AN ENERGY BUDGET FOR THE SOUTH AFRICAN ABALONE *HALIOTIS MIDAE*

by

REVITAL BARKAI

Thesis submitted in fulfilment of the requirements for the degree of M.Sc. in the Faculty of Science at the University of Cape Town.

Supervisor: Dr. C.L. Griffiths February 1987

CONTENTS

ABSTRACT

This study aims to quantify both the individual and population energy budgets of the large edible gastropod *Haliotis midae*, and is divided into three major sections. Section 1 deals with diet and section 2 the consumption rate, absorption efficiency, respiration rate and rate of ammonia excretion, each of which were measured as functions of wet body mass. Each aspect was studied using animals from two sites subject to different temperature regimes. One of these was on the western Cape coast, off Marcus Island (at 14°C) and the other on the south western Cape, Cape Hangklip (at 19°C) Fig.1. Together with the existing knowledge on growth rate and fecundity of *H. midae* (Newman, 1967 and 1968), the third section is used to convert the above parameters to energy equivalents and to compile energy budgets for the individual animals as well as for the populations in the different study sites.

The diet of the South African abalone *Haliotis midae*, was deduced by examining the gut contents of a size range of individuals collected at the study sites in both summer and winter. A total of 18 algal species

was recorded in the guts. The most important food items overall were the kelp *Ecklonia maxima* (56% by volume) and *Plocamium spp.* (21%), although several other species occurred in significant proportions in individual samples. There was little size related variation in diet over the range 65-145mm shell width, except that *Ulva sp.* formed a significantly greater proportion of the diets of smaller individuals. The proportion of kelp consumed was higher on the west coast (66%) than on the south (46%), where much more *Plocamium spp.* was taken (39% of diet vs 3%). Samples collected in summer consisted over 80% of these two species, but winter samples from both sites contained a more varied diet. A comparison between diet and the availability of food items at the study sites indicates that some are selected for and others avoided.

From feeding periodicity studies, a well developed diurnal feeding rhythm was evident, consumption being restricted to the period 16h00-08h00. Food intake averaged 8,1% wet flesh mass d^{-1} at 14°C and 11.4% at 19°C. The daily consumption rate was related to body mass by the relationships $C(g) = 0.54\ W(g)^{0.67}$ at 14°C and $C(g) = 0.35\ W(g)^{0.77}$ at 19°C. Absorption efficiency averaged 37% and was independent of body size. Equations relating respiration rate to wet body mass were : $R(\mathrm{ml02h}^{-1}) = 0.03\ W(g)^{0.83}$ at 14°C and $R = 0.03\ W^{0.94}$ at 19°C. No significant differences were detected between day and night rates or between fed and starved individuals. The rate of ammonia excretion (μmole h^{-1}) was related to wet body mass (g) by the equations $U = 0.22\ W^{0.43}$ at 14°C and $U = 0.03W^{0.85}$ at 19°C.

The energy budget of individual abalone shows that about 63% of the energy content of the food consumed (C) is lost as faeces (F) and a further 32% expended on respiration (R). Energy losses in the form of ammonia excetion are negligible, accounting for less than 1% of consumption. Some 5% of energy intake, or 13% of absorbed ration (A) is thus available for growth and reproductive output (Pg & Pr). In juveniles (<100mm) this is all allocated towards somatic growth, while in adults an increasing proportion of production is expended on reproductive output. Although feeding, respiration and exretion rates all increase with temperature the proportions of energy allocated to the various components of the energy budget appear to be consistent . Population energy budgets were calculated from density and size distribution surveys at two study sites. At Marcus Island, on the Cape west coast the population has a standing stock of 82g (wet flesh weight) m^{-2}, consumes about 3 260KJ$m^{-2}y^{-1}$ algae and has a P/B ratio of 0.46y^{-1}, whereas at Cape Hangklip, on the Cape south coast, the population biomass is 133gm^{-2}, consumes 8 613KJ$m^{-2}y^{-1}$ and has a P/B ratio of 0.70y^{-1}. These figures indicate that a high proportion of kelp bed primary production is directly consumed by grazing abalone in areas where populations have not been reduced by human exploitation.

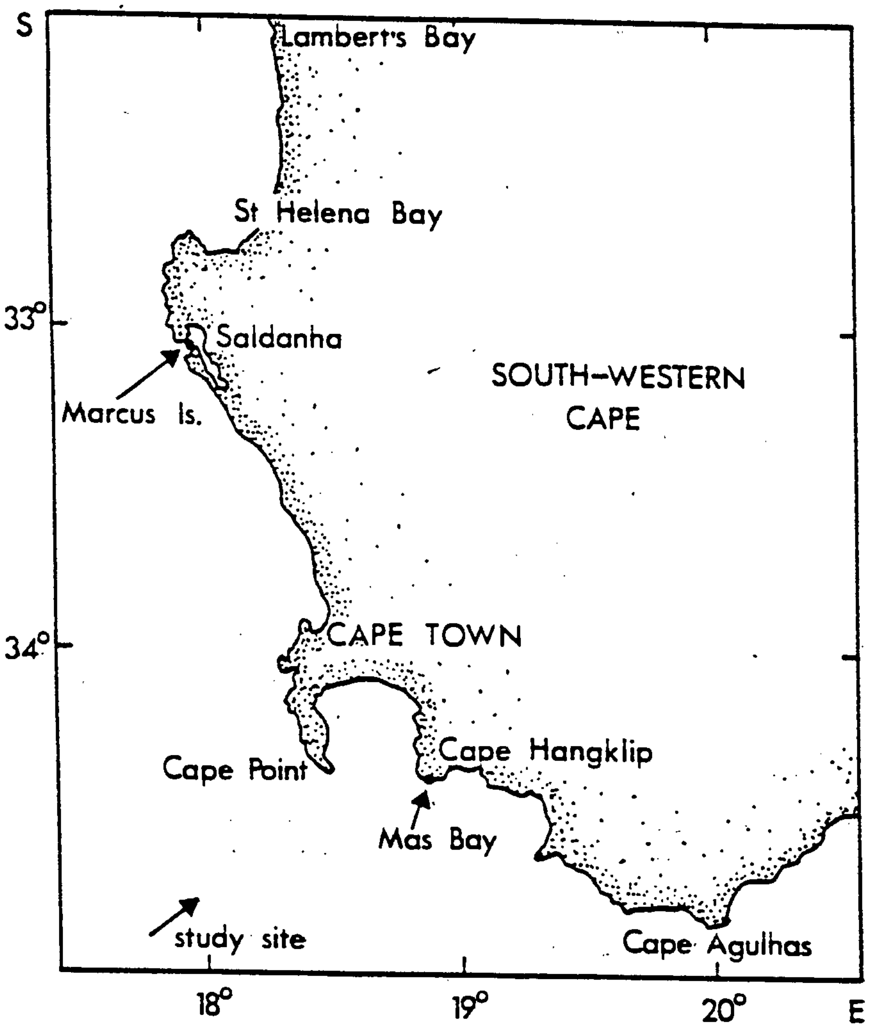

Fig. 1: The study sites and some of the places mentioned in text

DIET AND FOOD AVAILABILITY

INTRODUCTION

Abalone have been exploited by man for centuries, both on account of the food value of the muscular foot and for their shells, which are used as ornaments and manufactured into jewelry. Major *Haliotis* fisheries are located in California, Australia, New Zealand, Japan, Guernsey and South Africa.

Four species of abalone occur along the west and south-west coasts of South Africa. Three of these, *Haliotis parvum* Linn., *H. spadicea* Donaven and *H. queketti* Smith, are small non-commercial species, while the "perlemoen", *H. midae*, is the subject of a substantial fishery. *H. midae* is found on rocky shores between the low water mark and about 10m depth, (although rarely extending to 35m) and is most abundant between St. Helena Bay and Cape Agulhas. It reaches a maximum size of about 200mm shell width at an age of over 30 years (Newman 1968). The movements, reproduction, growth and distribution of H.midae have been reported upon by Newman (1966, 1967, 1968, 1969), but as yet nothing is known of its diet or feeding habits.

Aspects of the feeding biology of important Haliotidae have been carried out in many other parts of the world. Stephenson (1924) described the method of feeding in *H. tuberculata* from Guernsey and Crofts (1929) discussed selective feeding in this species. The gut contents of Japanese awabi *H. kamtschatkana* and *H. gigantea* were described by Veda and Okada (1939), while Sakai (1962) investigated the feeding habits of *H. discus hannai* with respect to growth and gonad maturation and studied its preferences for 12 different species of algae. Cox (1962) described the diets of eight Californian species and Leighton and Boolootian (1963) the food preferences and growth of the black abalone *H. cracherodii*. In New Zealand the diet and feeding habits of *H. iris, H. australis* and *H. virginea* have been investigated by Sinclair (1963), Tunbridge (1967) and Poore (1972) while the Australian species *H. laevigata, H. roei, H. ruber, H. cyclobates* and *H. scalaris* have been studied by Shepherd (1973).

In this investigation we aim to provide comparative data on the diet of the South African abalone *H.midae* from two study sites subject to different temperature regimes. An attempt is also made to assess the effects of body size and season on the composition of the diet and to compare the spectrum of food available with that actually consumed.

METHODS

Sampling

Haliotis midae samples were collected from each of two study sites, Marcus Island in Saldanha Bay on the Cape west coast (33°03'S17°58'E) and Masbaai near Cape Hangklip on the Cape south coast (34°22'S18°50'E), during summer (Dec 1983 - Jan 1984) and winter (July-Aug 1984). Each sample consisted of approximately 90 individuals covering as wide a size range as possible and collected by SCUBA divers from 3-4m depth. All collections were made in the morning (07h00 - 09h00) when preliminary sampling had shown the gut to be at its fullest.

Immediately on return to shore the wet flesh mass, sex and shell width of each individual was recorded and the crop and stomach removed and preserved in 10% formaldehyde. In the laboratory each gut was rated according to fullneses, from 0 (empty) to 10 (full). The algal food was then examined under a dissecting microscope, where most of it could be specifically identified. The allotted fullness points were then apportioned between the various species of algae in the gut according to their relative volumes, following the method of Shepherd (1973). Finally the point values for each algal species were summed, either by size class, study site or season, and compared statistically.

Coincident with the collection of abalone, algal samples were obtained from areas of maximum *H. midae* abundance. These consisted of 0,1m^2 metal quadrats placed on the rock surface. The approximate percentage cover of both attached and drifting algae within each quadrat was estimated by species and recorded underwater - following which the algae were collected and placed in labelled plastic bags for later confirmation of identification and weighing, both wet and dry (60°C for 4 days). Eighteen such quadrats were collected at each study site, nine in summer and nine in winter.

Statistical analysis

One way analysis of variance was used to compare the diets of abalone of different size classes, as well as those from the different study sites and seasons. Multiple analysis of variance (Scheffe's method) was applied when the one way analysis indicated significant difference ($\alpha = 0.05$) (Scheffe, 1959). In addition two way ANOVA was used in order to separate the effects of locality and season. Percentage data were angular transformed.

RESULTS

Pooled results showing the proportions, by volume, of various algal species recorded in the guts of *Haliotis midae* and on adjacent rock surfaces at each of the study sites in summer and in winter are given in Table 1.1. A total of 33 algal species were identified from the quadrat samples and 17 of these were also found in the stomachs of *H. midae*. One further species was recorded in the gut contents samples, but not from the quadrats.

Table 1.1 Percentage by volume of algal species in the stomachs of *Haliotis midae* and in the flora of Hangklip and Marcus Island in both summer and winter

Species	Order	Percentage by volume									
		Hangklip				Marcus Island				Mean (%)	
		Winter		Summer		Winter		Summer			
		Gut	Flora	Gut	Flora	Gut	Flora	Gut	Flora	Gut	Flora
		Green algae									
Ulva spp.	Ulotrichales	3,50	0,70	–	–	11,50	0,50	0,03	–	3,76	0,30
Caulerpa holmesiana	Siphonales	0,25	8,60			2,60	–	–	–	0,71	2,15
C. filiformis		–	–	–	1,00	–	–	–	–	–	0,25
Codium platylobium		–	11,50	–	3,00	–	–	–	–	–	3,62
C. stephensiae		–		–	2,00		–	–	–	–	0,50
C. fragile capense		–	–	–	2,00	–	–	–	–	–	0,50
Other		–	–	–	–	0,40	–	0,04	0,60	0,02	0,15
Total green algae		3,75	20,80	0,00	8,00	14,50	0,50	0,07	0,60		
		Brown algae									
Ecklonia maxima	Laminariales	45,75	34,00	46,40	38,00	52,00	40,00	80,60	47,00	56,20	39,75
Sargassum spp.	Fucales	–	6,00		2,00	–	–	–	–	–	2,00
Total brown algae		45,75	40,00	46,40	40,00	52,00	40,00	80,60	47,00		
		Red algae									
Gelidium amansii	Nemaliales	–	–	1,70	1,00	–	–	–	–	0,43	0,25
Chaetangium erinaceum		–	9,00	–	17,00	–	1,00	–	–	–	6,75
Amphiroa ephedraea	Cryptonemiales	–	0,70	–	2,00	–		–	–	–	0,68
Aeodes orbitosa		–	–	–	–	7,50	2,00	7,30	8,50	3,70	2,63
Phyllymenia spp.		–	–	–	–	12,00	7,00	–	–	3,00	1,75
Pachymenia cornea		–	–	–	–	–	–	–	11,80	–	2,95
Cheilosporum cultratum		–	–	–	1,00	–	–	–	–	–	0,25
Kallymenia agardhii		–	–	–	–	–	4,00	–	–	–	1,00
Gigartina radula	Gigartinales	2,25	0,70	6,00	25,00	–	–	0,14	–	2,10	6,42
Caulacanthus ustulatus		–	–	–	–	–	–	0,14	3,40	0,04	0,85
Hypnea spicifera		13,14	0,70	–	–	–	–	–	–	3,30	0,18
Gymnogongrus dilatatus		–	–	–	–	–	1,00	–	–	–	0,25
G. glomeratus		–	–	–	–	–	1,00	–	–	–	0,25
Iridaea capensis		–	–		–	–	3,00	–	–	–	0,75
Schizymenia obovata		–	–	–	–	–	10,00	–	–	–	2,50
Plocamium corallorhiza		23,25	19,00	45,90	6,00	–	–	0,07	–	17,31	6,25
P. cornutum		–	–	–	–	–	–	0,04	–	0,01	–
P. rigidum		8,11	2,00	–	–	6,00	0,50	–	–	3,53	0,63
P. suhrii		–	–	–	–	–	1,00	0,60	0,60	0,15	0,40
Pterosiphonia cloiophylla	Ceramiales	–	–	–	–	7,00	21,00	5,76	21,00	3,20	10,50
Carpoblepharis flaccida		–	–	–	–	–	–	3,14	0,30	0,80	0,07
Tayloriella tenebrosa		–	–	–	–	–	–	2,14	0,20	0,54	0,05
Ceramium spp.		–	–	–	–	–	1,00	–	–	–	0,25
Falkenbergia rufulanosa		3,75	5,00	–	–	–	–	–	–	0,94	1,25
Botryoglossum platycarpum		–	–	–	–	0,70	7,00	–	–	0,18	1,75
Neuroglossum binderianum		–	–	–	–	–	–	–	4,60	–	1,15
Other		–	2,10	–	–	0,30	–	–	2,00	0,08	1,02
Total red algae		50,50	39,20	53,60	52,00	33,50	59,50	19,33	52,40		

Further trends in feeding pattern can be deduced by examining the data with respect to body size, study area and season.

