# THE INTERTIDAL AND SHALLOW SUBTIDAL FOOD WEB OF SUB-ANTARCTIC MARION ISLAND

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Plate 1. A group of Marion Island starfish, *Anasterias rupicola*, co-operatively attacking a limpet, *Nacella delesserti*, which would be too large for an individual starfish to capture (see Part 3).

A photograph of a watercolour painting by Vanessa Blankley.

# FOREWORD

The work presented here is the major portion of the research I did whilst employed as a marine biologist on the Marion Island Marine Biology Programme. This programme is logistically supported and financed by the Department of Transport as advised by the South African Scientific Committee for Antarctic Research. Professor J.R. Grindley of the School of Environmental Studies, University of Cape Town is leader of the programme and Professor G.M. Branch supervised this project. The support and advice of the above organizations and people is gratefully acknowledged. Special thanks are due to Professor Branch for all the time, patience and constructive criticism he has given me and my work. Thanks also to my colleague Peter Haxen for his help and companionship in the field and laboratory. More specific help and advice given by other people are acknowledged in the following papers.

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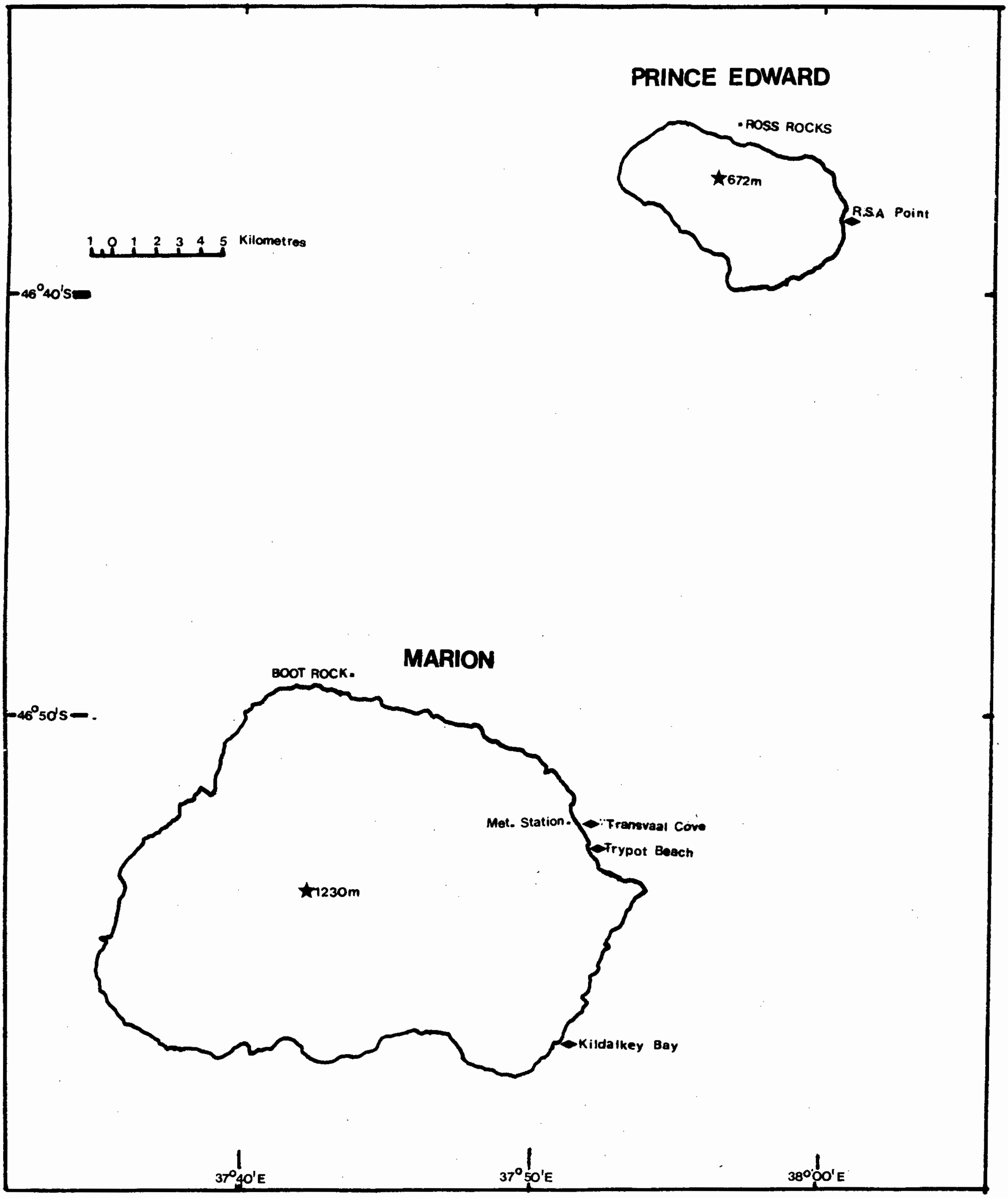

Fig. 1 Outline map of Marion and Prince Edward islands showing the locations of the major study sites (◆).

# INTRODUCTION

The sub-Antarctic Prince Edward Island group, consisting of Marion Island and Prince Edward Island (Fig. 1), was annexed by South Africa in 1947-1948 and subsequently declared a nature reserve. Isolated oceanic islands have always presented interesting opportunities for biological research on both the marine mammals and birds which use them for breeding purposes and the resident, often specially adapted, fauna and flora which colonise them. The ice-capped, windy and wet Marion and Prince Edward Islands are young volcanic islands, less than 300 000 years old, and house a considerably less diverse biota than the much older Crozet and Kerguelen sub-Antarctic Archipelagos (Van Zinderen Bakker, 1971). In view of the relative simplicity, small size and isolation of the Marion Island ecosystem one of the major goals of the South African Scientific Committee for Antarctic Research (SASCAR) has been to provide a comprehensive model describing the functioning of the system. Thus since the start of official biological research in 1965 many studies have been undertaken in the fields of ornithology, plant ecology, mammalogy and limnology. Marine biological research has been relatively neglected and at the outset of the present project the only work available on the Marion Island littoral fauna, apart from various taxonomic reports, was that of De Villiers (1976) who described species composition and zonation patterns of the shores. The present study, along with Mr Peter Haxen's research on the inshore macro-algae, was aimed at bridging the gap in our knowledge of the intertidal and shallow subtidal communities of Marion Island.

Community structure is a broad topic encompassing a variety of research approaches aimed at identifying the factors responsible for the organisation of a set of sympatric species populations. Very broadly, hypotheses based on biological factors such as competition and predation are emphasised in some studies whilst physical factors like wave action and ice abrasion are the central tenet of other studies. Obviously any single biological community, by definition, has to be a complex entity and although its structure may be reliably defined by significant hypotheses resulting from a single research approach (e.g. biomass or temperature tolerance) the validity of these hypotheses can only be established once the results of other research approaches on the system (e.g. competition or predation) become available.

Research done in the present study should thus be seen as only a subset of the possible research directions that could have been taken in working on the littoral community of Marion Island. The main interests of the study were predator-prey interactions and biomass although aspects of reproduction and ecological behaviour were also investigated.

By studying predators, their prey and the relative abundance of animals in any littoral community, it should be possible, firstly, to discover which are the most important ecological members of the system and secondly, to describe the main patterns of energy flow. These are the major aims of the present study.

The most obvious predators of inshore organisms are the three species of resident birds. Thus studies of the diets and feeding habits of the Kelp Gull *Larus dominicanus*, Lesser Sheathbill *Chionis minor* and Imperial Cormorant *Phalacrocorax atriceps* were undertaken. The abundant starfish *Anasterias rupicola* is a voracious predator of intertidal and subtidal organisms and a study of its diet and feeding ecology was essential for a better understanding of interactions in the benthic community. The unusual social and feeding behaviours of *Anasterias rupicola* proved to be intriguing and prompted further research on its co-operative feeding and brooding habits. Only three species of fish occupy the subtidal zone but they occur at fairly high densities and are important mobile predators of a wide variety of organisms. Hence an analysis of these fishes' diets and feeding interrelationships was also undertaken. As a result of these studies the relative importance of the various prey species emerged and the importance of the dominant limpet *Nacella delesserti* as a major source of food for the Kelp Gull *Larus dominicanus*, the cod *Notothenia coriiceps* and the starfish *Anasterias rupicola* was most striking. A separate study of the biomass and production of *Nacella* was undertaken to provide more information on this central species. In addition a study on the biomass and standing crop energy values of the other prey species was also done. In conclusion, rough energy requirements for the seven predators were calculated and, knowing their major prey, provided data for the construction of a quantitative food web.

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# PART 1

# MARINE FOOD OF KELP GULLS, LESSER SHEATHBILLS AND IMPERIAL CORMORANTS AT MARION ISLAND (SUBANTARCTIC)

## ABSTRACT

Kelp gulls *Larus dominicanus* feed extensively on the intertidal limpet *Nacella delesserti,* and the bivalve *Gaimardia trapesina* from the upper fronds of the off-shore kelp *Macrocystis pyrifera.* Seven monthly collections of *Nacella* shells deposited on Boulder Beach by feeding gulls showed that a mean of 441 ± 236 shells accumulate there per month. *Nacella* from the 40,0 - 55,0 mm size class are most heavily preyed on whilst smaller *Nacella* are swallowed whole and the shells regurgitated later. Regurgitations of crushed *Gaimardia* shells were analysed and each found to contain an average of 8,5 ± 4,2 *Gaimardia* from the 20 - 25 mm size class. Gulls also feed to some extent on the starfish *Anasterias rupicola,* and the fishes *Notothenia macrocephala* and *Harpagifer georgianus.*

The Lesser Sheathbill *Chionis minor* feeds on intertidal seaweed and fauna and also on invertebrates from amongst kelp jetsam but is less dependent on marine food sources than the gulls and cormorants. Analysis of *Chionis* faeces and observations of feeding activities provided data for a description of their major marine prey. The sheathbill feeds mainly on the intertidal alga *Porphyra* but also consumes many *Hyale* amphipods, *Ectemnorrhinus* beetles, limpets

(*Kerguelenella lateralis* and *Nacella*) and littoral insect larvae. They also peck the soft parts from intertidal *Anasterias*, feed on the polychaete *Platynereis australis* and remove small *Nacella* (35 mm) from rocks at low tide. *Nacella* shells at gull feeding sites are scoured for flesh remains.

