology or ecological significance. From existing information (Branch & Griffiths, 1988; Field & Griffiths, 1991;) and the abundance measurements obtained in Chapter 1, it is apparent that anemones can be prominent members of rocky shore assemblages in the south-western Cape. Information to determine the impact of this group as consumers in these systems is, however, lacking. None of the anemones examined in this study were found to contain symbiotic zooxanthellae within their tissues (Chapter 2), which suggests that all their energy requirements are met by the prey that they capture. The high densities in which anemones are frequently found suggests that they could have a considerable impact on local prey populations. From information obtained during this study, it is now possible to calculate their population consumption.

Using the abundance data obtained in Chapter 1, together with the information of the actual prey consumed by the anemones (Chapter 2) and the turnover times for the different prey items (Chapter 3), an attempt is made below to give the first quantitative estimate of annual consumption rates of each species. 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

To determine the quantitative importance of seven species of intertidal sea anemones as secondary consumers in rocky shore ecosystems, anemone assemblages from two sites in the south-western Cape, Wooley's Pool in False Bay and Blouberg in Table Bay (Fig. 1.1), were examined.

Line transects were used at each site to estimate the abundance and distribution patterns of the different anemone species (Chapter 1). The diets of the anemones at the two sites were investigated by means of gut content analysis (Chapter 2). This provided information on the types of prey most frequently consumed by each species and also the quantities (in terms of mass) in which they were captured. From these results it was apparent that the anemones can be grouped into four distinct feeding groups. *Anthothoe stimpsoni* is microphagous, *Actinia equina* and *Bunodosoma capensis* are both generalists, *Bunodactis reynaudi* from Wooley's Pool, *Anthopleura michaelseni* and *Pseudactinia flagellifera* and *P.varia* are macrophagous, while *B. reynaudi* from Blouberg feeds predominantly on bivalves (specialist bivalve-feeder).

To estimate the quantity of natural prey consumed per unit time, it was necessary to determine the turnover time of the prey items. Digestion rates of the most frequently consumed prey items were therefore assessed by feeding the anemones with each and noting the length of time that it took before the food bolus was egested (Chapter 3). These rates were then used to estimate number of turnovers per year and hence annual consumption rates. In these calculations it was assumed that the digestion rate of each prey item is constant in one year and that prey turnover time is dependent on the relative size of prey to anemone.

The annual consumption of a particular prey item by each species was estimated as:

Average number of prey item in coelenteron \times turnovers per year \times anemone abundance (m^{-1})

The overall annual consumption of anemones as a group was also determined by combining the annual consumption estimates of the different species at each site.

RESULTS

Previously established measures used to determine the annual consumption of prey types by the seven species of sea anemones examined are presented in Table 4.1. In this table, the number of anemones for which coelenteron contents were examined, their preferred prey categories and the rate at which these are digested, together with the anemone abundance per linear metre of shore are given. Anemone densities at the Wooley's Pool site varied from 5 per linear metre (m^{-1}) in *Pseudactinia varia* to 466 m^{-1} for *Anthothoe stimpsoni*. The average density of *Bunodactis reynaudi* (the only species found at Blouberg) was 901 m^{-1} (Chapter 1). The consumption rates of the anemone species at each site are discussed individually below:

WOOLEY'S POOL

Actinia equina

Examination of the diets of 87 *A. equina* showed pelecypods to be the most abundant dietary item (0.77 per individual), followed by isopods (0.25) and then amphipods (0.15). However, since digestion times for isopods, at 23 hours, were almost double those of amphipods (12 hours), individual annual consumption rates of amphipods (110 per annum) were greater than those of isopods (95 per annum). Bivalves, mostly the tiny *Nucula nucleus*, 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% or 27 000 were bivalves - the highest of all species studied.

Anthothoe stimpsoni

The diets of a sample of 185 *A. stimpsoni* were analysed. Isopods were the most abundant component in the diet (0.63 per individual), while gastropods were considerably less frequent (0.06 per individual). Turnover times of the prey were similar (28 hours for isopods and 30 hours for gastropods) and consequently the annual consumption of isopods (197 per anemone) greatly exceeded that of gastropods

Table 4.1: Consumption rates of seven species of intertidal sea anemones from two sites in the south-western Cape. 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 Chapter 2, is also included. The number of prey eaten per anemone per year is the product of turnovers per year 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.