Relationship between diet and body size

The abalone collected ranged in size from 65mm-145mm shell width. In order to test for any relationship between body size and diet the data for each 10mm size group of animals was averaged for each study site and season. The results are shown in Fig 1.1.

At least two and no more than six algal species were found in the stomachs of any particular size group. At Hangklip *Ecklonia maxima* and *Plocamium spp.* formed the bulk of the diet of all size classes, together comprising some 80% of food consumption. Although there was an apparent trend for *E. maxima* to make up an increasing proportion of the diet of larger individuals, there was no statistically significant relationship ($\alpha = 0.05$) between the proportion of this or any other species in the diet of abalone of different sizes.

At Marcus Island, where *Plocamium spp.* are relatively rare, *E. maxima* was by far the most important component of the diet. This was especially

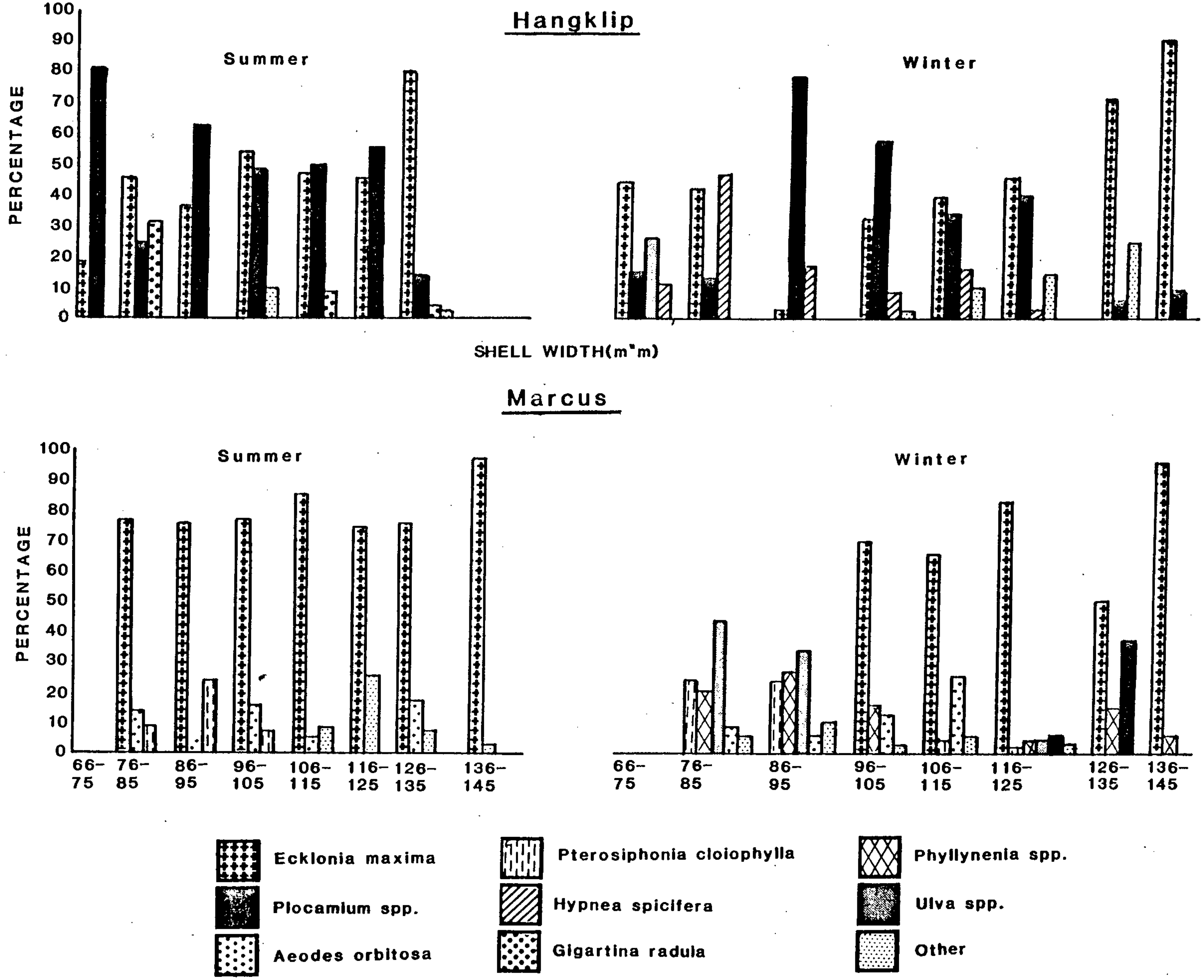

Fig. 1.1 Percentage by volume of algal species in the guts of H. midae of different sizes.

true in summer, where it made up about 80% of the diet of all size groups. In winter kelp was still important, particularly in the larger size classes, but several other species were taken in significant amounts, notably *Aeodes orbitosa, Pterosiphonia cloiophylla, Phyllymenia spp.* and *Ulva spp.* Again while several of the species appeared to decline in importance with size of abalone most of the trends were not statistically significant. Only *Ulva spp.* from the winter sample showed a significant decline in abundance, from a peak of 45% of the diet of individuals 75-86mm in shell width to only 0- 5% in larger abalone.

Effects of season and study site on composition of the diet

Using pooled data for all size classes, the relative proportions of major algal species found in the stomachs of *H. midae* from our two study sites, both in summer and winter, are illustrated in Fig 1.2. The study sites at Marcus Island and Hangklip experience markedly different water temperature regimes of 12°C and 19°C respectively in summer and 13°C and 14.5°C in winter. (Unpublished daily data of Seafisheries

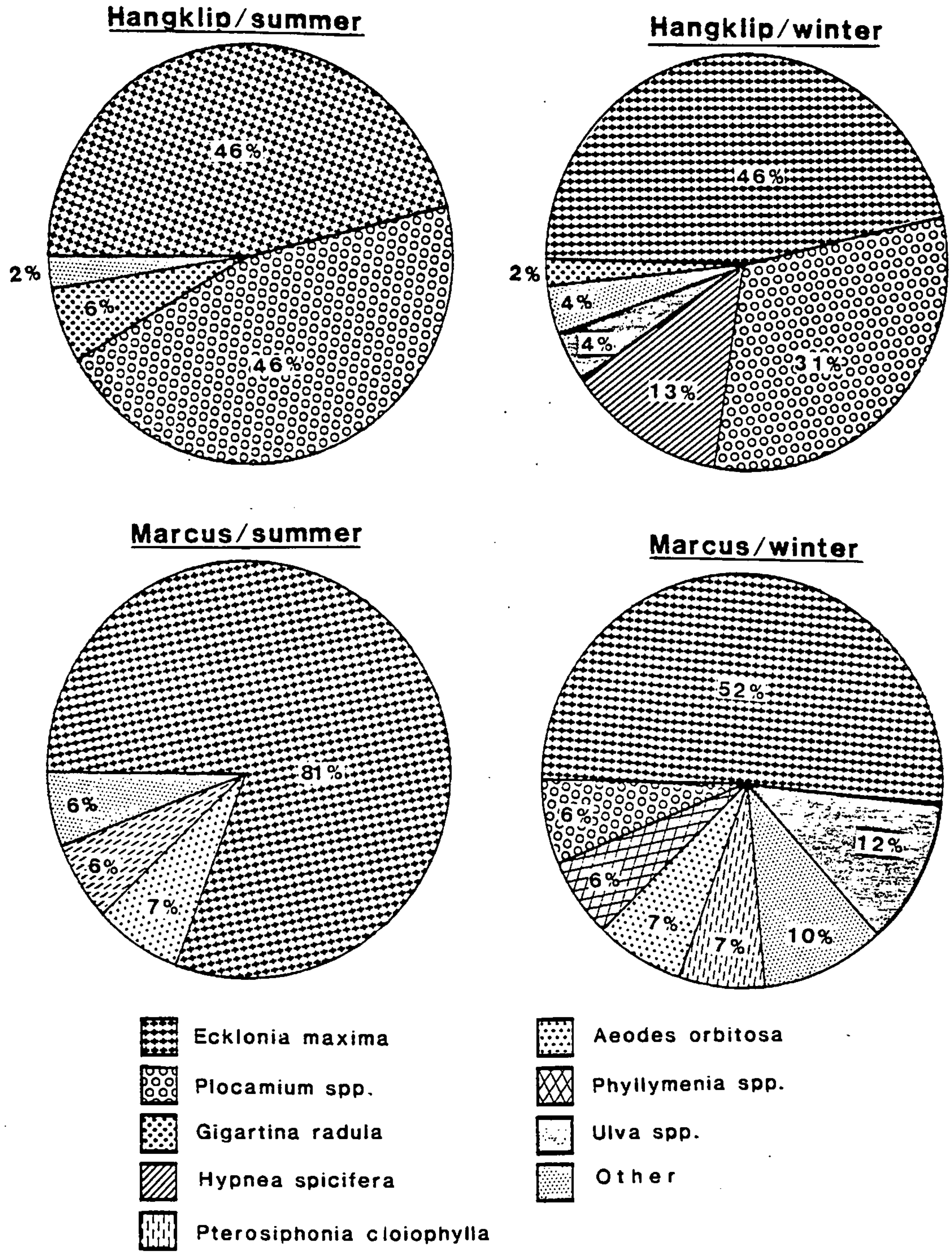

Fig. 1.2 The percentage of total stomach volume occupied by the most important algae eaten by *H. midae*.

Research Institute and Botany Department, UCT and Shannon and Stander 1977). Examining seasonal trends first, it is evident that the diets at both sites are more diverse in winter than in summer. The summer sample from Hangklip consisted 92% of *Ecklonia* plus *Plocamium* and that from Marcus Island 81% of *Ecklonia*. In Hangklip only one other species accounted for more than 3% of consumption and in Marcus Island only three. By contrast six species occurred in proportions exceeding 3% each in the winter diets at both sites. Of these *E. maxima, Plocamium spp.* and *Ulva spp.* were common to both sites, while *Hypnea spicifera, Falkenbergia rafullanosa* and *Gigartina radula* were significant at Hangklip and *Aeodes orbitosa, Pterosiphonia cloiophylla* and *Phyllymenia spp.* in samples from Marcus Island. Averaging the data across study sites and season the most important component of the diet of abalone was kelp *E. maxima* (56% by volume), followed by *Plocamium corallorhiza* (17%). No other algal species made up more than 4% of the diet overall, although no less than seven species comprised between 2% and 4% of food consumption. Comparing the two study sites the main difference, apart from substitution of species mentioned above, lies in the relative importance of

E. maxima and *Plocamium spp.* in the diet. At Marcus Island *E. maxima* is the overwhelming dominant, never present in less than 4x the proportion of the second ranking species. By contrast at Hangklip *Plocamium spp.* were much more important, being taken in equal amounts to *E. maxima* in summer (46% each) and at a ratio of 3:2 (46% to 31%) in winter.

Relation of diet to algal availability

The relative proportions of major algal species in the guts of *H. midae* and on adjacent rock surfaces at the two study sites are depicted in Fig **1.3**A and logarithmic selectivity indices (Berg 1979) shown in Fig **1.3**B. The selectivity index = log10 % food item in gut divided by that on the rock surface. A value greater than zero thus indicates selection for the species in question and a negative value that it is avoided.