King cormorants *Phalacrocorax atriceps* dive for demersal prey in the shallow subtidal but probably more in the deeper *Macrocystis* holdfast zone and beyond. Two regurgitations and the stomach contents of a dead chick were the only samples obtained from the poorly established island population. Fish *H. georgianus* and *N. macrocephala*, crustaceans *Nauticavis marionis*, unidentified squid and polychaetes formed the bulk of the stomach contents. These three resident avian species, exploiting the rich littoral food sources at the primary, secondary and tertiary levels, provide a strong trophic link between the terrestrial and local marine systems.

## INTRODUCTION

The three resident bird species of Marion and Prince Edward Islands, the Kelp Gull *Larus dominicanus*, Lesser Sheatbill *Chionis minor* and Imperial Cormorant *Phalacrocorax atriceps* are important predators of intertidal and inshore marine organisms. The birds' diets are little affected by human activities and pollution. One polluting factor is waste food, normally thrown out by the staff of the research station, which is eaten by local gulls, sheathbills and sub-Antarctic Skuas *Catharacta antarctica.* During the major part of this study all waste food was retained and frozen for removal by the relief ship. The installation of an incinerator for food disposal has been recommended.

The Kelp Gulls feed mainly on marine animals but also scavenge and prey on terrestrial invertebrates (Burger 1980). The terrestrial Lesser Sheathbills are wide niched feeders which use the intertidal zone as one of their feeding habitats. Imperial Cormorants feed exclusively on marine species and this study is only a preliminary assessment of their diet. The inshore marine environment is thus important to the livelihood of these three avian species and the aim of this study is to describe their trophic relationships with sea life.

## MATERIALS AND METHODS

All shells of the limpet *Nacella (Patinigera) delesserti* which had been deposited by feeding gulls on Boulder Beach, a 150 m stretch of rocky beach in front of the research station, were collected in October 1979. Subsequent monthly collections were made until May 1980 and were sorted into 5 mm size classes to provide information on the size distribution and numbers of *Nacella* preyed upon. Timed observations of gulls hunting and consuming *Nacella* provided data for the estimation of individual feeding rates.

Intact regurgitations were collected from sites where Kelp Gulls congregated. The lengths of regurgitated *Nacella* shells were recorded for comparison with the beach samples. Regurgitations consisting solely of crushed shells of the bivalve *Gaimardia trapesina* were dried at 60°C for 24 h and then weighed to the nearest 0,1 g. Fresh samples of over 100 *Gaimardia* were dissected and flesh and shells dried separately at 60°C to determine the number of *Gaimardia* represented in an average regurgitation.

Further observations of gull feeding activities were made elsewhere at Marion Island and also at Prince Edward Island.

Lesser Sheathbill faeces were collected on 17 different occasions from the intertidal and splash zones between January and May 1980. Prey remains were sorted to species level and all invertebrates counted. The percentage volume of seaweeds and invertebrates was estimated by eye. Starfish (*Anasterias rupicola*) which had been attacked by Lesser Sheathbills were collected and examined in the laboratory to assess which parts had been eaten. Observations of sheathbills feeding in the intertidal zone provided additional qualitative information on their diet. *Nacella* shells from sheathbill nests were measured and counted.

Two regurgitations from adult cormorants and the stomach contents of a dead chick were examined for prey species composition. Observations of the feeding habits of this species were made where possible.

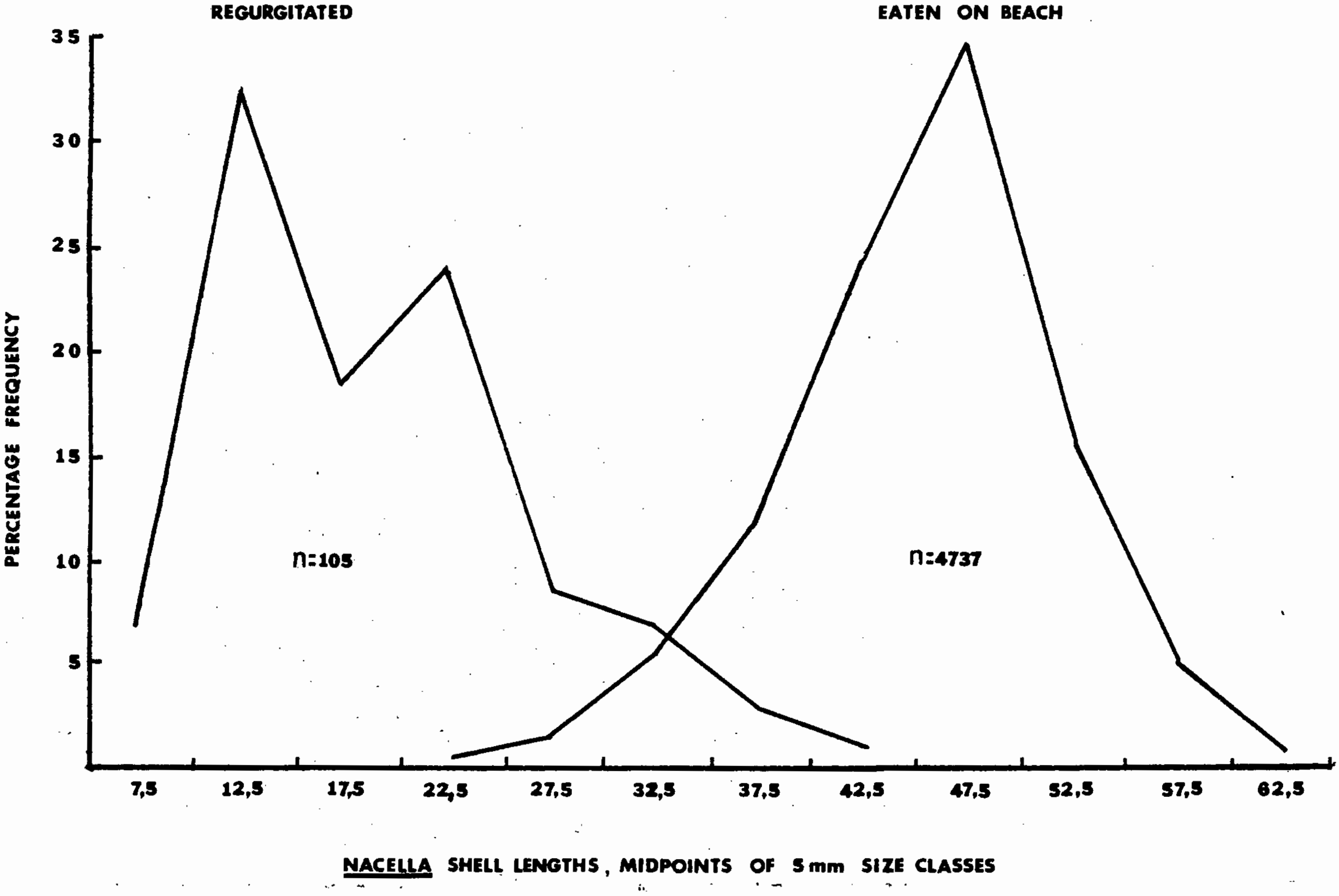

Fig. 1 Size class distribution of *Nacella* shells regurgitated by Kelp Gulls *Larus dominicanus* (N = 105) versus shells deposited on the beach by feeding gulls at Marion Island (N = 4747).

## RESULTS

### Kelp Gulls

Kelp Gulls fed mainly on intertidal *Nacella* and the offshore bivalve *Gaimardia trapesina*. Starfish (*Anasterias rupicola*) and the fish *Harpagifer georgianus* and *Notothenia macrocephala* were also eaten. The gulls hunted for limpets in shallow water during calm conditions. They floated on the surface within a few metres of the shore looking into the water directly beneath them. After stabilizing their position over a suitable limpet, they plunged their heads and sometimes most of their bodies into the water to capture a limpet from depths of up to 400 mm. Observations on seven gulls showed that a total of 77 dives in 195 minutes resulted in the capture and ingestion of 27 *Nacella*, indicating that one in three dives was successful and about seven minutes were needed to search for, catch and consume one *Nacella* including unsuccessful capture attempts. Small limpets were swallowed whole and shells regurgitated later, whilst larger specimens were carried to the shore and the soft parts eaten there. It took gulls one to two minutes to eat a captured limpet. Generally *Nacella* with shell lengths ranging from 40 mm to 35 mm were most heavily preyed on (Fig. 1). Regurgitated shells were comparatively rare.

Empty *Nacella* shells accumulated on the beach after the gulls had fed on the limpets; 2089 shells were removed during the initial clearing and thereafter a mean monthly total and standard deviation of 441 ± 236 was found from November 1979 to May 1980. No data were collected for March when unusually heavy seas swept the entire beach. No more than three gulls were ever seen hunting limpets simultaneously at Boulder Beach and the shells deposited on the beach were probably the result of feeding by the six to 15 gulls usually counted in the vicinity of the research station. Specific sites were chosen for the consumption of limpets on the shore. Large numbers of shells (up to 400) were collected from small eating sites (approx. 0,5m²) elsewhere on the island, i.e. Paddy Rocks, Trypot Beach, Kildalkey Bay and at Prince Edward Island.

The gulls also flew to the *Macrocystis* kelp beds (50 - 150 m offshore) to feed on the fragile pink bivalve *Gaimardia trapesina*. *Gaimardia* formed dense colonies on *Macrocystis* fronds and the gulls removed whole shells (15 - 30 mm long) from the upper fronds and swallowed them. The shells were crushed in the stomach and regurgitated later. Regurgitations after feeding on *Gaimardia* usually consisted entirely of *Gaimardia* shells indicating that the gulls fed to capacity on this bivalve, although any soft-bodied prey would not have been represented in regurgitations. A sample of 13 whole *Gaimardia* disected from Marion Island Kelp Gull stomachs had a mean longitudinal shell diameter and standard deviation of 22,9 ± 1,9 mm (J. Cooper, unpubl. data). Thirty-two intact *Gaimardia* regurtitations had a mean dry mass of 9,6 ± 2,5 g which would represent the shells of 8,5 ± 4,8 *Gaimardia* from the 20 - 25 mm size class. The extent of gulls' predation on *Gaimardia* is especially noticeable at Prince Edward Island where regurgitated *Gaimardia, Nacella* shells and odd bones have formed layers in the peat and built up into series of strata 500 mm deep.