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	0.25	23 \pm 0.61	381	95	60	5 715
	Amphipoda	0.15	12 \pm 0.58	730	110	60	6 600
	Pelecypoda	0.77	15 \pm 0.48	584	450	60	27 000
<i>Anthothoe stimpsoni</i> (N=185)	Isopoda	0.63	28 \pm 0.67	313	197	466	91 891
	Gastropoda	0.06	30 \pm 0.91	292	18	466	81 64
<i>Anthopleura michaelsoni</i> (N=57)	Cirripedia	0.61	29 \pm 1.36	302	184	25	4 600
	Pelecypoda	0.18	32 \pm 1.23	274	49	25	1 225
	Gastropoda	1.23	26 \pm 1.09	337	415	25	10 363
<i>Bunodosoma capensis</i> (N=72)	Isopoda	0.19	27 \pm 1.24	324	62	35	2 155
	Amphipoda	0.19	23 \pm 0.85	381	72	35	2 520
<i>Pseudactinia flagellifera</i> (N=59)	Isopoda	0.36	29 \pm 0.66	302	109	18	1 957
	Pelecypoda	0.22	47 \pm 1.44	186	41	18	738
	Gastropoda	0.55	33 \pm 0.37	265	146	18	2 628
<i>Pseudactinia varia</i> (N=60)	Isopoda	0.19	30 \pm 0.63	292	55	5	275
	Gastropoda	0.96	38 \pm 0.61	231	222	5	1 110
	Echinoidea	0.15	34 \pm 0.34	258	39	5	195
<i>Bunodactis reynaudi</i> (N=65)	Cirripedia	0.94	25 \pm 0.16	350	329	49	16 121
	Pelecypoda	0.85	60 \pm 1.51	146	124	49	6 076
	Gastropoda	0.44	30 \pm 0.69	292	128	49	6 272
BLOUBERG							
<i>Bunodactis reynaudi</i> (N=90)	Polychaeta	0.18	37 \pm 0.93	237	43	901	38 437
	Pelecypoda	1.18	72 \pm 1.11	122	144	901	129 744
	Gastropoda	0.63	43 \pm 1.09	204	129	901	116 229

(18 per anemone). *A. stimpsoni* is the most abundant anemone at this site (466 m⁻¹) and as a result of this has the highest population consumption (100 055 prey items m⁻¹ y⁻¹) of all species at Wooley's Pool. Isopods accounted for 92% or 91 891 of this annually.

Anthopleura michaelseni

Gastropods were the most important group in the diets of 57 *A. michaelseni* and were consumed (1.23 per anemone) twice as frequently as cirripedes (0.61 per anemone), while pelecypods were relatively scarce (0.18 per anemone). Turnover times were not markedly different, but gastropods were digested slightly faster (26 hours) than cirripedes (29 hours). Because of this quicker digestion rate, however, gastropods remained the most important food item (415 per anemone y⁻¹) forming 64% (or 10 363 m⁻¹ y⁻¹) of the total population consumption per year (16 188 prey items), while cirripedes contributed only 28% (4 600 m⁻¹ y⁻¹). Overall *A. michaelseni* was the most important consumer of gastropods at Wooley's Pool.

Bunodosoma capensis

The diets of 72 specimens revealed that no particular prey item dominated the diet. Isopods and amphipods were consumed in relatively low quantities and with equal frequency (0.19 per individual anemone). Turnover times for the two prey items were similar - amphipods being digested in 23 hours, while isopods took slightly longer (27 hours). Because of the low occurrence of these prey items in the guts, the estimated amount of prey consumed annually by this species is low (62 isopods and 72 amphipods per anemone). The overall population of 35 *B. capensis* m⁻¹ consumed 2 520 amphipods m⁻¹ y⁻¹ and 2 155 isopods m⁻¹ y⁻¹.

Pseudactinia flagellifera

The diets of 59 *P. flagellifera* were investigated. Gastropods were the most abundant prey item in the diets (0.55 per individual), followed by isopods (0.36 per individual) and then pelecypods (0.22 per individual). Pelecypods had the longest turnover time (47 hours) and consequently contributed only 14% or 738 to the annual population consumption of 5 323 prey items. Gastropods made up nearly half (49% or 2 628 m⁻¹) of the dietary items consumed by the population. However, because isopods were digested more rapidly (29 hours) than gastropods (33 hours), their proportional contribution to the total population consumption was enhanced to 37% or 1 957 m⁻¹ y⁻¹.