The two most abundant species in the algal flora at Hangklip, *Ecklonia maxima* and *Plocamium corallorhiza* were also the most important components in the diet and both were selected for. The only other species preferentially selected were *Hypnea spicifera* and *Ulva spp.*, but both these were relatively rare, possibly

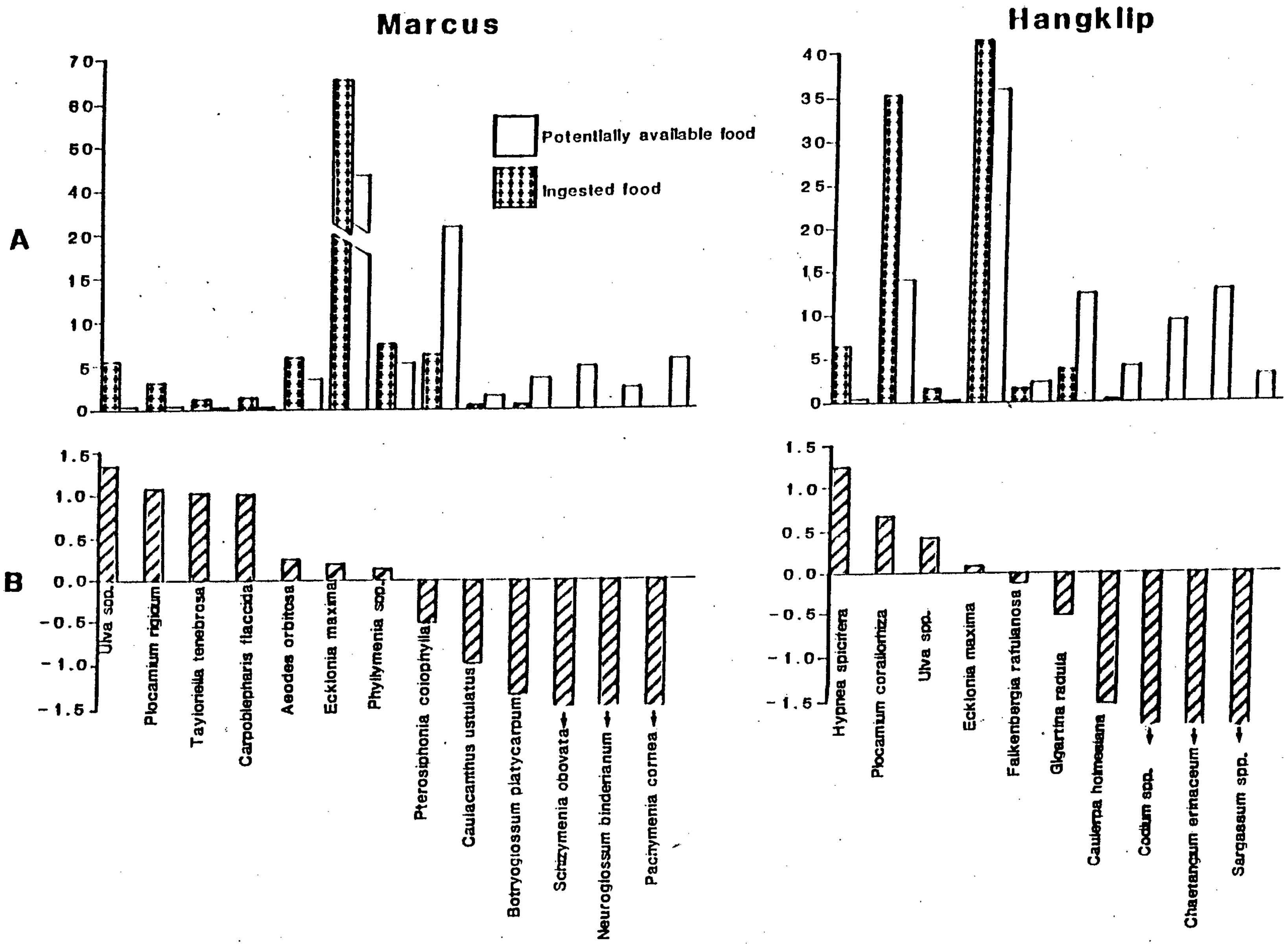

Fig. 1.3 (a) Percentage composition of algal flora available in the collecting site and in the stomachs of *H. midae* and (b) selectivity index of *H. midae*

$$S = \log_{10} \frac{(\%\text{food item in gut})}{(\%\text{food item on rock})}$$

because of grazing pressure. Several other species abundant on rock surfaces were rare or absent in the diet of *H. midae*, eg. *Codium spp.*, *Sargassum spp.*, *Caulerpa holmesiana*, *Chaetangium erinaceum* and *Gigartina radula*.

At Marcus Island both the flora and the stomach contents samples were dominated by *Ecklonia maxima*. Many of the more common species in the area were avoided by abalone while others rare in the environment, such as *Ulva spp.*, *Plocamium rigidum*, *Tayloriella tenebrosa* and *Carpoblepharis flaccida* were apparently strongly selected for, although uncommon on the rocks.

DISCUSSION

Our results clearly demonstrate that *Haliotis midae* is an entirely herbivorous species. Although taking a wide range of algae the preferred food item is kelp, *Ecklonia maxima*, with *Plocamium spp.* also a major element of the diet on the south coast. The diets of abalone 65-145mm in shell width are similar, except that *Ulva spp.* are taken in larger proportions by the smaller size classes. This may well be explained by the fact that both *Ulva spp.* and small abalone tend to be more abundant in shallower water. There are significant differences in the diet at the two study sites - particularly as regards the importance of *Plocamium spp.* in the diet - and also a diversification of the species taken in winter relative to summer.

The relative importance of site versus season in determining the composition of the flora and the gut contents of abalone are compared in Table 12. As regards the flora, study site appears to be a more important variable than season. In particular *Plocamium spp.* and *Gigartina radula* are significantly more abundant at Hangklip than at Marcus Island and *Pterosiphonia cloiophylla* less abundant. Similarly there are stronger differences in the diets of abalone at the two sites than in different seasons. This is particularly evident in the proportions of *Plocamium spp.* and *Phyllymenia spp.* taken, although the latter is also eaten exclusively in winter.

These findings correlate well with those of other workers. Kelps, such as the bull kelp *Nereocystis*, giant kelp *Macrocystis*, elk kelp *Pelagophycus* and boa kelp *Egregia*, are the main food items of red, pink,

	Gut			Flora		
Species	Site P	Season P	Explained P	Site P	Season P	Explained P
Ecklonia maxima	0.001**	0.089	0.001**	0.408	0.478	0.499
Plocamium spp.	0.000***	0.849	0.000***	0.000***	0.001**	0.000***
Ulva spp.	0.160	0.001**	0.003**	0.291	0.146	0.168
Hypnea spicifera	0.002**	0.002**	0.000***	0.310	0.162	0.191
Aeodes orbitosa	0.003**	0.852	0.011*	0.125	0.798	0.276
Phyllymenia spp.	0.000***	0.000***	0.000***	0.193	0.126	0.237
Plerosiphonia cloiophyla	0.016*	0.978	0.051	0.001**	0.831	0.005**
Gigantina radula	0.318	0.318	0.417	0.006**	0.013*	0.003**

* 0.05>P>/0.01
** 0.001>P>/0.001
*** P<0.001

Table 1.2

The relative importance of site (Hangklip and Marcus Island) and season (winter and summer), on the percentage by volume of major species of algae in the gut content of H. midae and in the benthic flora, based on two way analysis of variance.

white and green abalone from California (Cox, 1962) and are the preferred foods in selection experiments (Leighton, 1966). Brown algae also predominate in the diets of *H. tuberculata* from Guernsey (Stephenson 1924), the Japanese *H. gigantea* and *H. kamtchatkana* (Veda and Okada, 1939), *H. discus hannai* (Sakai 1962) and the Californian *H. cracherodii* (Leighton and Boolootian, 1963). Australian species, on the other hand, show a preference for red algae and reject most browns, subsisting predominantly on red algae and seagrasses, depending upon the possibilities of the habitat (Shepherd, 1973). *Ecklonia* was only eaten when red algae were scarce. Similarly the New Zealand *H. iris* and *H. australis* take mostly red algae at all times of year although browns, like *Ecklonia*, dominate the attached flora. Kelps were, however, taken at sites where Macrocystis was the dominant algal species (Poore, 1972).

In a study of the feeding patterns of pre-commercial *H. iris* Tunbridge (1967) concluded that abalone showed "more a rejection of certain species rather than an active seeking out of preferred types". The present results suggest that *H. midae* essentially adopts a similar feeding pattern, selecting from a wide group of acceptable species largely according to their abundance in the surrounding habitat.

ACKNOWLEDGEMENTS

I am grateful to A Barkai, C D McQuaid and P B Hanekom for assistance with the field work and R Simons, who helped with the identification of algae. Financial support was provided through the Benguela Ecology Programme of the South African National committee for Oceanographic Research and a U.C.T. Postgraduate Research Scholarship .

REFERENCES

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

CROFTS, D.R. 1929 - Haliotis. In L.M.B.C. Memoirs on Typical British Marine Plants and Animals 29: 1-74.

COX, K.W. 1962 - California abalones, family Haliotidae. Calif. Dep. Fish Game Fish. Bull. 118: 6-66.

LEIGHTON, D.L. 1966 - Studies of food preference in algivorous invertebrates of southern California kelp beds. Pac. Sci. 20: 104-113.

LEIGHTON, D. and BOOLOOTIAN, R.A. 1963 - Diet and growth in the black abalone, *Haliotis cracherodii*. Ecol. 44(2): 227-238.

NEWMAN, G.G. 1966 - Movements of the South African abalone, *Haliotis midae*. Investl. Rep. Div. Sea Fish. S. Afr. 56: 1-20.

NEWMAN, G.G. 1967 - Reproduction of the South African abalone, *Haliotis midae*. Investl. Rep. Div. Sea Fish. S. Afr. 64: 1-24.

NEWMAN, G.G. 1968 - Growth of the South African abalone, *Haliotis midae*. Investl. Rep. Div. Sea Fish. S. Afr. 67: 1-24.

NEWMAN, G.G. 1969 - Distribution of the abalone (*Haliotis midae*) and the effect of temperature on productivity. Investl. Rep. Div. Sea Fish. S. Afr. 74: 1-7.

POORE, G.C.B. 1972 - Ecology of New Zealand abalones, *Haliotis* species (Mollusca:Gastropoda). N.Z.J. Mar. Freshwater Res. 6(1+2): 11-22.

SAKAI, S. 1962 - Ecological studies on the abalone, *Haliotis discus hannai*.Iho-I. Experimental studies on the food habit.Bull.JPN. Soc. Sci. Fish. 28(8): 766-779.

SCHEFFE, H. 1959 - The analysis of variance. Wiley, N.Y. 477 pp.

SHANNON, L.V. and STANDER, G.H. 1977 - Physical and chemical characteristics of water in Saldanha Bay and Langebaan lagoon. Trans. roy. Soc. S. Afr. 42(3+4): 441-459.

SHEPHERD, S.A. 1973 - Studies on Southern Australian abalone (Genus *Haliotis*). I. Ecology of five sympatric species. Aust. J. Mar. Freshwater Res. 24: 217-257.

SINCLAIR, M. 1963 - Studies on the Paua, *Haliotis iris* Martyn in the Wellington district, 1945-46. Zool. Publ. Victoria Univ. Wellington. 35: 1-16.

STEPHENSON, T.A. 1924 - Note on *Haliotis tuberculata*. J. Mar. Biol. Assoc. U.K. 13(2): 480-495.

TUNBRIDGE, B.R. 1967 - Feeding habits of Paua. N.Z. Mar. Dep. Fish. Tech. Rep. 20: 1-18.

VEDA, S. and OKADA, Y. 1939 - Studies on the food of useful Gastropoda in Japan. I. Two species of

Japanese abalone, *Haliotis gigantea* Gmelin and *H.kamtschatkana* Jonas. Bull. JPN. Soc. Sci. Fish. 8: 51-57.

CONSUMPTION, ABSORPTION EFFICIENCY, RESPIRATION AND EXCRETION.

INTRODUCTION

The South African abalone, *Haliotis midae*, is a large edible gastropod found on shallow sublittoral rocky shores between St Helena Bay, on the west coast, and the southern Transkei, to the east. A substantial commercial fishery has been in existance since the 1950's and is concentrated in a relatively small area between Cape Agulhas and Cape Point, where abalone reach their greatest abundance. In 1962 the Division of Sea Fisheries initiated a research programme aimed at investigating those aspects of abalone biology which could be of use in the effective management of the available stocks. This led to studies of abalone movement, reproduction, growth, distribution and the influence of temperature on reproduction (Newman 1966, 1967, 1968, 1969). The mechanism of shell elevation has subsequently been investigated by Trueman and Brown (1985) and the influence of body size, season and location on the diet quantified by Barkai and Griffiths (1986).

As yet there is no published information on such aspects of the physiology of this important species as feeding rate, absorption efficiency, respiration rate, or excretion. Indeed, such data have been determined for very few herbivorous gastropods. The following account attempts to provide such information. Together with existing data on density, growth and reproductive output this will enable us to compile a population energy budget for *H. midae* (Barkai and Griffiths, in prep.).

METHODS

As in our earlier dietary study (Barkai and Griffiths, 1986) comparative material was collected from two study sites, one on the west coast, at Marcus Island (33°03'S, 17°58'E), where water temperatures average 14°C, and the other on the south coast, at Cape Hangklip (34°22'S, 18°50'E) where the mean temperature was 19°C. The methods used to estimate each of the parameters measured are outlined separately below.

Feeding periodicity and consumption rate

Initial attempts to induce abalone to feed in the laboratory were unsuccessful, making it necessary to deduce feeding rate and periodicity from the examination of stomach contents collected in the field at different times of day. This was accomplished using a cyclical feeding model developed by Eggers (1977), Elliot and Persson (1978) and Lane et al (1979). The model assumes that the day can be divided into separate feeding and elimination periods. Stomach fullness follows a curve $ds/dt = I(t) - Ks$, where $I(t)$ is the feeding rate at time t, K the instantaneous elimination rate h^{-1} and S the food content of the stomach, each expressed in % body weight. Elimination rate is estimated from the rate of decline of stomach contents during the fasting phase

$$S_2(t) = S'\exp[-k(t-t')]$$

and feeding rate from the feeding portion of the cycle

$$S_1(t) = (So - Ic/k)\exp[-k(t-t_0)] + Ic/k$$

From the two curves daily individual food intake $C = Ic(t-to)$ can be calculated (Lane et al 1979). To obtain the necessary data samples of 10-20 abalone were collected from fixed sites at 3-5m depth every

3h over a 24h period. Once landed each individual was taken from its shell and the stomach contents removed. Both wet flesh mass and stomach contents mass were then recorded separately, using a top loading balance. Samples from Marcus Island were collected in December 1984 and those from Cape Hangklip in September 1985, temperatures at the time of collection being 14°C and 19°C respectively.

Absorption efficiency

Absorption efficiency was estimated using the Conover Ratio method, in which percentage absorption is calculated from the differing proportions of organic matter in the food and faeces (Conover, 1966). Since *H. midae* held in the laboratory did not feed normally faeces had to be recorded from freshly collected field samples and the diet deduced by sacrificing a control group. This experiment was restricted to the Marcus Island site in summer, where a single algal species, *Ecklonia maxima*, comprises the vast bulk of the diet (Barkai and Griffiths, 1986).