TABLE 1 Analysis of Lesser Sheathbill *Chionis minor* faeces from Marion Island. N = 140 faeces

| Species | Counts | % Volume |
|---|---|---|
| Seaweeds | | |
| *Porphyra* | | 87 |
| *Ulothrix* | | 3 |
| *Rhodymenia* | | 4 |
| *Lithothamnia* | | 1 |
| Invertebrates & others | | |
| *Hyale grandicornis* | 210 | 5 |
| *Kerguelenella lateralis* | 96 | |
| *Ectemnorrhinus similis* | 78 | |
| Insect larvae | 31 | |
| Stones and gravel | 30 | |
| *Jassa falcata* | 17 | |
| *Nacella delesserti* | 8 | |
| Kelp flies | 5 | |
| *Shakeltonia* sp. | 2 | |
| *Laevilitorina caliginosa* | 1 | |
| *Exosphaeroma gigas* | 1 | |
| *Gaimardia trapesina* | 1 | |

TABLE 2 Combined analysis of two regurgitations and one sample of stomach contents from the Imperial Cormorant *Phalacrocorax Atriceps* at Marion Island

| Prey Species | Frequency | Wet Mass (g) | % Wet Mass |
|---|---|---|---|
| *Nauticavis marionis* | 33 | 14,0 | 10 |
| *Harpagifer georgianus* | 13 | 31,2 | 22 |
| Squid beaks | 9 prs | (1,5) | (1) |
| *Notothenia macrocephala* | 2 | 13,5 | 9,6 |
| Salp (unident.) | 1 | 2,0 | 1,4 |

Ossicles of the starfish A. *rupicola* occurred in about 5% of the regurgitations studied and on two occasions gulls were observed to peck and soften starfish before swallowing them. Only one gull was observed catching a fish, H. *georgianus* (60 mm long), which it caught in a shallow intertidal pool by quickly seizing it in its beak, and a single specimen of the fish N. *macrocephala* (90 mm long) was recovered from a gull chick at a nest site.

### Lesser Sheathbill

The Lesser Sheathbill regularly consumed intertidal organisms on the Marion Island shore. The analysis of faeces showed that seaweeds, especially *Porphyra*, formed the major portion of the diet (Table 1). The limpet *Kerguelenella lateralis*, amphipod *Hyale grandicornis*, beetle *Ectemnorrhinus similis* and small *Nacella* were the most important animal components of the diet. The Lesser Sheathbill was seen to remove intertidal *Nacella* up to 35 mm long from rocks and to eat their flesh. They also fed on the starfish A. *rupicola* from shallow gullies at low tide. Twenty-six starfish which had been attacked by sheathbills had a mean diameter and standard deviation of 42,9 ± 15,6 mm. Parts of the arms were pecked from 54% of the sample, stomach and pyloric caecae removed from 46% and gonads from 27%. One sheathbill was seen to peck and soften a small (15 mm) starfish and swallow it whole but otherwise only selected parts of larger starfish were consumed. Sheathbills also fed on individuals of the polychaete *Platynereis australis* which they removed from their tubes at low tide. This was seen on nine occasions during eight months of fieldwork.

They also ate the remaining flesh from *Nacella* shells left by gulls. A mean and standard deviation of 9,1 ± 4,6 *Nacella* shells were found at eight sheathbill nests but their large size ($\bar{x}$ = 44,4 mm) suggests that these shells were taken there from gull feeding sites rather than representing predation by sheathbills. Lesser Sheathbills are known to decorate their nest entrances with various pale coloured objects (Burger 1979).

## Imperial Cormorant

Imperial Cormorants dived for fish and other prey in the shallow subtidal amongst bull kelp *Durvillaea antarctica* and in the deep *Macrocystis pyrifera* kelp holdfast zone (10 - 15 mm deep) and probably even further and deeper offshore. The results show that the fish *H. georgianus* and *N. macrocephala* formed the largest part of the cormorant diet although they also took the shrimp *Nauticavis marionis*, squid and polychaetes (Table 2). Mean body length and standard deviation of the 13 *H. georgianus* was 53,2 ± 12,2 mm and 114,7 ± 9,1 mm for the three *N. macrocephala*.

## DISCUSSION

The Kelp Gull has a wide distribution in the Antarctic and sub-Antarctic where limpets form the major part of its food supply although it is also an opportunistic scavenger (Ealey 1954; Downes *et al.* 1959; De Villiers 1976; Simpson 1976; Maxon & Bernstein 1980). The Kelp Gulls of Marion Island preyed almost exclusively on two marine molluscs *Nacella delesserti* and *Gaimardia trapesina*. The high densities of both these prey species and the regularity with which they are eaten make them an important food source for the gulls. Snorkelling amongst the *Macrocystis* revealed that few *Gaimardia* occupy the upper fronds compared to the dense encrustations two to three metres deeper, suggesting that gulls take a heavy toll of this bivalve near the surface. *Nacella* is abundant in the belt where gulls hunt although less so than in water a metre or two deeper, but this could simply be caused by the shorebreak and not as the result of gull predation pressure. Kelp Gulls thus use two fairly specialized hunting techniques at Marion Island which reward them with a substantial supply of limpets and bivalves. The superior scavenging ability of the aggressive sub-Antarctic Skua on land has probably put pressure on the gulls to utilize marine organisms.

The Lesser Sheathbill is basically an opportunistic feeder which will investigate any likely source of food. Its littoral diet at other sub-Antarctic islands is not as well documented as that of the Kelp Gulls but is reported to feed on kelp flies (Ealey 1954), seaweeds (Downes *et al.* 1959) and seaweeds and limpets (Jones 1963). The most comprehensive study on Lesser Sheathbills is that of Burger (1980) who listed the intertidal zone and kelp jetsam as two of their 10 feeding habitats. Similarly Burger (1980) listed 11 basic categories of food consumed by sheathbills of which four were of littoral origin, namely *Porphyra;* limpets, chitons and starfish; amphipods; and kelp flies and larvae. The large quantities of seaweed which they ingest are voided in a fairly undigested state and further research will determine how much food energy they derive from them. Amphipods are plentiful amongst intertidal algae but no unusually high concentrations were found in faeces, suggesting that they are either not readily available for exploitation by sheathbills or they are not actively sought (Burger 1980). Lesser Sheathbills feeding on invertebrates (kelp flies, larvae and oligochaetes) from amongst kelp jetsam were not investigated in this study but Burger (1980) records this food source. Intertidal macroinvertebrates such as limpets, starfish and polychaetes are probably afforded a fair degree of protection against exploitation from sheathbills by the heavy coverage of the bull kelp *Durvillaea antarctica* over gullies and rock pools at low tide.

Little is known of cormorant feeding habits from Antarctic islands and Downes *et al.* (1959) only reported that the stomach contents of the Imperial Cormorant at Heard Island consisted mostly of notothenid fish *Notothenia cynobranchia,* squid beaks, isopods and amphipods. In the present study Imperial Cormorants were found to be strongly piscivorous and the many small, fairly slow swimming fish which occurred in shallow water were readily pursued and captured. The diet of the cormorants at Marion Island is obviously more complex than described here and the unidentified salp and giantpolychaetes in the regurgitations, previously unknown from Marion Island, may originate from much deeper offshore waters. Further work on the food of cormorants at Marion Island will be very useful but the small populations and erratic recruitment would make sampling of gut contents difficult (A.J. Williams, pers. comm.).

There is little possibility of competition for marine food by the three species of birds because they all essentially feed on different kinds of prey from different habitats. No serious attempt was made to assess the impact on marine organisms by the birds although Kelp Gulls seemed to deplete *Nacella* and *Gaimardia* stocks in the zones where they were available as prey. Lesser Sheathbills remove a large amount of *Porphyra* from intertidal and spray zone rocks and possibly eat a significant portion of this species' standing stock each year. Similarly, Imperial Cormorants could have a significant controlling effect on the local fish population. Since the three bird species are the only ones which remain on the island throughout the year and thus are entirely dependent on the local food, it seems likely that intraspecific competition for this food is an important factor controlling their population abundance.

All three species studied must cause some degree of mineral enrichment of island soil by their direct placement of marine minerals on to the soil in faeces and regurgitations. Quantitative estimates of guano production by the three species are given by Burger *et al.* (1978). Areas inhabited by Kelp Gulls had soils and plant significantly enriched with nitrogen and phosphorous (Smith 1978). The effect of scattered sheathbill faeces on soil enrichment and vegetation growth is still unknown and cormorants usually colonise cliffs at the ocean's edge, so presumably their guano only enriches their nesting sites before returning to the sea. Future work should be directed at determining the biological significance of these manuring activities.

The littoral environment of Marion Island is a rich source of food for the three resident avian species which forage within it, and exploitation of these resources at the primary (seaweeds), secondary (limpets, bivalves, amphipods and shrimps) and tertiary levels (starfish and fish) provides a strong link between the terrestrial and local marine systems.

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# PART 2

# ECOLOGY OF THE STARFISH *ANASTERIAS RUPICOLA* (VERRILL) AT MARION ISLAND (SOUTHERN OCEAN)

## ABSTRACT

The ecology of the Marion Island starfish *Anasterias rupicola* (Verrill) is described from studies of its feeding habits, biomass, habitats, population structure, growth, longevity and reproduction.