Pseudactinia varia

The examination of 60 *P. varia* revealed that gastropods were the most common items (0.96 per anemone) in the diet, while isopods and echinoderms were consumed far less frequently (0.19 and 0.15 per anemone respectively). Isopods had the fastest turnover time (30 hours), while gastropods were the slowest prey item to be digested (38 hours). 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 anemone species (5 m^{-1} of shore) and hence the annual consumption by this population was the lowest of all the anemone species examined at 1 580 items $m^{-1} y^{-1}$, of which 70% or 1 110 were gastropods.

Bunodactis reynaudi

Cirripedes featured as the most frequently consumed prey item (0.94 per individual) in the diets of the 65 *B. reynaudi* that were examined from Wooley's Pool. These were followed closely by pelecypods (0.85 per individual), while gastropods were less common (0.44 per individual). However, because pelecypods took at least twice as long (60 hours) as the other food items to be digested (25 and 30 hours for cirripedes and gastropods respectively), their individual annual consumption (124 per anemone) was considerably less than the rate for cirripedes (329 per anemone) and was in fact also lower than the rate for gastropods. Cirripedes made up 57% or 16 121 m^{-1} of the total annual population consumption of 28 469 m^{-1} , while 21% or 6 076 m^{-1} were pelecypods and 22% or 6 272 m^{-1} were gastropods.

BLOUBERG

Bunodactis reynaudi

The diets of 90 *B. reynaudi* were examined at this site. Results indicated that pelecypods were the dominant prey item in the diet (1.18 per individual), being consumed more than twice as often as gastropods (0.63 per individual). Polychaetes were less frequent in the guts (averaging 0.18 per anemone). Despite the fact that these soft-bodied prey were digested in half the time (37 hours) of the shelled pelecypods (72 hours), their annual consumption remained low (43 per anemone y^{-1}). Pelecypods still remained the most frequently ingested prey item (144 y^{-1}), however, the faster turnover time of gastropods (43 hours) increased their individual consumption to 129 per annum. Because of the very high abundance of *B. reynaudi* at Blouberg (901 m^{-1}), population consumption of prey at this site was exceedingly high (28 4410 $m^{-1} y^{-1}$). Both pelecypods and gastropods were consumed in very large quantities (129 744 $m^{-1} y^{-1}$ and 116 229 $m^{-1} y^{-1}$ respectively, equivalent to 46% and 41% of the annual population consumption respectively).

If the density of anemones at the Blouberg site (901 m^{-1}) is taken into account, the importance of pelecypods (144 per individual y^{-1}) and gastropods (129 individual $^{-1} \text{ y}^{-1}$) in the diet of *B. reynaudi* is consistent with consumption rates for these prey groups by *B. reynaudi* at Wooley's Pool (124 and 128 individual $^{-1} \text{ y}^{-1}$ respectively).

TOTAL ANNUAL CONSUMPTION

Total annual consumption of the major prey groups by anemones are shown in Table 4.2. Only groups that occurred in at least 10% of the gut contents of at least one anemone species were considered. Digestion rates of certain prey groups were determined experimentally (Chapter 3) for each anemone species. The turnover times of food items not established experimentally were calculated in the following manner:

1) If the digestion rate had been determined experimentally for other anemone species, but not for the one in question, the turnover time was taken to be the mean rate obtained from all the species 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. Total numbers of prey eaten by the different sea anemones species at each of the two sites are presented in Table 4.2.

While prey from a particular group was often consumed by several anemone species, most food categories formed the bulk of the diet of only one or two of these species. For example at Wooley's Pool, the number of isopods eaten by *A. stimpsoni* ($91\ 891 \text{ m}^{-1} \text{ y}^{-1}$) was far greater than the number consumed by other species. Even if the high abundance of *A. stimpsoni* (466 m^{-1}) is taken into account, the number of isopods consumed per anemone per year still surpasses that of the other species (Table 4.1). *A. stimpsoni* consumes (197) more than double that of *A. equina* (95) and more than three times the amount eaten by *B. capensis* (62).