Thirty abalone over the size range 100-600g wet mass were collected shortly after dawn, when the guts were known to be full. Half of these were sacrificed and the gut contents preserved for dietry analysis. The remainder were returned to separate aquaria, where they were held for 24h at 14°C. Faeces produced over this period were siphoned onto preashed GFC filter papers, rinsed with isotonic ammonium formate and dried for 24h at 60°C, cooled and reweighed. The organic fraction of the faeces, or mass loss on ashing, was compared with that for food, derived by treating fresh samples of algae from the collection site in the same way as the faeces and weighting the results according to the proportion of each algal species in the diet.

Absorption efficiency was then calculated using the formula

Absorption efficiency (%) = F - E x 100 / (F(1-E))

where F = fraction (ie. organic matter) lost by ashing the food

E = fraction (ie. organic matter) lost by ashing the faeces.

Respiration rate

Abalone for respiration rate study were collected from either Marcus Island or Cape Hangklip during early morning in April 1984. On return to the laboratory the shells were cleaned of algae and epifaunal organisms and the abalone allowed to attach to the walls of suitably sized perspex respiration chambers, where they were left to acclimatise for 4-5h in running seawater of the appropriate temperature (14°C for Marcus Island, 19°C for Cape Hangklip). The chambers were subsequently closed by lids which incorporated inlet and outlet pipes and YSI oxygen electrodes and were placed in a water bath of the correct temperature. After flushing the chambers with fresh seawater from a reservoir tank the inlets and outlets to the chambers were closed and the decline in oxygen tension recorded on a multichannel recorder, while gently agitating the water with magnetic stirrers. After 15mins, or when oxygen tensions fell to 80% saturation, the tops were reopened and the chambers flushed with air-saturated seawater before repeating the procedure. Some 5-10 readings for each individual were obtained in this way and averaged.

In order to determine whether time of day or feeding condition influenced respiration rate this entire experiment was carried out both by day (10h00- 17h00h) and at night (22h00-02h00) and again after the experimental animals had been held in a large closed circuit aquarium system for 4 weeks without food. The results were then statistically compared. Four way ANOVA was applied (Sokal and Rohlf, 1969) using SPSS/X statistical software on a Univact 1100 computer.

Ammonia excretion

Rates of ammonia excretion were measured for 5-6 size classes of abalone from each of the two study sites. Four individuals of closely matched size were selected within each of the size classes, which ranged from about 100- 1000g wet mass (58-140mm shell width). Each individual was placed in a separate plastic container together with an appropriate measured volume of sea water and held at a temperature equivalent to that at the collection site. Duplicate water samples were collected (for 4 hours) from each container at hourly intervals, as well as from a control, and deep frozen immediately. Ammonia was analysed according to the method of Grasshof (1976), modified for use with 5ml samples and the results for each group averaged and converted to give total ammoinia excretion rate h^{-1} individual^{-1}.

RESULTS

Feeding periodicity and consumption rate

The feeding pattern of *Haliotis midae* appears to conform closely to the cyclical feeding model used, a feeding phase occurring over the late afternoon and night and an elimination phase by day. This pattern is confirmed by the statistical results, analysis of covariance showing that mean stomach content weights differed significantly at different times of day ($P<0.001$). Daily fluctuations in the mass of the gut contents as a percentage of body mass in the two study sites, are shown in Fig 2.1, together with the fitted curves. Calculated feeding and elimination parameters are summarized in Table 2.1.

It is also possible to use these data to calculate the relationship between body mass and total daily food consumption, by splitting the samples from each site into four separate size classes and analysing these separately. The results are shown in Fig 2.2 and indicate that consumption rates are higher at Cape Hangklip than in the colder water of Marcus

			Marcus Island	Cape Hangklip
t_0	-	start of feeding period	(17h35)	(16h07)
t_1	-	start of elimination period	(07h52)	(03h51)
		Duration of feeding period (h)	14 h. 17 min	11h. 44 min
S_0	-	gut contents at t_0 (% body mass)	1,0%	1,0%
S_1	-	gut contents at t_1 (% body mass)	4,8%	5,5%
I_c	-	Rate of feeding (% body mass h^{-1})	0,83%	0,93%
K	-	elimination rate (" " ")	0,16%	0,14%
R	-	total daily ration (% body mass)	8,1%	11,4%

Table 2.1 Feeding periodicity and consumption rate parameters for *Haliotis midae* calculated from Fig 2.1.

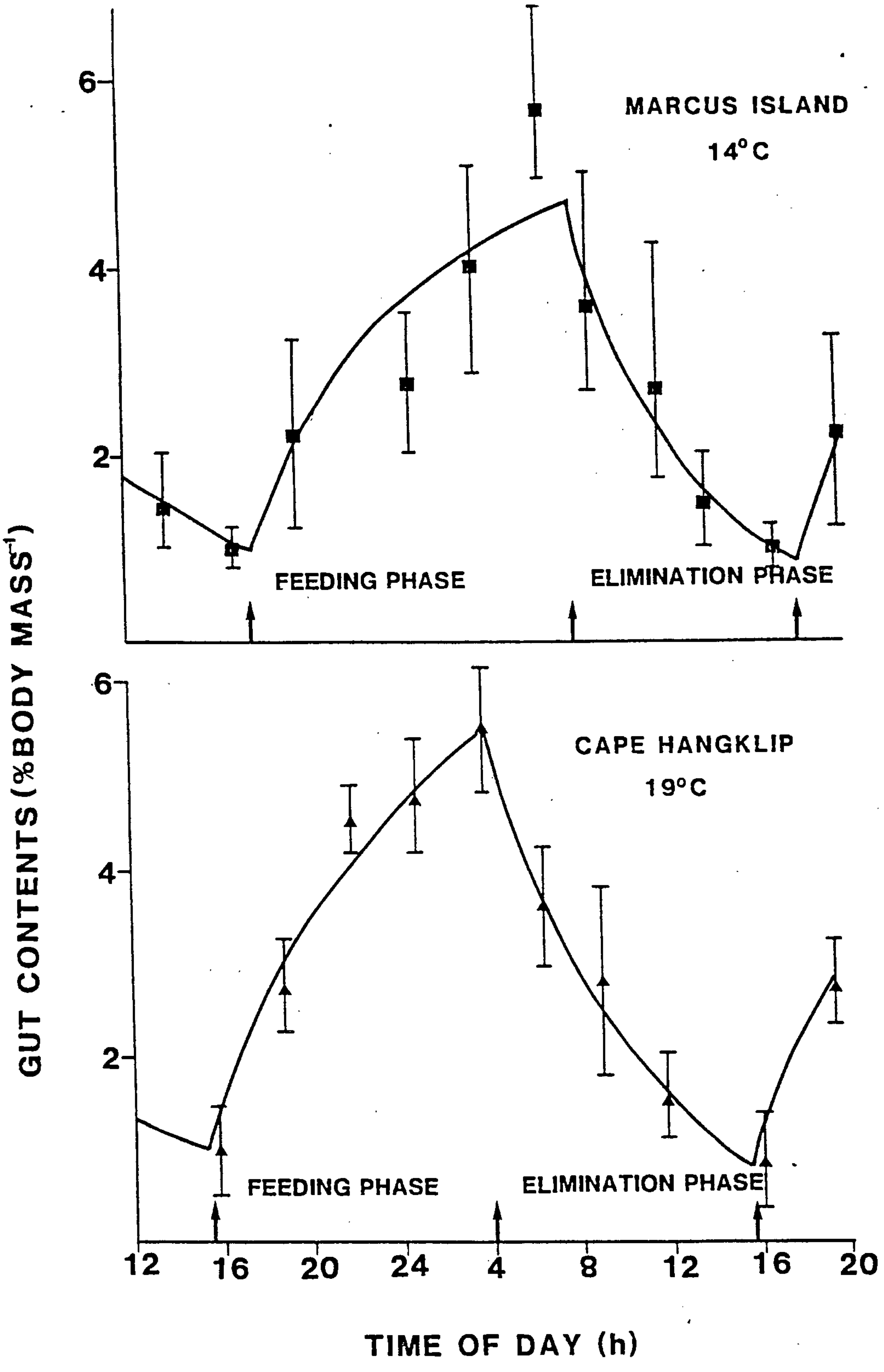

FIG 2.1. Dirunal feeding cycles for *Haliotis midae* from Marcus Island at 14°C (above) and Cape Hangklip, at 19°C (below). The data points indicate mean wet mass of stomach contents as percentage of mean wet body mass for a sample of 10-20 individuals taken on each occasion. Vertical bars are standard deviations. Curves have been fitted according to the cyclical feeding model described in the text.

Island. Daily food consumption (g wet mass) is related to wet body mass by the equations:

$C = 0.54\ W^{0.67}$ ($n = 16$; $r^2 = 0.98$)

at Marcus Island and

$C = 0{,}35\ W^{0.77}$ ($n = 16$; $r^2 = 0.98$)

at Cape Hangklip.

This in effect means that mass specific food intake declines from about 9- 6% of body mass d^{-1} over the range 200-700g mass at 14°C and 11-7% at 19°C.

Absorption efficiency

The mean absorption efficiency obtained from Conover Ratio estimates was 37% ($n = 15$; $SD = 10.3$), the only species of algae found in the guts being *Ecklonia maxima* (92%) and *Aeodes orbitosa* (8%).There was no detectable relationship between absorption efficiency and body mass over the range 100-600g wet flesh mass (one way ANOVA, $p(F) > 0.05$).

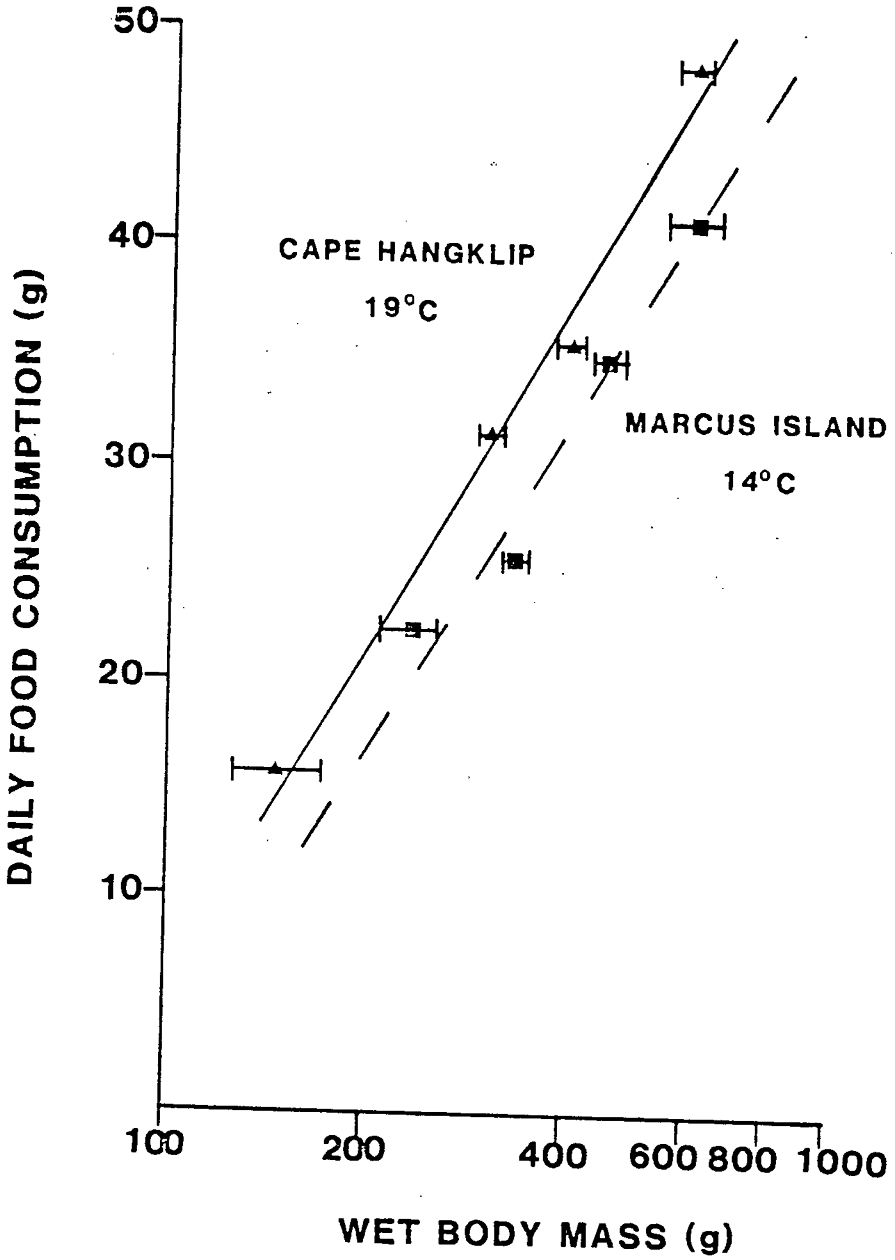

FIG 2.2. Daily food consumption (g wet mass) as a function of wet body mass for *Haliotis midae* from two study sites, Marcus Island (14°C ■) and Cape Hangklip (19°C)▲

Respiration rate

No differences could be detected between respiration rates measured by day or by night, nor between freshly collected and starved individuals, (4-way ANOVA, $P<0.05$). The data were therefore pooled and used to derive relationships between body mass and respiration rates at the two temperatures used. These relationships are depicted in Fig 2.3. The equations relating oxygen consumption (ml O_2h^{-1}) and wet body mass (g) being:-

$$R = 0.03\ W^{0.83}\ (n = 22;\ r^2 = 0.96)\ \text{at}\ 14^{\circ}C$$

and

$$R = 0.03\ W^{0.96}\ (n = 23;\ r^2 = 0.94)\ \text{at}\ 19^{\circ}C$$

This means that mass-specific respiration rate falls from 15-10µl $g^{-1}h^{-1}$ over the size range 50-500g wet body mass at 14°C, but remains more consistent at 24-21µl $g^{-1}h^{-1}$ at 19°C. Q_{10} values range from 3,1 at 50g to 3,9 at 500g over this temperature range.