*A. rupicola* is the most conspicuous littoral macro-invertebrate predator at Marion Island and has a mean density of 17,5 individuals m$^{-2}$ in the intertidal and infratidal zones. *Anasterias* tends to congregate in relatively sheltered sites and attains maximum densities of 171 m$^{-2}$. The diet of *A. rupicola* is recorded from 404 cases of predation, 40% of which occurred on the limpet *Nacella delesserti.* Three other important prey are the polychaete *Platynereis australis* and isopods *Dynamenella huttoni* and *Exosphaeroma gigas.* *Anasterias* may feed either as solitary individuals or clustered together in groups on single prey. Solitary starfish show size-limited predation and are limited to capturing prey smaller than themselves. However *Anasterias* which collectively attack large prey are able to overcome the restriction of size-limited predation. Counts of feeding versus non-feeding starfish in the field show that there is an average of 11,7% of the *Anasterias* population feeding at any one time. *Anasterias* which were confined with *Nacella* in cages were monitored each month and provided data for a linear regression to predict the daily intake of food by a given mass of *Anasterias*. It is estimated from calculations that *Anasterias* removes 31,0 *Nacella* $m^{-2}$ $y^{-1}$. *Anasterias* appears to grow very slowly and the only discernable growth was recorded in brooded juveniles which showed an overall increment in diameter of 1,26 mm in 6 - 8 months. It is suggested that *Anasterias* takes at least 39 years to attain its maximum diameter of 110 mm. Intertidal *Anasterias* are preyed on by the lesser sheathbill *Chionis minor* and the kelp gull *Larus dominicanus*. *Anasterias* performs a keystone rôle in the organization of the littoral community at Marion Island and its co-operative feeding behaviour, brooding habit and slow growth make it an interesting species worthy of further study.

## INTRODUCTION

Carnivorous starfish are important members of many intertidal communities and the effects of their predation on the structure of the marine communities to which they belong have been noted in the tropics (Endean & Stablum 1973), on temperate rocky shores (Menge, 1972; Paine 1969) and in the Antarctic (Dayton *et al.* 1974). At Marion Island in the sub-Antarctic (46°54'S, 37°45'E) *Anasterias rupicola* (Verrill) is the most conspicuous littoral macro-invertebrate predator. De Villiers (1976) noted that *A. rupicola* fed predominantly on the abundant limpet *Nacella (Patinigera) delesserti*, and Simpson (1976) briefly recorded the prey of *Anasterias directa* and *A. mawsoni* at Macquarie Island but otherwise very little is known of the habits of this southern asteroid genus. The unusual degree of social co-operation displayed by *Anasterias rupicola* in the capture and digestion of large prey is described in more detail in Part 3 of this thesis and is a further indication of why this species should be singled out for further studies. The main aim of the present study was to describe the feeding ecology of *Anasterias* at Marion Island, especially in relation to its major prey *Nacella delesserti*. Other aspects of the ecology of *Anasterias* including its abundance, habitats, population structure, growth, longevity and reproduction were also examined to provide a more comprehensive background for the study.

## MATERIALS AND METHODS

### Study site and general conditions

The major study site was Transvaal Cove, a rocky boulder beach on the north-east coast of Marion Island. Intertidal *Anasterias* were studied by wading in pools and amongst boulders at low tide and the subtidal population was examined by snorkelling to depths of four metres. Conditions ranged from very calm to days when 3 - 5 metre waves swept the entire beach. Underwater visibility was always very good, considering the poor available light, and the sea only became murky after storms, when detritus remained suspended in the water. Other sites around the island were visited and examined and a brief survey of the subtidal community at the neighbouring Prince Edward Island (46°38'S, 37°57'E) was conducted in May 1980. The study extended over a period of thirteen months, between May 1979 and May 1980.

## Biomass and population structure

*Anasterias* densities were recorded from 184 random quadrats (0,1 m²) in the intertidal and infratidal zones. The maximum diameter of each starfish was measured to the nearest millimetre and its wet mass was recorded to the nearest 0,1 g. Population structure was determined by ordering all the diameters of *Anasterias* from the quadrats into 5 mm size classes.

## Diet

*Anasterias* that were feeding could usually be recognised by their conspicuously humped feeding posture, but failing this, starfish were turned over and their stomachs examined for prey. Both prey and starfish were collected and *Anasterias* diameter and prey length were measured to the nearest millimetre. The wet masses of prey and starfish were recorded to the nearest 0,01 g. Dry masses of *Anasterias* and its prey species were determined by drying representative specimens to constant mass at 60°C, and calculating length-mass regressions which were used to calculate the mean dry mass of prey species.

## Feeding rates

On 18 occasions a 20 - 40 m stretch of beach was carefully searched and all feeding starfish were counted and checked to see whether they were feeding or not. The number of starfish feeding divided by the total number of starfish examined gave a proportional rate for those feeding.

Caged *Anasterias* were fed with *Nacella* to determine feeding rates. Cages were constructed from cylindrical P.V.C. piping, 250 mm long and 80 mm in diameter. The ends of the cages were closed off with stainless steel mesh (mesh size 1 mm$^2$) and the cages were tied with strong nylon twine to *Durvillaea antarctica* holdfasts in a sheltered gulley. Between one and 19 *Anasterias* were measured and placed in each of these cages and 10 - 15 *Nacella* of known shell lengths were confined with them. After one month limpets that had been eaten were replaced with fresh specimens. At the end of about two months (59 - 65 days) the experiment was terminated, although one cage was monitored for five months. A reliable regression equation relating *Nacella* shell length to dry body mass was used to determine the mass of flesh consumed by *Anasterias* from the limpets they had killed. Two control cages, one containing only *Anasterias* and the other only *Nacella* were monitored for 110 and 94 days respectively and provided data on mortality rates of *Nacella* in cages (negligible) and on the growth of *Anasterias* under conditions of food deprivation. Limpets and starfish used in the caging experiments were collected randomly from the shore so that the size-frequency distributions of the samples resembled that of the natural population from which they came, although juveniles ( $<15$ mm) were rarely used. Results from the caging experiments were pooled and the number and shell-free dry mass of *Nacella* eaten by the 85 *Anasterias* in two months were calculated. Calorific content of dry *Nacella* flesh was determined from representative samples using an AMPC micro-bomb calorimeter. The average daily intake of *Nacella* flesh by the starfish in each cage was plotted against the total dry mass of the caged starfish. The linear regression so obtained permitted estimation of the energy requirements for a given biomass of *Anasterias*.

The amount of time required by *Anasterias* to digest a meal of *Nacella* was recorded in the field by providing a starfish with a limpet and returning at regular intervals to the site until the digestive process was complete.

Estimates of the number of *Nacella* removed by *Anasterias* $m^{-2}.yr^{-1}$ were calculated firstly from biomass of *Anasterias* combined with the feeding rates of caged *Anasterias*, and secondly from the formula given by Menge (1972), modified to suit the needs of the present study:

$$\text{Number of } \textit{Nacella} \text{ consumed } m^{-2}.yr^{-1} = \frac{A \times B \times C}{D} \quad (E)\ (F)$$

where:

A = the average proportion of *Anasterias* observed feeding;

B = the proportion of *Nacella* in the diet;

C = the number of foraging hours available per day (assumed to be 12 for the intertidal population)

D = the time spent consuming an average *Nacella* (hrs);

E = the number of starfish $m^{-2}$;

F = number of days spent foraging per year (assumed to be 250, allowing for heavy seas and reproductive activities).

## Growth rates

Specimens of *Anasterias* were tagged with numbered fish tags threaded with eight pound nylon monofilament fish line which was inserted through and tied around the dorsal-distal portion of one arm in the way described by Paine (1976) for tagging *Pisaster ochraceus*. It was planned to recapture and record the mass and diameter of the tagged animals on a monthly basis but the process obviously caused discomfort and most starfish had pulled their tags out within three weeks. Records of changes in mass and diameter of starfish held in cages (see above) were used to assess growth rates.

## Brooding

Thirty nine brooding *Anasterias* were collected between June 1979 and May 1980 and the mean size of juveniles in the broods were compared every two months to calculate the growth rate of juveniles. Mean sizes were calculated from the diameters of c.a. 20 individuals from each of the broods.

# RESULTS

## Biomass, habitats and population structure

Mean density of *Anasterias* was 17,5 ± S.D. 43,2 individuals $m^{-2}$. In terms of biomass, the mean dry mass of *Anasterias* was 15,7 ± 6,8 $g.m^{-2}$ (=117,5 ± 47,9 kJ $m^{-2}$). One hundred and twenty six quadrats contained no starfish but in the quadrats where *Anasterias* did occur it had a mean density of 57,5 ± 64,0 $m^{-2}$ and the ten densest quadrats (each 0,1 $m^2$) contained a total of 171 starfish. *Anasterias* is thus a patchily distributed species, tending to aggregate in certain areas. Specific sites, which were usually sheltered from wave action, were noted to contain consistently more starfish than various other sites throughout the year of study. These localities presumably offered local optimal conditions for *Anasterias*, in terms of shelter and available food. The main habitats for these aggregations were found under rocky ledges, underneath stable boulders and in sheltered gullies. Small *Anasterias* ($\leqslant$ 20 mm) were mostly found amongst debris which had accumulated under boulders where they live in association with a plentiful community of amphipods, isopods and polychaetes. Larger *Anasterias* were found in less cryptic habitats on horizontal rocky surfaces, usually in areas close to stands of the abundant limpet *Nacella delesserti* which occur at a mean density of 75,0 $m^{-2}$. Very few *Anasterias* were found amongst thick layers of algal turf (e.g. *Rhodymenia* and *Corallina* spp.) and their rarity amongst small unstable boulders was also noted. Live *Anasterias* were very rarely encountered above the water level at low tide except when engaged in a struggle