The important consumers of amphipods were *A. equina* ($6\ 600 \text{ m}^{-1}$) followed by *A. stimpsoni* ($4\ 660 \text{ m}^{-1}$) and then *B. capensis* ($2\ 520 \text{ m}^{-1}$).

Only two anemone species were significant consumers of cirripedes with *B. reynaudi* by far the most important of these ($16\ 121 \text{ m}^{-1}$) followed by *A. michaelsoni* ($4\ 600 \text{ m}^{-1}$).

Table 4.2: 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
WOOLEY'S POOL									
<i>Actinia equina</i>	5 715	6600	-	27 000	(480)	-	(660)	(9 060)	-
<i>Anothoe stimpsoni</i>	91 891	(4 660)	-	(4 194)	8 164	-	(16 398)	-	-
<i>Anthopleura michaelseni</i>	(1 050)	(250)	4 600	1 225	10 363	(375)	(175)	-	-
<i>Bunodosoma capensis</i>	2 155	2 520	-	(875)	(1 085)	(210)	(875)	(630)	-
<i>Pseudactinia flagellifera</i>	1 957	(738)	(234)	738	2 628	(954)	-	-	-
<i>Pseudactinia varia</i>	275	(205)	(95)	(360)	1 110	195	(70)	(70)	(105)
<i>Bunodactis reynaudi</i>	(294)	-	16 121	6 076	6 272	(294)	-	(343)	(1 715)
TOTAL	103 337	14 973	21 050	40 468	30 102	2 028	3 178	10 103	1 820
BLOUBERG									
<i>Bunodactis reynaudi</i>	(14 416)	(8 109)	-	129 744	116 229	-	38 437	-	(8 109)

Table 4.3: 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	2 586.2	17 229.8	3 050.9	16.2	7 505.5	30 851.1
Blouberg	49.8	17.7	-	82 482.6	66 527.3	-	196.4	33 010.1	182 283.9

The greatest proportion of pelecypods ingested at Wooley's Pool were eaten by *A. equina* ($27\,000\text{ m}^{-1}\text{ y}^{-1}$). This was more than four times the number consumed by *B. reynaudi* ($6\,076\text{ m}^{-1}\text{ y}^{-1}$). Even when the anemone density is taken into account, *A. equina*, that is more abundant (60 m^{-1}) than the other species, still consumed more pelecypods (450 per anemone y^{-1}) than the other Wooley's Pool species - *B. reynaudi* that consumed more than the remaining species, ingested only 124 pelecypods per year (Table 4.1).

More gastropods were consumed by *A. michaelsoni* ($10\,363\text{ m}^{-1}\text{ y}^{-1}$) than any of the other species at Wooley's Pool. *A. simpsoni* consumed $8\,164\text{ m}^{-1}\text{ y}^{-1}$, while *P. varia* ate the least, almost ten times less than the amount consumed by *A. michaelsoni* ($1\,110\text{ m}^{-1}\text{ y}^{-1}$). If however, the anemone abundance is taken into account (Table 4.1) and only the annual consumption per anemone is considered, the ranking of anemones that most frequently consumed gastropods, is changed. *A. michaelsoni* remained the principal consumer of gastropods (415 anemone $^{-1}\text{ y}^{-1}$). However, *P. varia* that ingested 222 gastropods per anemone per year follows next, and *A. simpsoni* now ranks last, since each anemone consumed only 18 gastropods per year.

Turning to the overall numbers of prey items consumed by the anemone assemblages. Isopods are the prey group most heavily exploited by anemones at Wooley's Pool ($103\,337\text{ m}^{-1}\text{ y}^{-1}$). The number consumed is 2.5 times more than the number of pelecypods (the second most important prey item) ingested and almost 3.5 times the number of gastropods, which ranked third. These are followed, by cirripedes ($21\,050\text{ m}^{-1}\text{ y}^{-1}$) then amphipods ($14\,973\text{ m}^{-1}\text{ y}^{-1}$) and insects ($10\,103\text{ m}^{-1}\text{ y}^{-1}$).