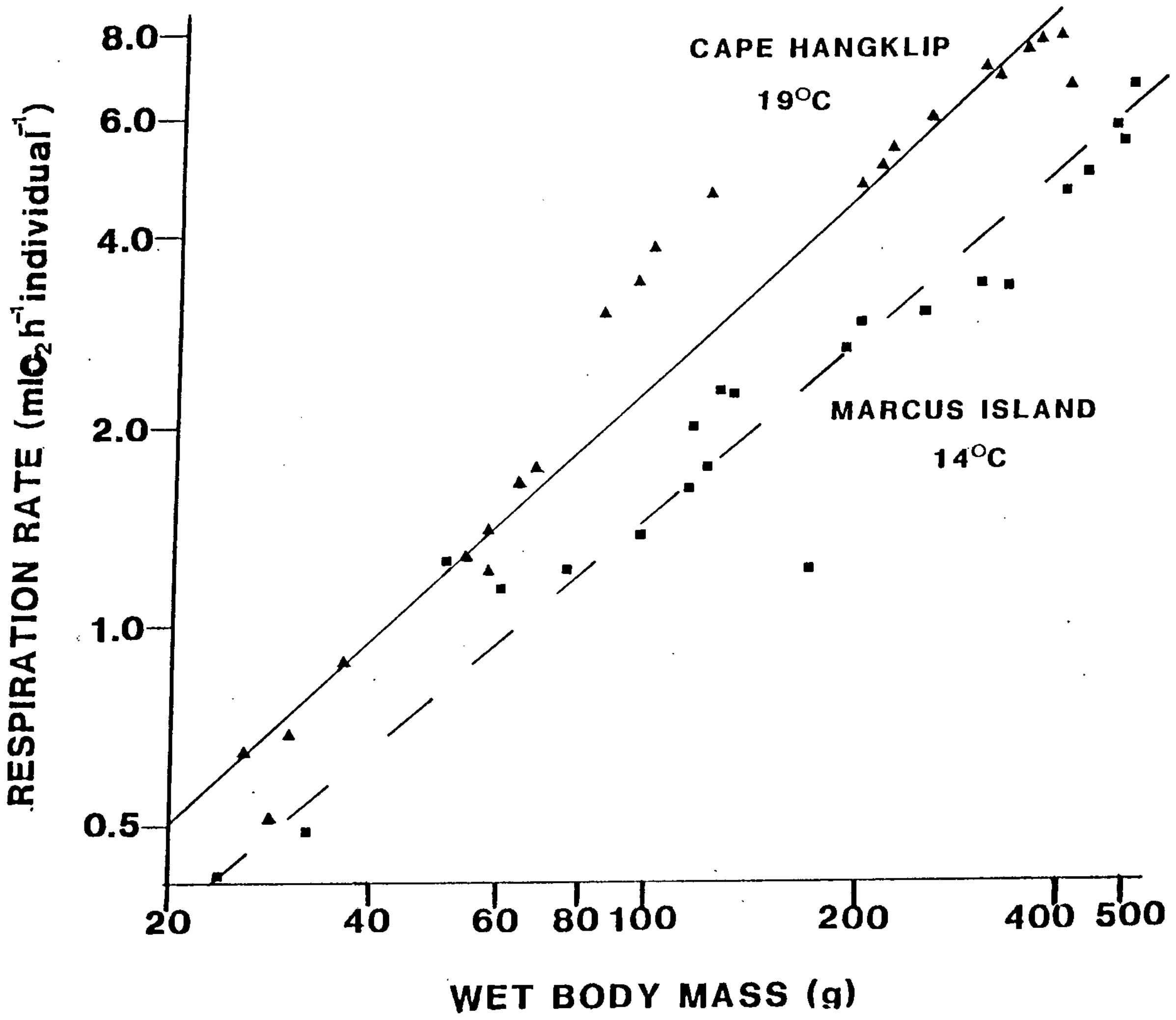

FIG. 2.3. The relationships between respiration rate (ml O_2h^{-1}) and wet body mass for *Haliotis midae* from two study sites, Marcus Island (14°C) ■ and Cape Hangklip (19°C)▲

Ammonia excretion

Relationship between rate of ammonia excretion and wet body mass at 14°C and 19°C are depicted in Fig 2.4. Equations relating these two parameters are:

U (µmole h^{-1}) = $0.22\ W^{0.43}$ ($n = 20$, $r^2 = 0.88$) at 14°C and

U (µmole h^{-1}) = $0.03\ W^{0.85}$ ($n = 24$, $r^2 = 0.92$) at 19°C

Some authors have expressed comparable rates of ammonia excretion in µgr per unit dry body mass (see Bayne and Newell, 1983 for review) and these may be calculated by using the wet to dry mass relationship: Dry mass = 0.15 wet mass - 3.30 ($n=100$). The excretion rates then become :

$U = 10.72\ W^{0.39}$ at 14°C and $U = 4.37\ W^{0.75}$ at 19°C.

DISCUSSION

The cyclical feeding model depicted in Fig 1.1 clearly confirms the nocturnal pattern of grazing behaviour in *Haliotis midae* and correlates with our observations that abalone tended to remain inactive by

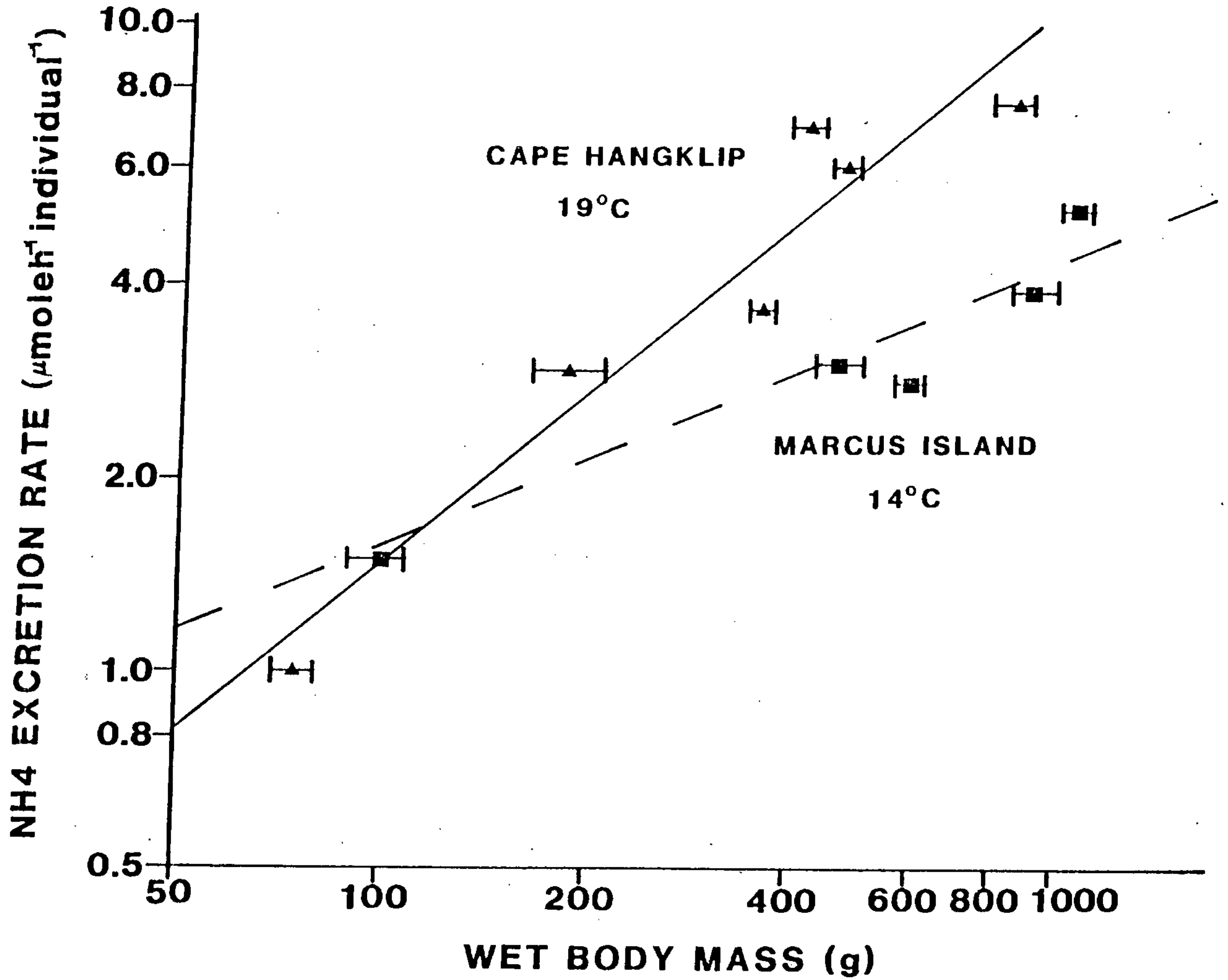

FIG. 2.4. Ammonia excretion rates (µmole h^{-1}) as a function of wet body mass in *Haliotis midae* arecovered from two study sites, Marcus Island ■ (14°C) and Cape Hangklip (19°C)▲ ⊢⊣ = SD

day, both in the field and in laboratory tanks, and to move about at night. Similar nocturnal feeding habits have been reported in other species of abalone, notably *H. tuberculata* (Stephenson, 1924; Crofts, 1929).

The feeding phase of the activity cycle appears to begin earlier in the evening and to follow at steeper course at Cape Hanglip than at Marcus Island. It also ends considerably earlier, but at a higher level of gut fullness. The earlier start time can be explained by the time of sampling, which was in September for the Hangklip experiment, but in December, when sunset occurs considerably later in the evening, for Marcus Island. The warmer temperature at Hangklip may increase both activity level and metabolic costs, resulting in a more rapid rate of food intake, but the fact that feeding ends earlier suggests that satiation has been achieved. This in turn could be taken to indicate that food is more readily available at Cape Hangklip than at Marcus Island, a postulation supported by the rich abalone fishery in this area (Marcus Island lies outside the commercially exploited range of *H. midae*).

Feeding rates are fairly rapid for a gastropod of this size, at 0.83 - 0.93% body mass h^{-1}, but are sustained for only about half of the day, so that the rate averaged over 24h is in fact between 0.45-0.48% h^{-1}. Plant food is digested with considerably lower efficiency than animal material and although some molluscs exhibit very high absorption efficiencies the Values for grazing forms given by Bayne and Newell (1983) vary from 12-76% with a mean of 54%. In this context the mean of 37% obtained here for *H. midae* is quite low. The absence of any correlation between absorption efficiency and body mass is supported by data from other gastropods given by Bayne and Newell (1983). Respiration rates in *H. midae* were strongly dependent upon both body size and temperature. The mass exponents of 0,83 and 0.94 at 14°C and 19°C respectively are somewhat higher than those reported in other *Haliotis* species by Jan et al (1981), and the mean for grazing gastropods of 0,67 given by Bayne and Newell (1983). They do, however, lie well within the range reported within the mollusca by Ghirretti (1966) and Bayne and Newell (1983). As is frequently the case the respiratory exponents exceeded those for consumption rate, the greater rate of increase in respiratory costs relative to food intake being one of the factors limiting the ultimate body size that can be attained.

Our experiments failed to demonstrate differences in rate of oxygen consumption between day and night, despite the fact that abalone are known to feed actively at night and to be quiescent by day. Uri and Kikuchi (1975) have recorded increased metabolic rates in *H. discus hanni* over the period from dusk to midnight, while diurnal respiration rhythms for other *Haliotis* species are also reported in Jan etal (1981). Possibly the chambers used in our experiments were too small to allow natural locomotary activity to take place, hence depressing nocturnal rates. In contrast there were marked differences in the metabolic rates of abalone from Marcus Island and Cape Hangklip. Given that the two groups were tested only at the temperature prevailing at their own site (ie. only acclimated rates were tested) the Q_{10} values of over 3 are unusually high.

Ammonia, which is assumed to be the dominant end product of protein catabolism (Bayne & Newell, 1983) shows a similar pattern of temperature and body mass relationship. The weight exponent of 0,75 at 19°C is considerably higher than that of 0,39 at 14°C, while overall rates, at least in the larger size classes, show a strong temperature dependance. The weight exponents found here fall within the same range as those for other marine gastropods. Stickle and Bayne (1982) give an exponent of 0,61 for *Thais lapillus* and Mace and Ansell (1982) ones of 0.64 and 1,12 for *Polinices alderi* (in Oban) at 10°C and 20° respectively.

Taken together these results suggest that the proportion of energy consumed that is made available for growth and reproductive output will decline with animal size. This is because absorption efficiency remains constant, but respiration rates (and at higher temperatures excretion rates) increase more rapidly in relation to body mass than does consumption. Similarly when temperatures are increased from 14°C to 19°C the respiration rate increases more rapidly than the consumption rate, so that unless there is a compensatory change in absorption efficiency a decline in energy balance should occur.

These suggestions are based on the assumption that the food consumed by abalone of different sizes and at the two study sites is of similar calorific value . But when different diet is taken into account the real proportion of the energy available for growth and reproduction may change. Our studies on the diet of *H. midae* , (Barkai and Griffiths, 1986), show little significant difference in the diet of animals of different sizes. There were, however, considerable differences between the diets of abalone from the two study sites, that at Cape Hangklip incorporating more *Plocamium*, which has is a higher calorific value (21.2) than the *Ecklonia maxima* (13.1) that comprises the bulk of the diet at Marcus Island . The precise numerical effects of these factors on the energy budget of *H. midae* at 14°C and 19°C will be calculated in a later publication (Barkai and Griffiths, in prep.) in which we will present full energy budgets for this species at 14°C and 19°C.

ACKNOWLEDGEMENTS

I am grateful to T.A. Probyn and B.A. Bennett of the University of Cape Town for their help and advice in methods and to A. Barkai who assisted in the field work. Financial support was provided through the Benguela Ecology Programme of the S.A. National Committee for Oceanographic Research.