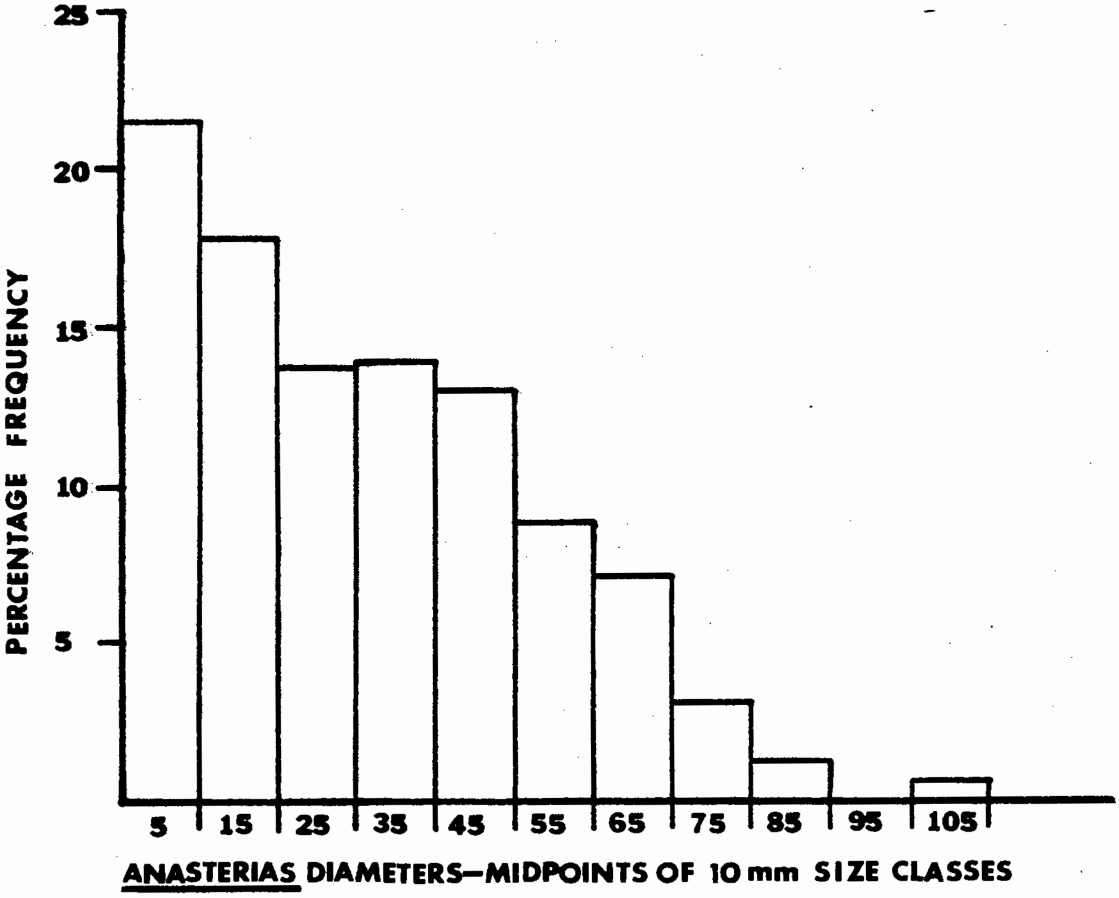

Fig. 1 Size class frequency distributions of *Anasterias* sampled from the biomass study (N = 322).

with its main prey, *Nacella*, or when cast up on to the higher shore by heavy seas. Relatively few *Anasterias* were encountered at depths exceeding five metres and densities of the starfish were greatest just below the intertidal zone and at depths of 1 - 3 m.

The size frequency distribution of A.*rupicola* sampled in the biomass study is shown in Fig. 1. Juveniles ( < 30 mm diameter) comprise 53% of the population and a gradual decrease in numbers with increasing diameter is apparent. The largest starfish had a diameter of 110 mm and a wet mass of 34,2 g.

## Diet, prey capture and size relationships

*Anasterias rupicola* is an exclusively carnivorous species and even very young individuals (4 - 5 mm diameter) actively capture small prey. Table 1 shows the main prey species of which the limpet *Nacella delesserti* is by far the most important. Whilst only 40% of *Anasterias* predation occurred on *Nacella*, in terms of dry mass the limpet comprised 90% of the diet. Three other important prey were the polychaete *Platynereis australis* and isopods *Dynamenella huttoni* and *Exosphaeroma gigas*. *Anasterias* captures its prey using its tube feet and arms and most prey are digested externally by evagination of the cardiac stomach, but small prey (such as amphipods) were often found to be withdrawn into the stomach cavity by larger starfish so that internal digestion took place. Fast-moving prey like amphipods and isopods were often noted to seek shelter under *Anasterias* where, instead, they ended up as a meal for the starfish.

TABLE 1 Species composition of the diet of *Anasterias rupicola* at Marion Island recorded as the % number of feeding observations on each species and the % contribution of each prey to the total dry mass of prey.

| | Prey species | % of feeding observations | % of prey biomass |
|---|---|---|---|
| 1. | *Nacella delesserti* (limpet) | 40 | 90 |
| 2. | *Platynereis australis* (polychaete) | 10 | 2 |
| 3. | *Dynamenella huttoni* (isopod) | 10 | 1 |
| 4. | *Lasaea consanguinea* (pelecypod) | 6 | 1 |
| 5. | *Kerguelenella lateralis* (siphonariid) | 5 | 1 |
| 6. | *Exosphaeroma gigas* (isopod) | 4 | 1 |
| 7. | *Jassa falcata* (amphipod) | 4 | 1 |
| 8. | *Kidderia minuta* (pelecypod) | 3 | 1 |
| 9. | *Hyale hirtipalma* (amphipod) | 3 | 1 |
| 10. | *Hemiarthrum setulosum* (chiton) | 3 | 1 |
| 11. | *Shakeltonia* sp. (amphipod) | 1 | 1 |
| | Others (18 species) | 11 | 5 |
| Totals: | 29 prey | n = 404 | 169 g |

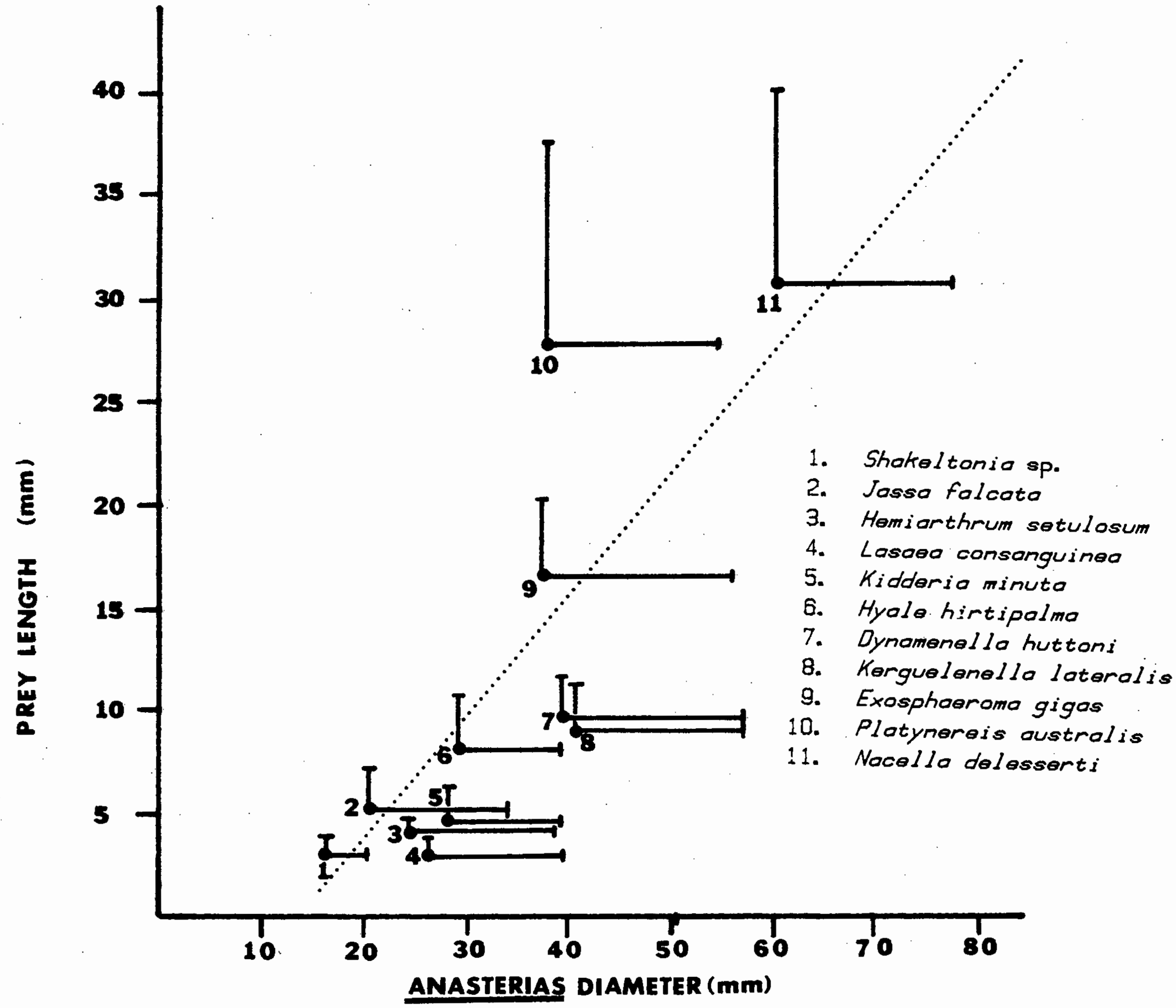

Fig. 2 Size-limited predation of *Anasterias* on its major prey species. Mean diameter (+1 S.D.) of *Anasterias* found feeding on each prey species is plotted against the mean length (+1 S.D.) of the prey. A significant linear regression ($y = 0{,}65\ x - 10{,}39$; $r^2 = 0{,}67$) fits the data (……).

*Anasterias* may feed either as solitary individuals or clustered together in groups on a single prey. In the case of solitary starfish, there is a positive correlation between the sizes of the starfish and the sizes of the animals on which they prey (Fig. 2). This suggests that predation by *Anasterias* is size-limited, large starfish being able to capture large prey, while smaller individuals are restricted to small prey. The smallest *Anasterias* (4 - 40 mm diameter) fed almost exclusively on prey less than 10 mm in length, such as amphipods, pelecypods and chitons. Larger *Anasterias* (20 - 60 mm) fed more on larger animals such as polychaetes and isopods whilst the largest starfish (40 - 80 mm) fed mostly on the limpet *Nacella*.

This size-limited feeding relationship is complicated, however, by the phenomenon of cluster-feeding on larger prey, for two to 14 *Anasterias* could be found clustered around and feeding on a single prey item. In the case of the limpet *Nacella*, groups of *Anasterias* atually co-operatively capture large limpets which they would not be able to deal with individually.