At Blouberg, pelecypods were the most abundant food group ($129\,744\text{ m}^{-1}\text{ y}^{-1}$). Gastropods however, also featured as a major component in the diet of *B. reynaudi* ($116\,229\text{ m}^{-1}\text{ y}^{-1}$). They were consumed three times more frequently than polychaetes ($38\,437\text{ m}^{-1}\text{ y}^{-1}$) and eight times more often than isopods ($14\,416\text{ m}^{-1}\text{ y}^{-1}$). Amphipods and crabs were consumed in equal quantities ($8\,109\text{ m}^{-1}\text{ y}^{-1}$).

Overall annual energy values of the major prey groups eaten by anemones at the two study sites are presented in Table 4.3. In terms of the energetic contribution to the requirements of anemones at Wooley's Pool, gastropods constitute the most important prey group ($17\,229.8\text{ kJ m}^{-2}\text{ y}^{-1}$ 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 prey items, isopods, yielded only $357.2\text{ kJ m}^{-2}\text{ y}^{-1}$.

Pelecypods (45%) and gastropods (36%) contributed most to the energetic requirements of anemones at Blouberg (82 482.6 kJ m⁻² y⁻¹ and 66 527.3 kJ m⁻² y⁻¹ respectively). Crabs (brachyura) are similarly important contributors (18%) to the energetic input of anemones at this site (33 010.1 kJ m⁻² y⁻¹), whereas polychaetes, which were the third most frequently consumed group, supplied only 196.4 kJ m⁻² y⁻¹ or 0.1% of the overall energetic contribution. The total overall consumption rates of all the major prey items consumed by anemones are estimated as 30 851.1 kJ m⁻² y⁻¹ and 182.283.9 kJ m⁻² y⁻¹ for Wooley's Pool and Blouberg respectively. This suggests that the total energetic content of prey populations sustaining the anemone assemblages at Blouberg, is nearly six times that which occurs at Wooley's Pool.

DISCUSSION

Most dietary studies simply document gut contents and assume these provide a true reflection of the diet. Merely examining the prey in the coelenteron is, however, insufficient, as it assumes that the turnover time is the same for each prey item, a situation that is known not to be true (Peterson & Bradley, 1978). By incorporating the turnover times of the various prey items, the overall picture of the actual diet eaten by different consumers can be estimated more accurately (Sullivan & Reeve, 1982), and hence their impact on the prey that they consume assessed. The energy flow through the system can then also be ascertained.

The initial study of the diets of intertidal sea anemones from two sites in the southwestern Cape, led to the conclusion that they could be separated into four distinct feeding groups (see Chapter 1). *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 michaelseni*, *Pseudactinia flagellifera* and *P. varia* were deemed to be macrophagous feeders, while *B. reynaudi* from Blouberg was found to be a specialist bivalve-feeder. When the turnover times of the different prey items are taken into account however, some of these conclusions are modified. *A. stimpsoni* is still essentially microphagous, depending to a large extent on isopods. *B. capensis* remains, 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 4.1). The pelecypods examined were the tiny bivalve *Nucula nucleus* (Table 3.2), the mass of which is very small. In order to derive sufficient nutritional benefit from this prey therefore, they

need to be consumed in very large numbers. The isopods and amphipods that were tested (*Cirolana* sp. and *Paramoera capensis* respectively) were of a similar mean size (0.04g and 0.03g respectively) and were found to be consumed in similar quantities. The macrophagous group remained unaltered. Generally, the number of prey captured by these species was lower than that consumed by the microphagous or generalist species. Since the prey is larger, fewer need to be consumed to meet the energy requirements of the anemones. Taking turnover time into account suggests that gastropods are also an important component in the diet of *B. reynaudi* from Blouberg, which originally appeared to be essentially a mussel-feeder. Although the quantity of mussels consumed by this species annually is still exceedingly high ($129\ 744\ m^{-1}$), the number of gastropods that were eaten was also very large ($116\ 229\ m^{-1}$).

The number of isopods consumed by the anemones appears to increase with increased height up the shore. *A. simpsoni*, found at the highest levels on the shore (Chapter 1), ate more isopods than any other species, followed by *A. equina* and *B. capensis* which occurred at lower shore levels. The two low shore species - *P. flagellifera* and *P. varia* utilize fewer isopods. The high number of isopods captured by *A. simpsoni* may merely be a result of the motility of the isopods. They may become trapped in the rock pools that *A. simpsoni* occupies when the tide recedes and be caught by the anemones whilst swimming about. A similar situation may occur in the cracks and crevices occupied by *A. equina* and *B. capensis*. The two *Pseudactinia* species are more likely to encounter larger prey that would provide more energy than a small isopod.