REFERENCES

Barkai, R. and C.L. Griffiths 1986. - Diet of the South African abalone *Haliotis midae*. S. Afr.J. mar. Sci. 4: 37-44.

Barkai, R. and C.L. Griffiths (in prep) - An energy budget for the South African abalone, *Haliotis midae*. S. Afr. J.Mar.Sci.

Bayne, B.L. and R.C. Newell 1983 - Physiological energetics of marine molluscs. In: The Mollusca Vol. 4 Physiology Part 1 eds Wilbur, K.M. and Saleuddin, A.S.M. Academic Press N.Y. 407-515 pp.

Crofts, D.R. 1929 - Haliotis. Liverpool Marine Biological Committee Memoires on Typical British Marine Plants and Animals. 29: 1-74.

Conover, R.J. 1966 - Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11: 338-345.

Egger, D.M. 1977 - Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290-294.

Elliot, J.M. and L. Persson 1978 - The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977-991.

Ghiretti, F. 1966 - Respiration . In: Physiology of Mollusca Vol. II eds K.M. Wilbur and C.M. Yonge Academic Press N.Y and London. 175-208 pp.

Grasshoff, K. 1976 - Methods of seawater analysis. Weinheim: Verlag Chemie. 317 pp.

Jan, R.Q., K.T. Shao and K.H. Chang 1981 - A study of dirunal periodicity in oxygen consumption of the small abalone (*Haliotis diversicolor supertexta* Lischke). Bull. Inst. Zool. Academia sinica. 20(1): 1-8.

Lane, E.D., C.S. Kingsley and D.E. Thornton 1979 - Daily feeding and food conversion efficiency of the diamond turbot: An analysis based on field data. Trans. Am. Fish. Soc. 108: 530-535.

Mace, A.M. and A.D. Ansell 1982 - Respiration and nitrogen excretion of *Polinices alderi* (Forbes) and *Polinices catena* (da Costa) (Gastropoda:Naticidae). J. Exp. Mar. Biol. Ecol. 60: 275-292.

Newman, G.G. 1966 - Movement of the South African abalone *Haliotis midae*. Investl Rep. Div. sea Fish. S. Afr. 56: 19pp.

Newman, G.G. 1967 - Reproduction of the South African abalone *Haliotis midae*. Investl Rep. Div. Sea Fish. S. Afr. 64: 24 pp.

Newman, G.G. 1968 - Growth of the South African abalone *Haliotis midae*. Investl Rep. Div. Sea Fish. S. Afr. 67: 24pp.

Newman, G.G. 1969 - Distribution of the abalone (*Haliotis midae*) and the effect of temperature on reproductivity. Investl Rep. Div. Sea Fish. S. Afr. 74: 7pp.

Sokal, R.R. and F.J. Rohlf 1969 - Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Company San Francisco. 776 pp.

Stephenson, T.A. 1924 - Notes on *Haliotis tuberculata* Part 1. J. Mar. Biol. Ass. U.K. 13(2): 480-495.

Stickle, W.B. and B.L. Bayne 1982 - Effects of temperature and salinity on oxygen consumption and nitrogen excretion in *Thais (Nucella) lapillus* (L). J. Exp. Mar. Biol. Ecol. 58: 1-17.

Trueman, E.R. and A.C. Brown 1985 - The mechanism of shell elevation in *Haliotis* (Mollusca Gastropoda) and a consideration of the evolution of the hydrostatic skeleton in Mollusca. J. Zool. Lond.(A) 250: 585-594.

Uri, N. and S. Kikuchi 1975 - Oxygen consumption of the abalone, *Haliotis discus hannai* in relation to body size and temperature. Bull. Tohoku Reg. Fish. Lab. 35: 73-84.

ENERGY BUDGET

INTRODUCTION

The South African abalone, *Haliotis midae*, is a large gastropod found on shallow sublittoral reefs from the western Cape Province to the Transkei, where it grazes on macroalgae (Newman 1965, Day 1974, Field et al 1977). Like other large Haliotidae from California, Japan, Australia, and New Zealand, *H. midae* is extensively utilized for food by man. Subsistence fisheries for *H. midae* have been in existence in South Africa since prehistoric times (Avery 1974, Van Noten 1974, Robertshaw 1977, Deacon 1979, Poggenpoel and Robertshaw 1981, Smith 1981, Deacon 1979), and a substantial recreational fishery persists to this day. Commercial exploitation, aimed mainly at the export market, began in the 1950's, but is restricted to the South Western Cape Province, where abalone are most abundant (Newman, 1969). The current commercial production of abalone is about 640,000Kg y^{-1} with a revenue value in excess of R5m ($2.35m U.S.), (Chief Directorate, Marine Development, Annual Report 1984). Because of the apparent vulnerability of this accessible and long lived mollusc to exploitation, studies of its movements, reproduction, growth and distribution were carried out by the then Division of Sea Fisheries during the 1960's (Newman 1966,1967,1968,1969). Subsequently Trueman and Brown (1985) have investigated the mechanisms of shell elevation and Barkai and Griffiths (1986, in press) the diet and various aspects of the physiology, namely feeding, absorption, respiration and excretion.

Scattered within these publications are most of the data necessary to calculate an energy budget for *H. midae*. In the following account we have attempted to convert these existing data into energy units and to provide the additional information necessary to compute both individual and population energy budgets. Very few energy budgets have been compiled for grazing gastropods, the available data having been reviewed by Bayne and Newell (1983). Comparable data for *H.midae* is of interest not only because of its economic importance, but also because of the unusually large size and long life cycle of this species relative to those of other gastropods that have been studied.

INDIVIDUAL ENERGY BUDGET

The relationships between body size and the various components of the standard energy budget equation: C= (Pg+Pr)+R+F+U are considered separately below. The data are then combined to provide a picture of the changing pattern of energy allocation throughout an individual's lifespan.

a) Consumption (C)

Haliotis midae are entirely herbivorous. The diet varies slightly with body size, season and locality, but the most important food items are kelp, *Ecklonia maxima*, the red algae *Plocamium spp*. and *Hypnea spicifera* while in juvenile abalone, *Ulva spp*.may also be significant (Barkai and Griffiths,1986).

Adult abalone show a marked diurnal feeding rhythm, consisting of an ingestion phase lasting from late afternoon to early morning and a day time elimination period. Using a cyclical feeding and elimination model Barkai and Griffiths (in press) were able to estimate rates of food consumption for natural abalone populations at two study sites, one on the west coast, (with a mean water temperature of 14°C) and the other on the south coast, (with mean water temperature of 19°C) of South Africa. Daily rations (g wet mass) were related to wet body mass by the following equations:

$$C = 0{,}54W^{0.67} \text{ at } 14^{\circ}C$$

and

$$C = 0{,}35W^{0.77} \text{ at } 19^{\circ}C$$

This in effect means that the ration declines from about 9-6% wet body mass d^{-1} over a size range 200-700g wet flesh mass at 14°C and 11-7% at 19°C.

These consumption readings may be converted to energy equivalents using the wet to dry mass conversions and calorific values for various sublittoral algal species given by Field et al (1980).

The resulting relationships between dry flesh mass and consumption rate (KJy^{-1}) are:

$$C = 1.1x10^{3}W^{0.58} \text{ at } 14^{\circ}C$$

and

$$C = 5.9x10^{2}W^{0.85} \text{ at } 19^{\circ}C$$

b) Growth rate (Pg)

Rates of growth of *H. midae* have been estimated by Newman (1968), using both tagging and population sampling techniques. He found the rate of growth, expressed in terms of rate of change in shell breadth, to be best represented by a Van Bertalanffy growth equation:

$$Lt = 19.33(1-e^{-0.0593(t-1.8820)})$$

In order to convert these increments in size to energy units it is necessary to know the relationships between shell width and both flesh and shell mass, and then to convert these weights to energy equivalents.

Wet flesh mass is related to shell width by the equation:

$$W\ (\text{g wet}) = 0.3608\ B(\text{cm})^{2.7736} \quad (\text{Newman, 1968})$$

Using ballistic bomb calorimetry we found the mean calorific value of *H.midae* flesh to be 18.96 (0.68 SD n=15) KJg^{-1} dry mass. The wet to dry mass ratio was 5:1, giving an energy equivalent of 3.8 KJg^{-1} for wet flesh. This allows conversion of Newman's equation to one relating shell breadth to energy content of the flesh:

$$\text{Flesh energy (KJ)} = 1.4B^{2.7736}$$

Newman (1968) did not consider increments in shell mass, but by measuring the dry mass of 100 *H.midae* shells we were able establish a relationship between shell breadth and dry shell mass:

$$\text{Dry shell mass (g)} = 0.05\ B^{3.24}(\text{cm})$$

Dry shell had a mean organic content of 26.5% and an energy content of 0.8 (+ 0.28 SD)KJg^{-1} whole dry mass. Shell energy content is thus related to shell breadth by the equation:

$$\text{Shell energy (KJ)} = 0.04\ B^{3.24}$$

It transpires from these calculations that *H.midae* consists of approximately 56% shell and 44% flesh in terms of dry mass, while the shell forms 13% and the flesh 87% of energy content. This figure is somewhat higher than that recorded for limpets by Branch (1981), but falls well below the 25-50% of the annual production invested in shell growth by bivalves such as *Aulacomya ater* (Griffiths and King, 1979), *Crassostrea virginica* (Dame, 1976), *Ostrea edulis* (Rodhouse, 1978) and *Geukensia demissa* (Kuenzler , 1961).

c) Reproductive output (Pr)

Various aspects of the reproductive biology of *H.midae*, including the structure of the gonads, sex ratio, size at maturity, reproductive cycle and fecundity, are described by Newman (1967). *H.midae* is a dioecious species, with males and females equally represented in the population. The extensive superficial gonad is cream coloured in males and green in females and lies around the digestive gland. Fifty percent sexual maturity is attained at a wet flesh mass of 140g, equivalent to a shell breadth of 8.0cm, with 100% of individuals mature at a size of 275g or 10.5cm shell breadth. (Newman, 1967)

There is some local variation in the reproductive cycle and intensity, but most populations studied spawned twice a year, once in spring or early summer and again in late summer or autumn. Other species of *Haliotis* which also spawn in late summer to autumn are *H.ruber* (Harrison and Grant, 1971), *H.iris* (Poore,1973) and *H.tuberculata* (Stephenson, 1924) while other species such as *H.rufescens* (Boolootain et al,1962) and *H.corrugata* (Tutschulte and Connell,1981) spawn during most of the year. Fecundity, expressed in terms of egg production (per individual spawning) is linearly related to wet flesh mass, according to the equation:

$$F\ (\times 10^{6}\ \text{eggs}) = 0.0198\ W(g) - 2.196$$

This converts to a power function relating fecundity to shell breadth (Newman,1967):

$$F\ (\mathrm{x}10^{6}\ \mathrm{eggs}) = 0.0004257\ B(\mathrm{cm})^{3.787}$$

In order to convert these fecundity estimates to units of energy it is necessary to know the calorific value per egg. This was obtained by dissecting ten gonads of matured females (shell width 11,4 cm), a few weeks before spawning season. Five subsamples were taken from each gonad in which total number of eggs were counted under a dissecting microscope. The eggs were then dried for 48 hours at 60° C. The dry weight of each of the 50 samples, was divided by the number of eggs and the results averaged to give a mean dry mass per egg of $3{,}94\mathrm{x}10^{-6}$ g. The energy content of gonad was 26.46 (± 1.35 SD) KJg^{-1} dry mass. Reproductive output is thus related to shell breadth by the equation:

$$\text{Reproductive output } (\mathrm{KJy}^{-1}) = 0.0886\ B^{3.787}$$

No date is available on reproductive output in males, but it appears from the changes in gonad bulk index given by Newman (1967) that reproductive output is similar in both sexes. For the purposes of energy budget calculation we have thus assumed that the energy expended on reproduction is the same in both males and females. Proportional intensity of spawning at South and West coast sites was estimated from the gonad bulk index curves given by Newman (1967).

d) Respiration (R)

Rates of oxygen consumption in *H.midae* have been measured at both 14°C and 19°C by Barkai and Griffiths (in press), who relate respiration rate to wet flesh mass by the equations:

$$R\ (\mathrm{ml}O_2h^{-1}) = 0.03\ W^{0.83}\ (g)\ \text{at}\ 14^{\circ}$$

and

$$R\ (\mathrm{ml}O_2h^{-1}) = 0.03W^{0.94}\ (g)\ \text{at}\ 19^{\circ}C$$

No differences in respiration rate could be detected between freshly collected and starved individuals, nor between readings made by night and by day.