Table 2 clearly shows that cluster feeding only occurs on the five largest prey species, and that there is a significant correlation ($r = 0,84$; $p < 0,01$) between the incidence of cluster-feeding and the mean soft dry mass of prey. The mean number of *Anasterias* in feeding clusters also increases with increasing mean prey mass and the largest cluster (14 *Anasterias*) occurred on a *Nacella*.

TABLE 2 Details of *Anasterias rupicola* cluster-feeding on its main prey species, showing the relationships between the % incidence of cluster-feeding, the dry mass of prey and the mean and maximum number of *Anasterias* clustering on the different species.

| Prey species | % predation occurring as clusters | Mean soft dry mass of prey ± S.D. (mg) | Mean No. of *Anasterias* in clusters ± S.D. | Maximum No. of *Anasterias* in clusters |
|---|---|---|---|---|
| *Nacella delesserti* | 69,8 | 11 000 ± 660 | 4,0 ± 2,2 | 14 |
| *Platynereis australis* | 34,2 | 83 ± 60 | 3,6 ± 2,5 | 11 |
| *Exosphaeroma gigas* | 31,3 | 178 ± 80 | 3,4 ± 2,1 | 7 |
| *Dynamenella huttoni* | 30,8 | 56 ± 30 | 2,8 ± 2,8 | 4 |
| *Kerguelenella lateralis* | 25,0 | 40 ± 30 | 2,6 ± 0,9 | 3 |
| *Hyale hirtipalma* | 8,3 | 6 | 2,0 | 2 |
| *Jassa falcata* | 6,7 | 5 | 2,0 | 2 |
| *Hemiarthrum setulosum* | 0,0 | 19,5 | - | - |
| *Kidderia minuta* | 0,0 | 7,6 | - | - |
| *Lasaea consanguinea* | 0,0 | 3,6 | - | - |
| *Shakeltonia* sp. | 0,0 | 1,8 | - | - |

## Feeding rates

From the 18 counts of feeding versus non-feeding starfish, a total of 146 feeders and 1102 non-feeders was recorded. Thus there is an average of 11,7% of the *Anasterias* population feeding at any one time, although this figure is only a rough estimate since various factors affecting feeding rates (e.g. seasonality and prey availability) were not taken into account.

Pooled data from the results of the ten caging experiments, where 71 *Anasterias* (totalling 86,5 g dry flesh mass) were enclosed with a total of 188 limpets, revealed that the starfish consumed 78 *Nacella* (63,6 dry g) in two months. Despite the artificial nature of the cages, and the fact that overall densities of *Anasterias* ($118/m^{-2}$) and *Nacella* ($113/m^{-2}$) in the cages were fairly high, the experiments provided useful data on the rates of *Anasterias* consumption of *Nacella*. The total dry mass of *Anasterias* in each of the ten experimental cages was plotted against their respective average daily consumption of *Nacella* flesh and yielded a significant linear regression ($r^2 = 0,77$; $p < 0,01$) for predicting the daily intake of food by a given mass of *Anasterias* (Fig. 3).

Using the mean biomass values obtained for *Anasterias* and energy values of *Nacella* flesh it can be calculated from the above data that *Anasterias* consumes the equivalent of 3,9 kJ of *Nacella* $m^{-2}.day^{-1}$. From this it can be tentatively derived that *Anasterias* consumes the equivalent of 1424 kJ of *Nacella* $m^{-2}.yr^{-1}$ or 84 average sized *Nacella*

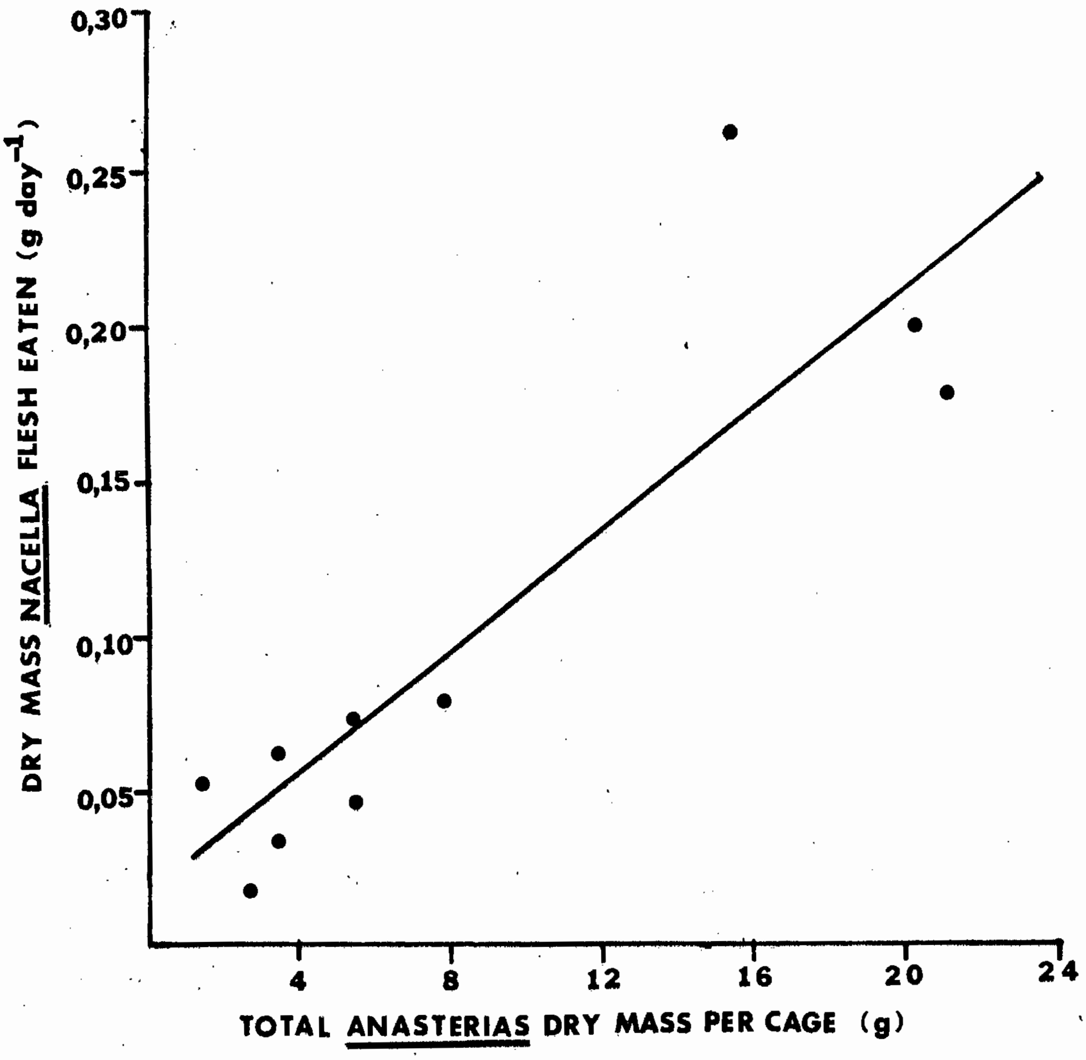

Fig. 3 The relationship between total dry mass of *Anasterias* in each of the experimental feeding cages and their corresponding daily intake of *Nacella* flesh. A significant linear regression fits the data ($y = 0{,}0098x + 0{,}0158$; $r^2 = 0{,}77$) and was used to determine consumption rates for a given biomass of *Anasterias*.

$m^{-2}.yr^{-1}$. These feeding rates are obviously maximal and only apply to areas where *Anasterias* has access to abundant supplies of *Nacella*.

On six occasions solitary starfish were supplied with a 40 - 45 mm limpet to record the time taken to digest a single *Nacella*. The original starfish was soon joined by others and feeding clusters consisting of 8 - 14 *Anasterias* were formed. These seeded clusters took a mean of 79,2 ± S.D. 10,7 hours to completely digest the limpets.

Using Menge's (1972) formula (given in the Methods) and the following data from the present study, a second measure can be obtained at the rate with which *Anasteria* removes *Nacella*:

$$\frac{0{,}117 \times 0{,}40 \times 12}{79{,}2} (17{,}5)\ (250) = 31{,}0 \textit{ Nacella } m^{-2}.\ yr^{-1}.$$

## Growth rates

Measuring the growth rate of *Anasterias* was a difficult task and the methods used produced unreliable results. Free-range growth experiments had to be abandoned since the tagged *Anasterias* pulled out the nylon filaments bearing their tags. *Anasterias* held in cages for the feeding experiments showed inconsistent increases and decreases in both diameter and wet mass after two months (Fig. 4) and no reliable pattern of growth could be found, even in the cage which was monitored for five months. Similarly, the *Anasterias* which were confined