Although only one species, *B. reynaudi* occurred at Blouberg, its density greatly exceeded the combined densities of all the anemones at Wooley's Pool (Chapter 1). This vastly increased abundance may be attributed to the presence of larger quantities of food items. Pelecypods (mainly the mussel *Mytilus galloprovincialis* (Table 3.2)) are a major component of the diet of this species, particularly at this site. The shore at Blouberg is exposed (Chapter 1), with much stronger wave action and consequently a higher biomass of filter-feeders (McQuaid & Branch, 1985, Field & Griffiths; 1991; Emanuel *et al.*, 1992) than the more sheltered Wooley's Pool site. Filter-feeders make up 72% of the total animal standing stock on the west coast (Newell *et al.*, 1982) and only between 5.5% and 57%, depending on the degree of wave action, in False Bay (Griffiths & Branch, 1991). Because of the increased wave action at this site, not only are there more mussels present, but they are more likely to be dislodged and tumbled around and hence may become available as prey to the anemones (Branch & Griffiths, 1988). Intraspecific competition for space is one of the principal causes of mortality in mussel populations (Griffiths, 1990). Growth rates at Blouberg are also high due to the

lower water temperature (Griffiths, 1981) and hence more self-thinning occurs, thus making more food available to the anemones. The number of pelecypods consumed by anemones at Blouberg greatly exceeds that at Wooley's Pool (Table 4.2). However, because of the greater abundance of anemones at the former site, the annual consumption per individual *B. reynaudi* is similar at the two sites.

Comparison of the ratio of the number of mussels (see Chapter 1) to the number of anemones present at each site, revealed that the number of mussels per anemone at Wooley's Pool is 2.1 fold greater than the corresponding value at Blouberg. However, because annual per capita consumption rates are similar (Table 4.1), this suggests that the actual proportion of mussels which are available for consumption by anemones is greater at Blouberg than at Wooley's Pool. This is because of the stronger wave action at Blouberg, which acts to dislodge mussels and so increase the fraction of the mussel population that constitute potential prey for the anemones. In assessing the maximum anemone density a habitat can sustain, it is therefore important to consider not only the absolute quantity of prey, but rather the proportion of prey which is actually available to the anemone. Van Erkom Schurink & Griffiths (1990) also noted that extensive mussel beds extend well into the subtidal zone at this site, and consequently their assessment of mussel stocks may underestimate the number of mussels that are actually present.

The number of gastropods consumed by the *B. reynaudi* population at Blouberg is considerably greater than at Wooley's Pool (Table 4.1). *Burnupena* sp. densities at the latter site are 27 per square meter, versus 35 per square meter at the former site (Van Herwerden, 1989). If the consumption rate per anemone at each site are considered, the results are almost identical (Table 4.1). While it is not possible to determine the impact of *B. reynaudi* on the gastropod populations from these data, it does suggest that mussels are the more important food source in sustaining the population.

The above discussion does not suggest that anemones are selective in the prey that they capture, but certain prey items are eaten in greater quantities than others (Chapter 2). This may result from an abundance of anemones in a particular area or a large quantity of a particular prey type, or because of the behaviour of either the anemones or the prey. The amount of food ingested by anemones is highly stochastic (Sebens, 1982b; Shick, 1991) and the frequency with which large prey are caught by anemones is generally extremely low. Sebens (1982b) estimated that *Anthopleura xanthogrammica* only captures a mussel every three to five days. This corresponds well with estimated prey capture rates of *B. reynaudi*, whose morphology, behaviour and habitat closely

resemble that of *A. xanthogrammica*, and which was found to ingest a mussel approximately every three days (Table 4.1). Anemones eat approximately the same daily ration, relative to their mass, as other similarly-sized, carnivorous marine invertebrates (Conover, 1978 in Shick, 1991).

It is of interest to compare the consumption rates of sea anemones with those of other predators occurring in the same area. Three invertebrate predators, the rock lobster *Jasus lalandii*, the starfish *Marthasterias glacialis* and the gastropod *Nucella cingulata* have been studied previously, and their effect on mussel (*Choromytilus meridionalis*) populations at various sites on the Cape Peninsula established. Results of these studies, together with the consumption rates of the anemone species that frequently consume mussels (*Mytilus galloprovincialis*) are presented in Table 4.4.