For energy budgeting purposes these rates may be converted to units of energy per gram dry mass using the previously estabilshed wet to dry mass ratio of 5:1 and an oxycalorific coefficient of 0.02 kJmlO$_2^{-1}$ (Hughes 1970). The relationship between dry flesh mass and respiration rates (KJy^{-1}) thus become:

$$R=33.07W^{0.81} \text{ at } 14^{\circ}C$$

and

$$R = 42.70W^{0.93} \text{ at } 19^{\circ}C$$

e) Faecal losses (F)

Rates of loss of faecal material may be estimated from the product of the feeding rate (above) and the absorption efficiency. Using the Conover Ratio method (Conover 1966), Barkai and Griffiths (in press) have estimated the absorption efficiency of H. midae feeding on a natural diet, primarily of *Ecklonia maxima*, as being 37.25%. No size specific variations in absorption efficiency were detected amongst abalone over a size range of 100-600g wet flesh mass, so this figure is assumed to apply to all size classes. These measurements were made at 14°C and the effects of temperature on absorption efficiency were not investigated, although studies on other molluscs indicate that absorption efficiency is not strongly influenced by temperature over the natural range at which animals survive in the field (Buxton et al, 1981, Winter, 1969, Ansell, 1981, Bayne and Newell, 1983).

f) Excretion (U)

The principal excretory product in molluscs is generally ammonia (Bayne 1976, Bayne and Scullard 1977, Mace and Ansell 1982, Stickle and Bayne 1982) and rates of ammonia production in *H. midae* are given by Barkai and Griffiths (in press). They relate rate of ammonia excretion to wet flesh mass (g) by the equations:

$$U\ (\mu\text{mole h}^{-1}) = 0.22W^{0.43} \text{ at } 14°\text{C}$$

and

$$U\ (\mu\text{mole h}^{-1}) = 0.03W^{0.85} \text{ at } 19°\text{C}$$

These values may be converted to energy equivalents from the relationships 1g ammonia = 20.5 kJ (Brafield and Llewellyn, 1982) and 1µmole ammonia = 18µg. The relationships between U in kJy^{-1} and dry flesh mass are:

$$U = 1.37W^{0.48} \text{ at } 14^{\circ}C$$

and

$$U = 0.58W^{0.85} \text{ at } 19^{\circ}C$$

g) Compiling the individual energy budgets

In order to examine the changing pattern of energy allocation throughout life individual lifetime energy budgets were constructed as follows:

Shell width and flesh mass were first calculated for abalone of set ages (annually from age 1-10, two yearly thereafter), using the growth equations given in section (b). Consumption rates and energy expended on each of the energy budget parameters were then calculated for animals of these sizes and the results plotted as cumulative curves (Fig. 3.1). Since several of the energy budget parameters, namely C,R and U, were measured at two

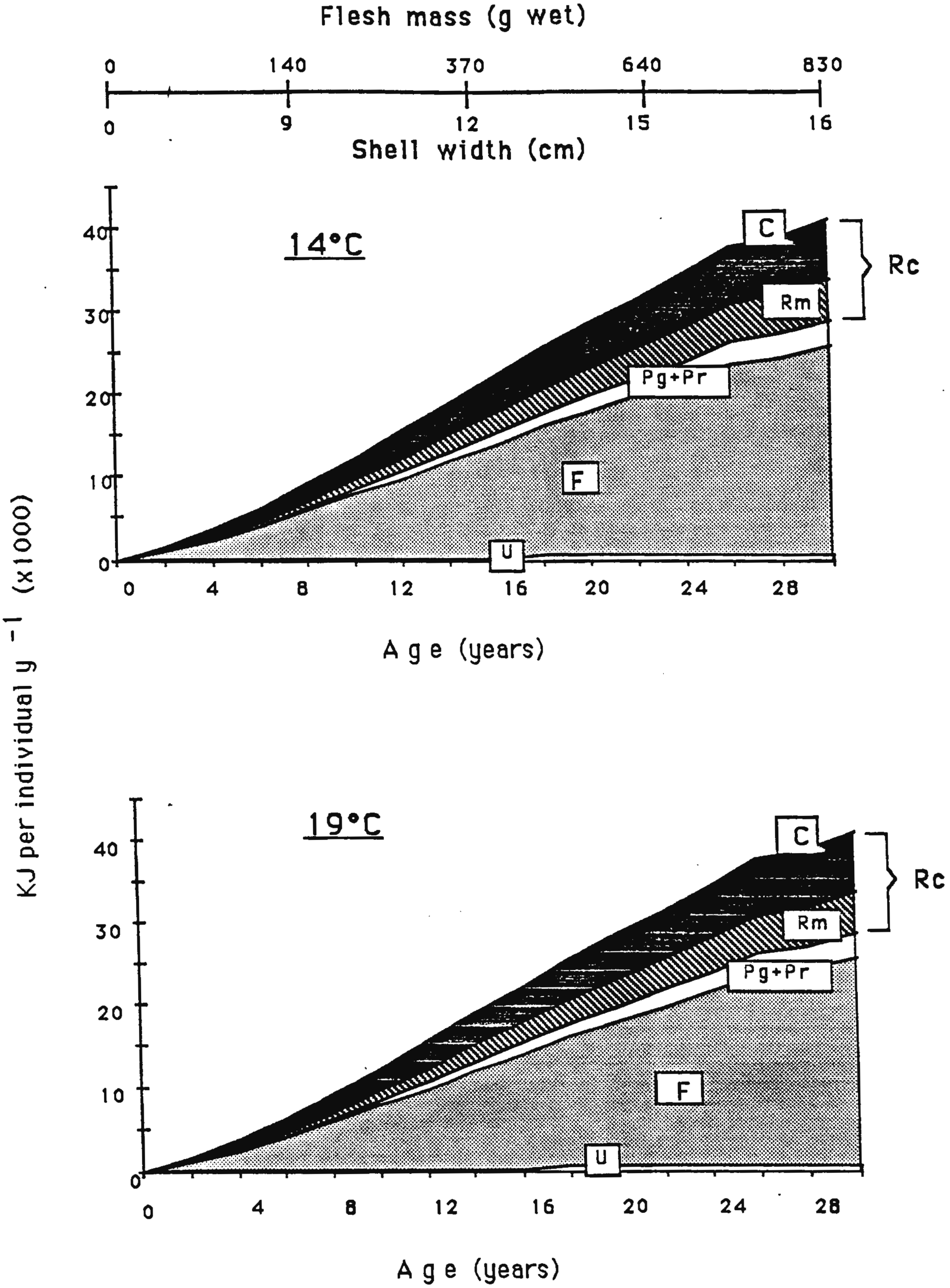

Fig 3.1

Patterns of energy acquisition and expenditure in <u>Haliotis midae</u> in two temperatures. The area shaded by black indicates imbalance in measured parameters i.e the difference between measured energy consumption and sum of expenditures on P+R+F+U.

temperatures, representative of South coast (19°C) and West coast (14°C) respectively, we have attempted to calculate separate plots for these two temperatures. Although it is possible to obtain separate estimates for reproductive output on the two coasts from the relative magnitudes of the fluctuations in gonad bulk index for the two populations, as depicted by Newman (1967), we have had to assume that growth and absorption efficiency are independent of temperature over this fairly narrow range. Evidence from the literature does indeed suggest that absorption efficiency is relatively insensitive to temperature (see section (e) above). We have no data on the influence of temperature on growth in *H. midae*. Although Newman (1969) assumed growth rates along the cooler west coast to be slower, the fact that the size frequency distributions of south and west coast populations are remarkably similar (Fig. 3.2) indicates that growth rates are probably similar in the two areas. According to Sakai (1962) who studied the growth rate of *H. discus hannai* in three different sites, the annual fluctuation in growth was not significantly correlated with temperature. While studies on the Australian abalone *H. laevigata* and

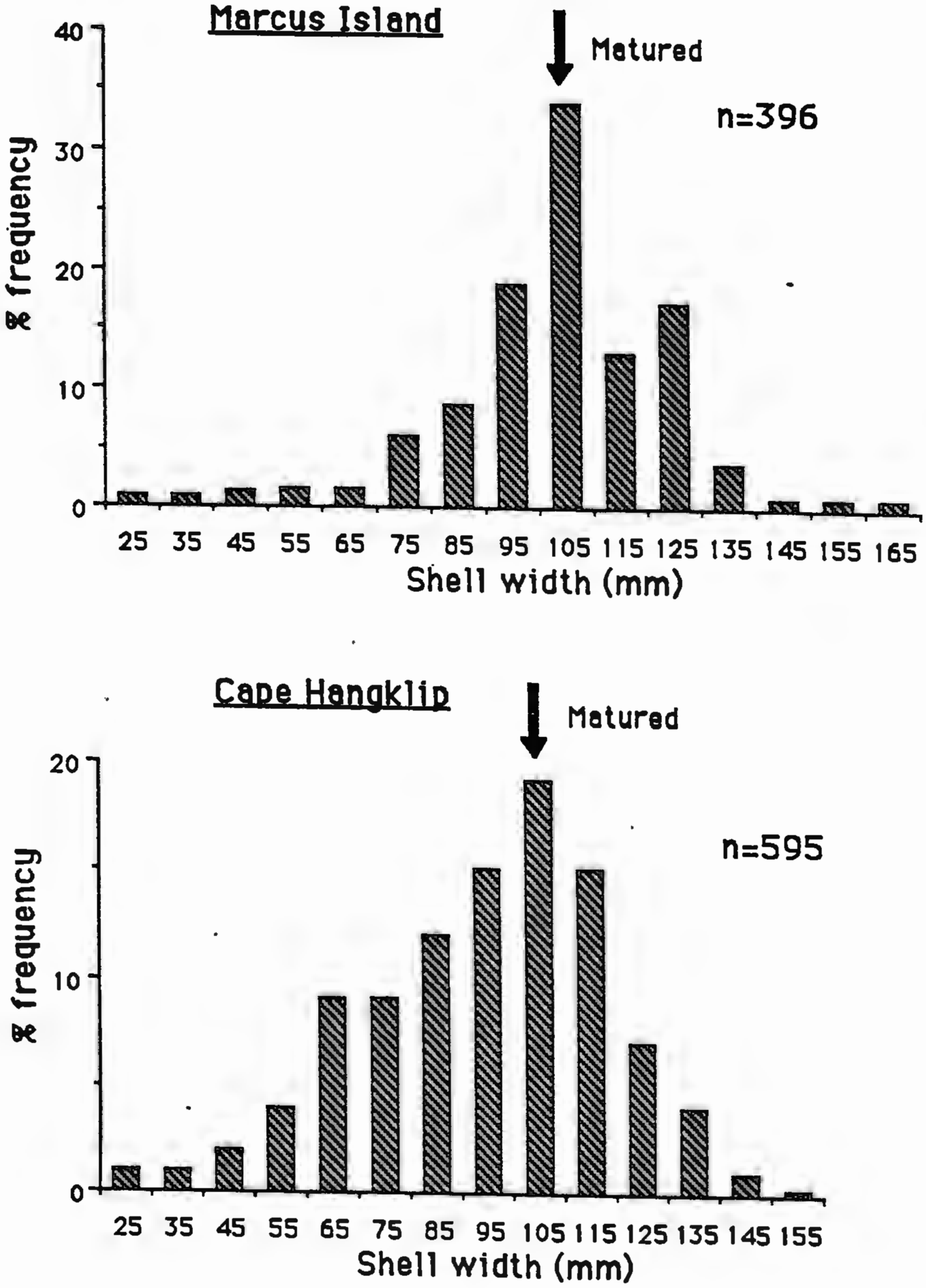

Fig 3.2

Size frequency distributions for populations of *Haliotis midae* from Marcus Island and Cape Hangklip.

H. ruber (Shepherd and Hearn, 1983) suggest differences in growth rate within a species between sites of different temperatures, these result predominantly from differences in the food supply.

Examining the two lifetime energy budgets in Fig.3.1, it is evident that the proportional allocation of energy to the various energy budget parameters is similar at both sites, but that overall rates are somewhat higher at 19°C than at 14°C. Approximately 63% of ingested energy is lost in the faeces. Excretory costs are very low, comprising less than 1% of ingested energy in all size classes.Some 5% of available energy is allocated to production, with an increasing proportion of this utilised for reproductive purposes in older individuals. By subtraction this would suggest that some 32% of energy is lost via respiration. Actual laboratory measures of R, however, indicate far lower rates of about 8% ingested energy.Similar imbalances between estimates of respiratory energy expenditure obtained by laboratory measurements (Rm) versus calculation by subtraction (Rc) have frequently been reported (Bayne and Newell, 1983) and probably result from suppression of normal locomotory activity within respirometer chambers. In order to compensate for these presumed underestimates some authors have arbitrarily multiplied Rm values by a factor of 2 or 3 (Bayne and Newell, 1983), although acceptance of the Rc value may be a more reasonable course to adopt and is the one we have applied to Fig. 3.2 and our subsequent population energy budget calculations.

POPULATION ENERGY BUDGETS

Estimates of population density and size distribution were obtained for both cool west coast and warmer south coast sites. A single location, Marcus Island, in Saldanha Bay (33°03'S, 17°58'E) was surveyed on the west coast but a mean of five sites in the vicinity of Cape Hangklip (34°22'S, 18°50'E) were taken as representative of south coast populations (Tarr , unpublished). In each case a belt transect method was used in which a weighted rope was laid across the sampling area parallel to the shore in not more than 10m depth and divers swam along the line recording all abalone within 1m of the rope. Random samples of about 500 animals were taken out of the water and measured for size frequency distributions in each site.

The mean density of *H. midae* was 0,3 animals m^{-2} or 82g (wet mass) m^{-2} on the west coast and 0,56 animals m^{-2} or 133 gm^{-2} on the south coast The size frequency distributions in the two areas were similar, the mean shell widths being 106mm and 100mm respectively (equivalent to wet flesh masses of 249 and 212g).

Population energy budgets were obtained by calculating the population densities of each 10mm size class of abalone (using overall density and size frequency figures) and reading off rates of energy aquisition and expenditure from the various equation given above.

Total rates of energy turnover, expressed in terms of $kJm^{-2}y^{-1}$ and percentages are given in Table 3.1.

For these calculations R is obtained by difference i.e. $R = C-(Pg+Pr+F+U)$.

DISCUSSION

The lifetime energy budget diagrams shown in Fig 3.1 indicate that there are only minor changes in the proportional allocation of energy with abalone age or size.

		C	Pg	Pr	Rc	F	U	$\bar{B}$	$P/\bar{B}$
14°C	$KJm^{-2}y^{-1}$	3,260	44	107	1052	2054	3	328KJm^{-2}	0.46
	%	100	1.4	33	32.2	63.0	0.1		
19°C	$KJm^{-2}y^{-1}$	8,613	78	297	2803	5426	9	532KJm^{-2}	0.70
	%	100	1.0	3.4	32.5	63.0	0.1		

Table 3.1 Total rates of energy turnover ($KJm^{-2}y^{-1}$ and %) for populatons of *H. midae* from Marcus Island (14°C) and Cape Hangklip (19°C).

Some 63% of the energy value of ingested food is lost in the faeces. This is somewhat higher than the average for grazing gastropods (51.8% + 14.9% SD) given by Bayne and Newell (1983), but within the range of values in the literature. The relatively low absorption efficiency can probably be attributed to the tough nature of *Ecklonia maxima* fronds, relative to those of most algae eaten by the smaller herbivorous gastropods.