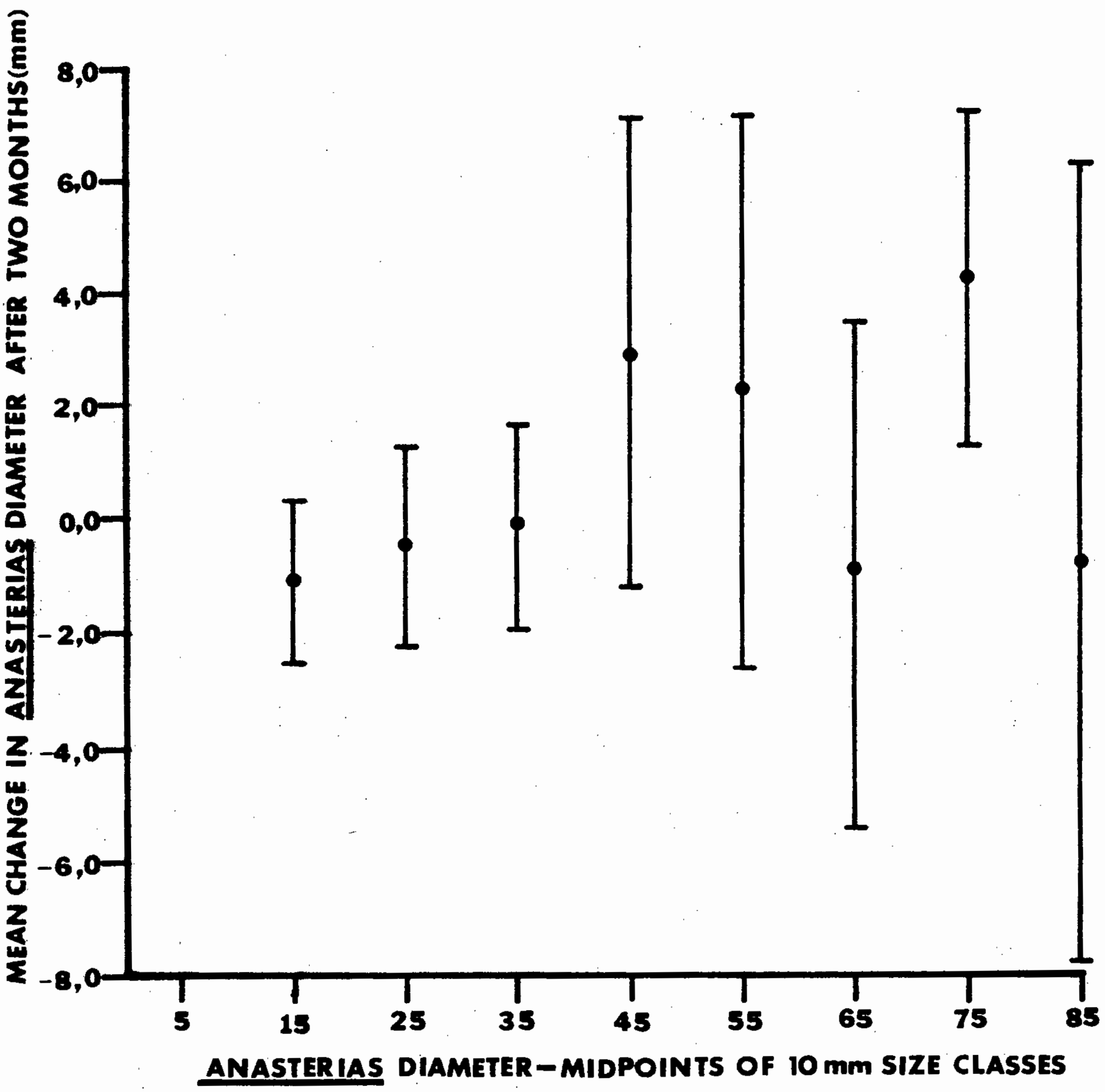

Fig. 4 Growth of *Anasterias* maintained in cages and fed on *Nacella* for two months. Mean changes in *Anasterias* diameter (± 1 S.D.) for each 10 mm size class show no general trend.

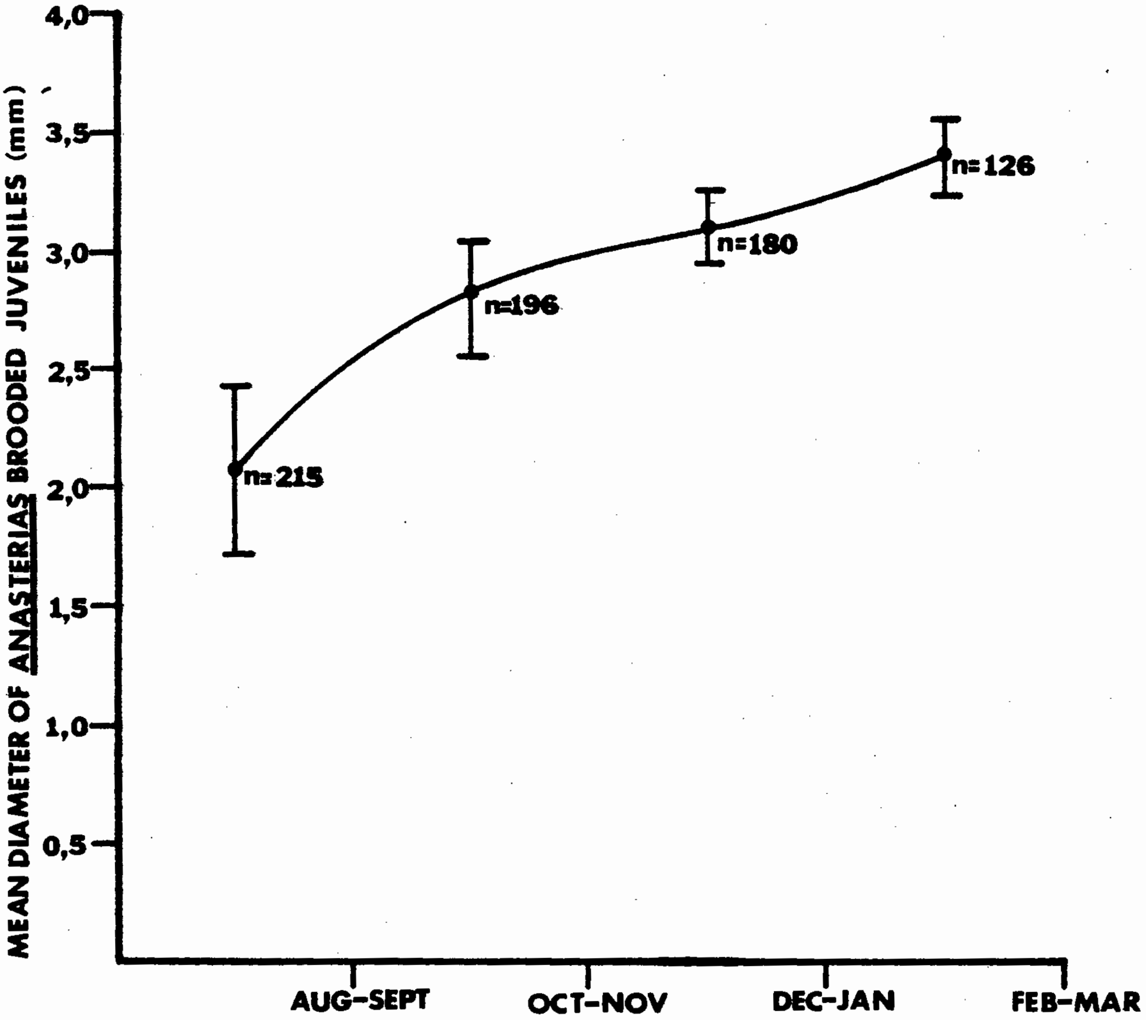

Fig. 5 Mean diameters of juveniles sampled from broods collected every two months during the 8 to 10 month brooding cycle of *Anasterias rupicola* (n = the number of representative juveniles measured).

without food for 110 days in the control cage suffered no mortality and showed no general trend of decrease in mass or diameter. These findings suggest that *Anaterias* grows very slowly so that changes in size are relatively undetectable. Menge (1972) found that well-fed *Leptasterias hexactis*, raised in the laboratory, showed readily discernible monthly increments in size.

The mean increments in diameter and mass of the 71 caged *Anasterias* were 0,47 mm and 0,48 g but the large standard deviations around both these figures (3,3 and 2,2 respectively) make further speculation about growth fruitless.

## Brooding

An indication of slow growth in *Anasterias* came from a study of its reproduction. *Anasterias* is a synchronous brooder and females larger than 21 mm in diameter appear to raise young once every two years (unpublished data). Brooders found in June and July carried up to 320 large yolky eggs 1,6 mm in diameter. Figure 5 shows a synchronised, regular pattern of growth of these brooded juveniles, which increased from a diameter of 2,16 mm in August-September to 3,24 mm in February-March of the following year, giving an overall increment of 1,26 mm in 6 - 8 months.

## DISCUSSION

Although A. *rupicola* exploits a wide range of prey species at Marion Island it is essentially monophagous on the limpet N. *delesserti* as its major source of food. Even the smallest *Anasterias* is able to feed on large, energetically rewarding *Nacella* by joining other starfish in the digestion and sometimes capture of a limpet (Part 3). At Macquarie Island, Simpson (1976) also noted that *Anasterias directa* and A. *mawsoni* formed feeding clusters on their two largest species of molluscan prey (25 - 35 mm) despite the fact that starfish densities there were only in the region of 1 - 2 $m^{-2}$. As seen in Fig. 2, there are clearly limitations on the size of prey that solitary A. *rupicola* can capture and co-operative behaviour thus appears to be a successful strategy allowing them to exploit large prey.

Mean densities of *Anasterias* recorded in the present study (17,5 individuals or 15,7 dry g $m^{-2}$) are fairly high especially compared to the density of 1 - 2 *Anasterias* $m^{-2}$ recorded by Simpson (1976). The high density of A. *rupicola* is reflected in the estimates of its food consumption from the caging experiments (84 *Nacella* or 1424 kJ $m^{-2}.yr^{-1}$) or from Menge's (1972) formula (31 *Nacella* or 525,5 kJ $m^{-2}.yr^{-1}$). Since the *Anasterias* in cages had unlimited access to *Nacella* their consumption rate is likely to be a maximum limit and the latter estimate is probably more accurate for the natural population. *Nacella* appears to be able to sustain its numbers under this heavy predation and has a mean density of 75,1 $m^{-2}$ with a net production of 40,77 g dry mass (or 798,3 kJ) $m^{-2}.yr^{-1}$) (Part 5). This figure for *Nacella* production does not include the input of juvenile recruits in the population and is thus a conservative estimate.

The tendency of *Anasterias* to form dense aggregations in specific areas is not too unusual for a starfish and Sloan (1980) lists 18 asteroid species known to form aggregations, mostly in response to super-abundant food resources. Aggregations of *Anasterias* appeared to be a response firstly to wave action, as no aggregations were found in relatively exposed situations, and secondly to food availability, and the most noticeable aggregations were usually found on horizontal surfaces directly below dense clumps of *Nacella* living on vertical surfaces. The starfish presumably exploit these stands of *Nacella* whenever possible - for instance during exceptionally calm conditions when they can move safely on vertical surfaces or when the limpets move downwards into starfish territory. *Anasterias* predation on *Nacella* is likely to occur at high frequencies in these areas which are densely colonised by limpets, and consumption rates probably reach levels as high as those recorded in the cages.