Table 4.4: 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 & Griffiths (1984) and *Nucella cingulata* from Wickens & Griffiths (1985).

Predator	Density per square metre	Number of prey per predator per day	Population consumption (No m ⁻² . y ⁻¹)
Anemones (Wooley's Pool)	16.5	0.17	1 024
Anemones (Blouberg)	712	0.39	101 353
<i>Jasus lalandii</i>	0.5	107	19 528
<i>Marthasterias glacialis</i>	6	0.84	1 840
<i>Nucella cingulata</i>	492	0.08	14 366

It is recognized that these predators were examined in areas where their abundance is maximal and that consumption rates obtained experimentally may be substantially overestimated. In the field there is only partial overlap in the distribution of the different predator species and where they do coexist, their densities are often greatly reduced. However, these data are considered to be acceptable for the comparative purposes of this study.

The three predators *J. lalandii*, *M. glacialis* and *N. cingulata* have all been shown to have a considerable impact on *C. meridionalis* populations in the areas where they were studied (Penney & Griffiths, 1984; Wickens & Griffiths, 1985). Each predator was found to be strongly size selective, with most of the predation being directed at the

smaller size classes ($< 50\text{mm}$) (Griffiths & Hockey, 1987). Comparing the annual consumption of mussels by anemones with those of other invertebrates known to affect the structure of mussel populations, it is evident that the anemones (*B. reynaudi*) are capable of consuming at least five times more mussels than *J. lalandii*, notably one of the most conspicuous predators of mussels in the south-western Cape (Griffiths & Hockey, 1987). However, because anemones are passive sessile feeders (Sebens, 1982a) and the vast majority of the mussels that they capture are loose individuals with virtually no chance of survival (Branch & Griffiths, 1988), they are not likely to have any effect on the structuring of the mussel population. Griffiths & Hockey (1987) calculated the losses in production of the mussel *C. meridionalis*, due to competition for space (self-thinning) at several sites in the south-western Cape, and estimated that 83.7% of the total mussel production is lost as a result of self-thinning. These mussels are then potentially available to the anemones as prey. Calculations to determine the proportion of this food utilized by the anemones, indicated that more than a quarter of the mussels that are accessible due to this self-thinning process are consumed by anemones at Blouberg (Table 4.5). At Wooley's Pool however, anemones eat approximately five times more mussels than are made available by this process. This suggests that other factors, such as, battering by rocks or debris, the foraging behaviour of motile predators, or humans collecting food or bait, by which mussels may also be dislodged, that have not been considered here, must be more important at this site. Mussel consumption by anemones at Wooley's Pool may also have been exaggerated because the anemones living within the mussel beds were not included in the density estimates, as they were at Blouberg (Chapter 1). Despite these limitations however, it is apparent that anemone consumption is significant and mussels loosened by self-thinning are an important food source for sea anemones. However, because most of these are likely to become stranded and hence be lost to the system, despite the large numbers in which they are consumed, anemones will have no effect on mussel population structure.

The barnacle *Tetraclita serrata* is the primary food-source of another gastropod, *Nucella dubia* (McQuaid, 1985). It has a relatively slow consumption rate (0.02 barnacles $\text{whelk}^{-1} \text{ day}^{-1}$), but because it is very abundant (86 m^{-2}), the annual population consumption is $678 \text{ barnacles m}^{-2}$, which McQuaid calculated to be 45% of the barnacle standing stock per year. The two anemone species for which data on *T. serrata* consumption are available are, *B. reynaudi* and *A. michaelsoni* from Wooley's Pool. These were found to eat 1 314 and 368 barnacles $\text{m}^{-2} \text{ year}^{-1}$ respectively, which suggests that the potential consumption of *B. reynaudi* is nearly twice that of *N. dubia*. However, the situation with respect to barnacles is the same as

that for bivalves consumed by anemones. All of those captured will be wave-tumbled, having been dislodged from the rocks, with little chance of survival and hence *B. reynaudi* will have no impact on the barnacle population.