The proportion of energy expended on respiration was estimated as 8% from laboratory measurements, but as 32% by subtraction. The fact that the average value for eight grazing gastropods is given by Bayne and Newell (1983) ie. 37.4% + 9.7% SD indicates that R was indeed underestimated during laboratory experiments and that abalone ranging free in the field consume some 4X more oxygen that those in laboratory chambers. Houlihan and Innes (1982), who studied the relationship between oxygen consumption and crawling speed and calculated the cost of transport in four intertidal gastropods, recorded an increase in oxygen consumption of up to 300% of the inactive rate, in both air and water. In the table of the scope for activity of eight mollusc species, they also show that the locomotion cost for gastropods may be about five times higher, than for example, in running vertebrates and ants, this being associated to a certain extent with mucus production. As feeding is also associated with increase in oxygen consumption (Bayne and Newell, 1983), it is quite expected that *H. midae* feeding purposes expresses much lower rates of oxygen consumption while confined in an experimental chamber in a completely inactive state than it would in the field.

Energy losses via ammonia excretion were negligible, but since very few readings of U have been made for gastropod populations, few comparative data exist. Some authors have suggested that mucus production may be responsible for significant excretory losses (Paine 1971; Calow 1974, 1977) but we were unable to measure mucus production in *H. midae*.

The proportion of energy allocated to production in *H. midae* was only 5%, lower than the 8.8% (± 6.2% SD) average given by Bayne and Newell (1983). The species is however larger and longer lived than any of those previously studied, so this is not unexpected. The proportion of production allocated to somatic growth is 100% until maturity is attained at about 80-105mm shell breadth (7-11 years old). Thereafter an increasing proportion of production is allocated to reproductive output, this reaching about 91% and 95% of total production at 150mm at 14°C and 19°C respectively.

Comparing individual energy budget at 14°C and 19°C we found very little change in the proportion of consumed energy allocated to the various metabolic rate processes, although the enery consumed per matured individual rose by up to about 80%.

Turning to the population energy budgets, the net production efficiencies (P/A) within invertebrates are lower in herbivores than in any other trophic category (Humphreys 1974). Bayne and Newell (1983) gave mean values for P/C and P/A in populations of grazing gastropods of 9% and 18% respectively. These data represent averages of species much smaller in size and shorter lived than *H.midae*. As lower production efficiency is also associated with long lived poikilotherms (McNeill and Lawton 1970) it is not surprising that *H. midae* shows lower values of 4,5% and 12,5% respectively. The low ratios are also an indication of a low proportion of young individuals and more stable population. The annual turnover rate of those populations of *H.*

midae is also low (P/B 0.5 and 0.7 at 14°C and 19°C respectively) reflecting the slow growth rate of the species but a high standing crop. These P/B ratios fit well to the expected ratio for long lifespan gastropods given by Robertson (1979) who predicts that a species living 25 years should have a P/B ratio of about 0.44. It is clear that *H. midae* populations at these high density sites are very important consumers. Thus the population at Marcus Island, which has a standing stock of 82g (wet flesh)m^{-2} (or 328 KJm^{-2}) consumes 3 260 $KJm^{-2}y^{-1}$ algae, almost all in the form of kelp, *E. maxima*. At Cape Hangklip the abalone population is even more dense at 133g wet m^{-2} (532 KJm^{-2}) and, at this higher temperature, consumes 8 613 $KJm^{-2}y^{-1}$. These figures are in contrast to those provided in the kelp bed community energy budget compiled by Newell et al (1982). These authors estimate total macrophyte production within a typical kelp bed (mean depth 10m) at $38x10^3$ $kJm^{-2}y^{-1}$ and suggest that only aout 12% of this production is directly consumed by grazers, mainly sea urchins, *Parechinus angulosus*. These calculations were however, based on measurements taken at study sites where abalone have been reduced to very low levels through sustained human exploitation. The primary production figures are, moreover, averages, and it has been well established that both the biomass and rates of primary production of kelp decline rapidly with depth (Velimirov et al 1977; Field et al 1980; Dieckmann 1980). Rates of primary reproduction in the dense shallow *Ecklonia maxima* beds in which most abalone live are thus likely to be very much higher than the average values given by Newell et al (1982). There is nevertheless, no doubt that where dense abalone populations persist, a high proportion of macrophyte production passes through the herbivore food chain. Much of this material will, however, subsequently be lost as faeces that may become available as food to the filter feeding community that dominates the offshore portion of kelp beds throughout the area (Velimirov et al 1977).

ACKNOWLEDGEMENTS

I am grateful to R.J.Q. Tarr of the Sea Fisheries Research Institute for useful information and advice in methods, to A. Barkai, S. Tugwell and K. Findlay of the University of Cape Town who assisted in the field work and to S. Tolosana and J. Burbidge for typing the script. Financial support was provided through the Benguela Ecology Programme of the South African National Committee for Oceanographic Research.

REFERENCES

Ansell, A.D. 1981 - Experimental studies of a benthic predator-prey relationship. Feeding, growth and egg collar production in long-term cultures of the gastropod drill *Polinices alderi* (Forbes) feeding on the bivalve *Tellina tenuis* (da Costa). J. Exp. Mar. Biol. 56: 1-21.

Avery, G. 1974 - Open station shell midden sites and associated features from the Pearly Beach area, south-western Cape. S. Afr. Archaeol. Bull. 29: 104-114.

Barkai, R. and Griffiths, C.L. 1986 - Diet of the South African abalone *Haliotis midae*. S. Afr. J. Mar. Sci. 4: 37-44.

Barkai, R. and Griffiths, C.L. in press - Consumption, absorption efficiency, respiration and excretion in the South African abalone, *Haliotis midae*. S. Afr. J. Mar. Sci.

Bayne, B.L., 1976 - Marine Mussels, their Ecology and Physiology. Cambridge University Press, London.

Bayne, B.L. and Newell, R.C. 1983 - Physiological energetics of marine molluscs. In: The Mollusca Vol. 4 Physiology Part I (Wilbur, K.M. and Saleuddin, eds.) 407-515. A.S.M. Academic Press N.Y.

Bayne, B.L. and Scullard, C. 1977 - Rates of nitrogen excretion by species of *Mytilus* (Bivalvia:Mollusca). J. Mar. Biol. Assoc. U.K. 57: 355-367.

Boolootain, R.A., Farmanfarmaian, A. and Giese, A.C. 1962 - On the reproductive cycle and breeding habits of two western species of *Haliotis*. Biol. Bull. 122: 183-193.

Brafield, A.E. and Llewellyn, M.J. 1982 - Animal Energetics. Blackie and Son, Glasgow.

Branch, G.M., 1981 - The biology of limpets: physical factors, energy flow, and ecological interactions. Oceanogr. Mar. Biol. Ann. Rev. 19: 235-380.

Buxton, C.D., Newell, R.C. and Field, J.G. 1981 - Response-surface analysis of the combined effects of exposure and acclimation temperature on filtration, oxygen consumption and scope for growth in the oyster *Ostrea edulis*. Mar. Ecol. Prog. Ser. 6: 73-82.

Calow, P., 1974 - Some observations on locomotory strategies and their metabolic effects in two species of freshwater gastropods, *Ancylus fluvuatilis* Mull. and *Planorbis contortus* Linn. Oecologia 16: 149-161.

Calow, P., 1977 - Ecology, evolution and energetics : A study in metabolic adaptation. Adv. Ecol. Res. 10: 1-62.

Conover, R.J., 1966 - Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11: 338-345.

Dame, R.F., 1976 - Energy flow in an intertidal oyster population. Estuar. Coastl. Mar. Sci. 4: 243-253.

Day, J.H., 1974 - A guide to marine life on South African Shores. 2nd ed. A.A. Balkema, Cape Town.

Deacon, J. 1979 - Guide to archaeological sites in the southern Cape. Occ. Publ. Dept. Archaeol. Univ. Stellenbosch 1: 1-149.

Dieckmann, G.S., 1980 - Aspects of the ecology of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula (South Africa). I. Seasonal growth. Bot. Mar. 23: 579-585.

Field, J.G., Jarman, N.G., Dieckman, G.S., Griffiths, C.L., Velimirov, B. and Zoutendyk, P. 1977 - Sun, waves, seaweed and lobsters: the dynamics of a west coast kelp-bed. S. Afr. J. Sci. 73: 7-10.

Field, J. G., Griffiths, C. L., Griffiths, R. J., Jarman, N. G., Zoutendyk, P., Velimirov, B. 1980 - Variation in structure and biomass of kelp communities along the south west Cape Coast. Trans. R. Soc. S. Afr. 44: 145-203.

Griffiths, C.L. and King, J.A. 1979 - Energy expended on growth and gonad output in the ribbed mussel *Aulacomya ater*. Mar. Biol. 53: 217-222.

Harrison, A.J. and Grant, J.F. 1971 - Progress in abalone research. Tasmanian Fish. Res. 5(1): 1-10.

Houlihan, D.F. and Innes, A.J. 1982 - Oxygen consumption, crawling speeds and cost of transport in four Meditteranean intertidal gastropods. J. Comp. Physiol. 147: 113-122.

Hughes, R.N., 1970 - An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (Da Costa). J. Anim. Ecol. 39: 357-381.

Humphreys, W.F., 1979 - Production and respiration in animal populations. J. Anim. Ecol. 48: 427-453.

Kuenzler, E.J., 1961 - Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. Oceanogr. 6: 191-204.

Mace, A.M. and Ansell, A.D. 1982 - Respiration and nitrogen excretion of *Polinices alderi* (Forbes) and *Polinices satena* (da Costa) (Gastropoda:Naticidae). J. Exp. Biol. 60: 275-292.

McNeill, S. and Lawton, J.H., 1970 - Annual production and respiration in animal populations. Nature Lond. 225: 472-474.

Newell, R.C., Field, J.G., Griffiths, C.L., 1982 - Energy balance and significance of micro-organisms in a kelp-bed community. Mar. Ecol. Prog. Ser. 8: 103-113.

Newman, G.G., 1965 - Abalone research in South Africa. S. Afr. Shipp. News Fish. Ind. Rev. 20(5): 93-101.

Newman, G.G., 1966 - Movement of the South African abalone *Haliotis midae*. Investl Rep. Div. Sea Fish. S. Afr. 56: 1-19.

Newman, G.G., 1967 - Reproduction of the South African abalone *Haliotis midae*. Investl Rep. Div. Sea Fish. S. Afr. 64: 1-24.

Newman, G.G., 1968 - Growth of the South African abalone *Haliotis midae*. Investl. Rep. Div. Sea Fish. S. Afr. 67: 1-24.

Newman, G.G., 1969 - Distribution of the abalone (*Haliotis midae*) and the effect of temperature on reproductivity. Investl Rep. Div. Sea Fish. S. Afr. 74: 1-7.

Paine, R.T., 1971 - Energy flow in a natural population of the herbivorous gastropod *Tegula funebralis*. Limnol. Oceanogr. 16: 86-98.

Poggenpoel, C.A. and Robertshaw, P.T., 1981 - The excavation of Smitswinkelbaai Cave, Cape Peninsula. S. Afr. archaeol. Bull. 36: 29-35.

Poore, G.C.B., 1973 - Ecology of New Zealand abalones, *Haliotis* species (Mollusca:Gastropoda) part 4. Reproduction. N.Z. J. Mar. Freshw. Res. 7(1+2): 67-84.

Robertshaw, P.T. 1977 - Excavations at Paternoster, south western Cape. S. Afr. archaeol. Bull. 32: 63-73.

Robertson, A.J. 1979 - The relationship between annual production:biomass ratios and lifespans for marine macrobenthos. Oecologia (Berlin), 38: 193-202.

Rodhouse, P.G. 1978 - Energy transformations by the oyster *Ostrea edulis* L. in a temperate estuary. J. Exp. Mar. Biol. Ecol. 34: 1-22.

Sakai, S. 1962 - Ecological studies on the abalone, *Haliotis discus hannai* In - III. Study on the mechanism of production of the abalone in the region of Onagawa Bay. Bull. Jap. Soc. Sci. Fish. 28(9): 891-899.

Shepherd, S.A. and W.S. Hearn, 1983 - Studies on Southern Australian abalone (Genus Haliotis). Part IV. Growth of *H. laevigata* and *H. ruber*. Aust. J. Mar. Freshw. Res. 34: 461-475.

Smith, A.B., 1981 - An archaeological investigation of Halocene deposits at Rooi Els Cave, south western Cape. S. Afr. archaeol. Bull. 36: 75-83.

Stephenson, T.A. 1924 - Notes on *Haliotis tuberculata* Part I. J. Mar. Biol. Assoc. U.K. 13(2): 480-495.

Stickle, W.B. and B.L. Bayne, 1982 - Effects of temperature and salinity on oxygen consumption and nitrogen excretion in *Thais (Nucella) lapillus*. J. Exp. Mar. Biol. Ecol. 58: 1-17.

Tarr, R.J.Q., 1966 - Size distributuon and count survey of *H. midae*. Sea Fisheries Institute of South Africa. Unpublished.

Trueman, E.R. and Brown, A.C. 1985 - The mechanism of shell elevation in *Haliotis* (Mollusca Gastropoda) and a consideration of the elevation of the Hydrostatic skeleton in Mollusca. J. Zool. Lond. 250(A): 585-594.

Tutschulte, T. and J.H. Connell, 1981 - Reproductive biology of three species of abalones (*Haliotis*) in Southern California. The Veliger 23(3): 195-206.

Van Noten, F. 1974 - Excavations at the Gordons Bay shell midden, south western Cape. S. Afr. archeol. Bull. 29: 122-142.

Velimirov, B., J.G. Field, C.L. Griffiths, and P. Zoutendyk, 1977 - The ecology of kelp bed communities in the benguela upwelling system. Helgol. Wiss. Meeresunters. 30: 495-518.

Winter, J.E. 1969 - On the influence of food concentration and other factors on filtration rate of food utilization in the mussels *Arctica islandica* and *Modiolus modiolus*. Mar. Biol. 4: 87-135.