Table 4.5: Anemone mussel consumption compared with mussel numbers available due to self-thinning. All size classes of both anemones and mussels are represented. Mussels numbers (from Van Erkom Schurink & Griffiths, 1990) were presumed to represent the 16.7% that survive intraspecific competition for space (Griffiths & Hockey, 1987) and were therefore converted to give the total stock of mussels km^{-1} . This was then reduced by 87.3% to represent the number of mussels available to the anemones due to self-thinning.

Site	Anemone density (km^{-1})	Mussel numbers consumed (km^{-1})	Number of mussels available (km^{-1})	Proportion consumed
Wooley's Pool	658×10^3	$40\,796 \times 10^3$	$8\,364 \times 10^3$	4.88
Blouberg	901×10^3	$127\,942 \times 10^3$	$493\,943 \times 10^3$	0.26

The situation concerning the consumption of motile prey is however very different, as these are often ingested alive and healthy, and are thus actually removed from the population. Isopods were the most important such prey group, in terms of numbers, eaten at Wooley's Pool (Table 4.2). Annual consumption of isopods by the anemone population at this site was estimated to be $357.2 \text{ kJ m}^{-2} \text{ y}^{-1}$ of intertidal zone (Table 4.3). Shafir & Field (1980) estimated the annual production of the predatory isopod, *Cirolana imposita* from the south-western Cape coast as $2\,229 \text{ kJ m}^{-2} \text{ y}^{-1}$. Anemones thus consume about 16% of the available isopod production. Bennett (1984) determined that intertidal fish on the south-western Cape coast exert enormous predation pressure on certain invertebrate populations. He estimated that they consume approximately 2.4% (or $350 \text{ kJ m}^{-2} \text{ y}^{-1}$) of the total invertebrate production. However, not all this production is available to fish and they are able to utilize only small crustacea, polychaetes and molluscs, consuming approximately 64% of the production of these groups. It would appear therefore that the impact that anemones could have on isopod populations could be severe. However, because they are indiscriminate, opportunistic feeders and do not actually target specific prey populations in the same way as fish, their impact is likely to be more stochastic.

In other parts of the world anemones have been shown to be significant consumers and as such may be important in controlling and indeed shaping the populations of their prey. In each of these cases however, spat or juveniles are targeted as prey. For

example, *Diadumene leucolena* from Chesapeake Bay in the USA is a voracious predator on oyster larvae and consequently has a substantial influence on oyster abundance in the area (MacKenzie, 1977). *Anthopleura ballii* on the south coast of Ireland may have a significant impact on *Pecten maximus* populations due to predation on the spat (Minchin, 1983). Similarly, *Anthothoe albocincta* in South Australia is a potential predator on abalone larvae (Shepherd & Gray, 1985).

Total overall consumption of anemones (Table 4.3) at Wooley's Pool ($30\ 851.1\ \text{kJ m}^{-2}\ \text{y}^{-1}$) and Blouberg ($182\ 283.9\ \text{kJ m}^{-2}\ \text{y}^{-1}$) are exceedingly high. When compared with energy budgets estimated for ecosystems in these regions (e.g. Newell *et al.*, 1982; Field & Griffiths, 1991) it appears that there is insufficient production compared with the amount calculated to have been consumed by the anemones. The reason for this is two-fold. Firstly, the study sites that were chosen are both areas of maximal anemone abundance. If anemone abundance was arranged over a longer length of coastline, incorporating both suitable and unsuitable sites, estimated anemone abundance and hence consumption would have been greatly reduced. Secondly, as has been mentioned previously, Van Erkom Schurink & Griffiths (1990) pointed out that extensive mussel beds on the west coast of South Africa often extend well into the sublittoral zone, sometimes to depths of over 40m and may be to hundreds of metres seaward of the low water mark. While the energy budgets mentioned above only considered mussel beds in the intertidal zone, these sublittoral beds are likely to be a major food source for the anemones - not only the mussels themselves, but also the many invertebrates that live within these beds.

From the above discussion it can be concluded that intertidal anemones in the southwestern Cape have the potential to consume very large amounts of prey. However, since they are opportunistic feeders and much of their prey is wave-tumbled and hence essentially lost to the population anyway, anemones are unlikely to feature in the structuring of sessile prey populations. However, when significant quantities of motile prey are captured, anemone predation may be a major factor in structuring prey populations.

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