All attempts to measure the growth rate of *Anasterias* in the present study were thwarted although the growth of brooded juveniles was successfully measured. The major reason for this failure appears to be very slow growth in A. *rupicola* which was relatively undetectable in the short study period. Barker (1979) found that juvenile *Stichaster australis* reached a diameter of 8 mm in 7 - 8 months after metamorphosis and take a further 11 months to attain a size of 24 mm. Chia (1966) records that another brooding starfish *Leptasterias hexactis*, broods eggs to the stage when young starfish metamorphose after two months, and Menge (1975) found that the same starfish lives 10,2 years after maturity. The 1,26 mm increment in diameter after 6 - 8 months shown by brooded *Anasterias* juveniles in the present study is thus suggestive of very slow growth, and it is proposed that the lengthy brooding period of *A. rupicola* indicates that this species could have a correspondingly long life span. If the mean bi-monthly increment in diameter (0,47 mm) of the well-fed caged *Anasterias* is at all reliable, then *Anasterias* takes at least 39 years to attain a maximum size of 110 mm, but considering the admittedly sparse evidence it may live even longer than this.

Few predatory starfish are preyed on by other predators, but at Marion Island the lesser sheathbill *Chionis minor* and kelp gull *Larus dominicanus* regularly devour intertidal *Anasterias* (Part 1 and Blankley 1981). Thus *Anasterias* does contribute to the higher trophic levels and is not simply a trophic dead end.

The present study shows that the activities of *Anasterias* make it a keystone species in the organisation of the littoral community at Marion Island and its co-operative feeding behaviour, brooding habit and slow growth certainly make it an interesting species which merits further study.

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# PART 3

# SOCIAL CO-OPERATION IN A SUB-ANTARCTIC STARFISH

## ABSTRACT

Carnivorous starfish are usually solitary feeders only able to prey on animals smaller than themselves. Many prey species become immune to starfish predation once they achieve a certain size. The starfish *Anasterias rupicola* (Verrill), which occurs on sub-Antarctic Marion Island, has the unique habit of gathering in groups to collectively attack and feed on large prey which would be impossible for an individual starfish to capture. As a result, its predation on its major prey species, the limpet ***Nacella delesserti,*** is no longer size-limited. *Anasterias rupicola* is one of the relatively few species of starfish which broods eggs and is also unique in that the females capture and feed on prey whilst still carrying their young.

True social behaviour is rare in echinoderms although the tendency to aggregate is considered to be a general characteristic of the phylum (Reese 1966). Such aggregations are proposed to be the summation of individuals' reactions to environmental stimuli mostly in response to feeding and reproductive cues (Feder & Christensen 1966; Binyon 1972). In studying the ecology of the sub-Antarctic starfish *Anasterias rupicola* (Verrill) at Marion Island (46°51'S, 37°52'E) we have recorded, for the first time, truly cooperative behaviour in an asteroid. Starfish frequently cluster gregariously, but *Anasterias* is unusual in that individuals band together to allow them to collectively capture and feed on large prey which they would not individually be able to handle. In addition, *Anasterias* females brood young for up to nine months, and their habit of actively feeding while brooding is unique among asteroids and allows them to provide the young with freshly captured food whilst they are still under maternal care.

Feeding and brooding starfish were collected from the intertidal and subtidal zones of Transvaal Cove, a rocky boulder beach on the north-east coast of Marion Island, between May 1979 and May 1980. Of the 404 cases of predation examined, 29 prey species were identified, but 40 percent of the predation occurred on the limpet *Nacella delesserti*, and in terms of dry mass *Nacella* provided 90% of the diet. *Nacella* is thus the primary source of food for *Anasterias* at Marion Island and since these two species are the dominant macroinvertebrates of the shores, their trophic interaction is an important feature of the Island's littoral ecology.

Predatory starfish are frequently limited to capturing prey of a particular size range, larger individuals being able to capture larger prey, whilst smaller specimens are only able to deal with prey below a certain size threshold (Menge 1972; Paine 1976). Because of this size-limited predation, the largest individuals of the prey are relatively immune to predation - a fact of some importance, considering that they are also the most productive breeders.

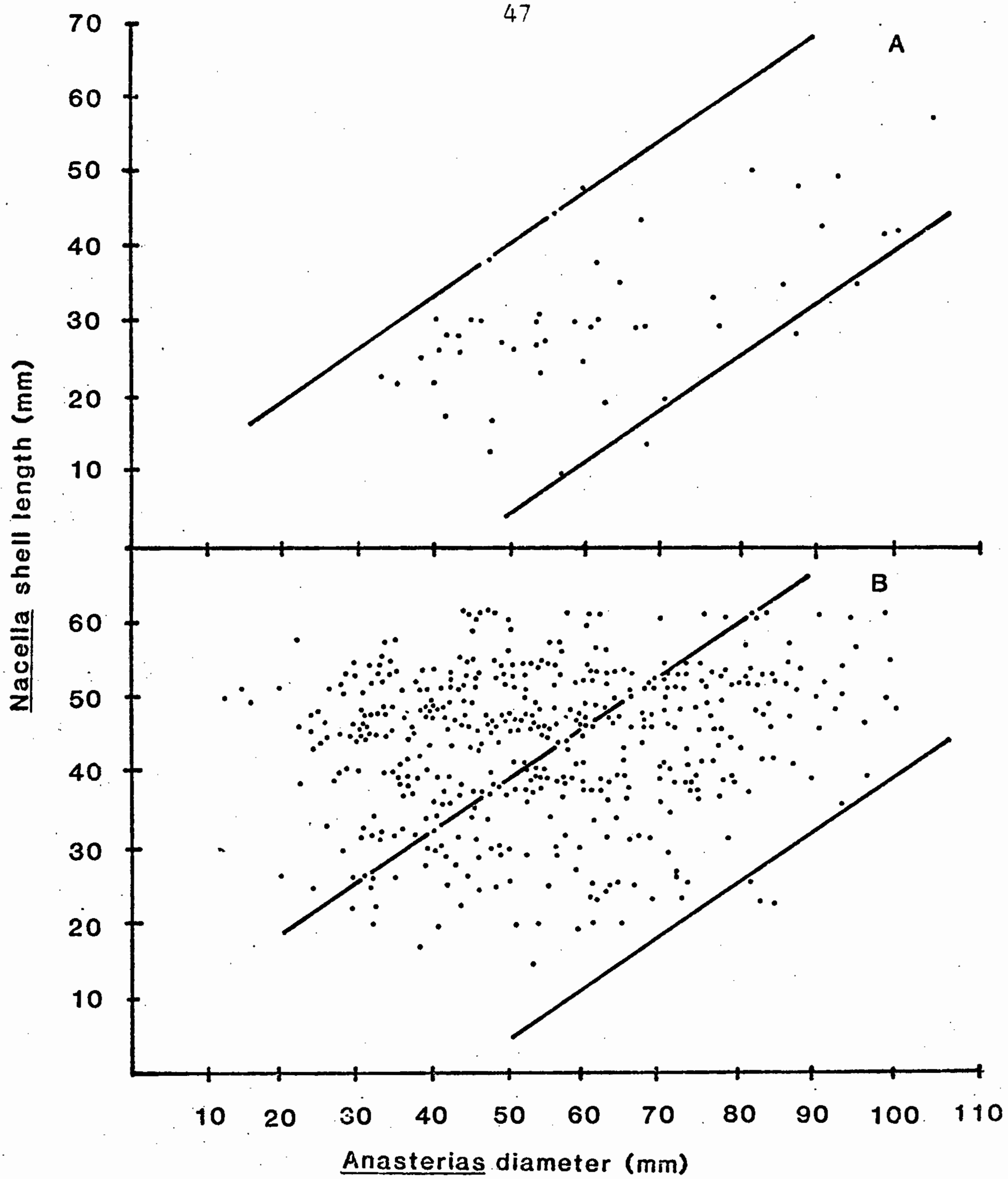

Fig. 1A Size-limited predation of *Nacella* by solitary *Anasterias*. The diameter of each starfish is plotted against the length of the limpet it was consuming. Upper and lower limit lines were fitted by eye and represent the largest and smallest sizes of limpets preyed on by a starfish of any given diameter. A significant linear regression fits the data ($y = 1{,}095x - 27{,}45$, $r^2 = 0{,}39$; $p < 0{,}01$) thus supporting the hypotheses that larger starfish selectively attack larger limpets and that smaller starfish are individually unable to capture limpets above a certain size threshold.

Fig. 1B Relationship between the sizes of *Anasterias* which were feeding in clusters and the shell length of *Nacella* on which they were preying. Under these conditions, there is no significant regression or correlation between the size of *Anasterias* and the size of limpets ($r^2 = 0{,}10$; $p > 0{,}05$) showing that when small starfish feed in groups they are no longer restricted to eating small limpets. The upper and lower size limits of *Nacella* that are eaten by solitary starfish (Fig. 1A) are inserted for comparison.

In cases where solitary *Anasterias* were found feeding on *Nacella*, a clear size-limited predation was shown to exist, larger *Anasterias* being able to feed on larger Nacella and seemingly spurning smaller limpets (Fig. 1A). This pattern of attack presumably allows the starfish to select limpets which will give a maximum return of food for the effort put into foraging and prey capture. In no case did solitary *Anasterias* capture limpets larger than themselves. Since *Nacella* reaches a maximum size of 65 mm, the largest limpets should be safe from attack from all but the very largest of starfish. However, by cooperative action, relatively small starfish can attack and feed on even the largest of limpets (Fig. 1B). Of 161 records of *Anasterias* predation of *Nacella*, 112 involved two or more starfish feeding on the same limpet, and up to 14 starfish could be found clustered around and digesting a single limpet. In many cases all of the starfish in a feeding cluster were smaller than the limpet they were eating, showing that group effort successfully overcomes the problem that small starfish have when attempting to feed on large prey. Figure 2 shows that solitary *Anasterias* captured limpets that were smaller than those eaten by clusters of starfish.

By artificially 'seeding' a cluster (i.e. by feeding a limpet to a starfish in an area densely populated by *Anasterias*), we were able to observe these feeding clusters more closely. Other starfish joined the original captor within 20 minutes so that two or three starfish soon became involved in the capture of the struggling limpet. Usually within 12 hours, nine to fourteen starfish had clustered on the kill and complete digestion of the limpet took two to three days. Starfish

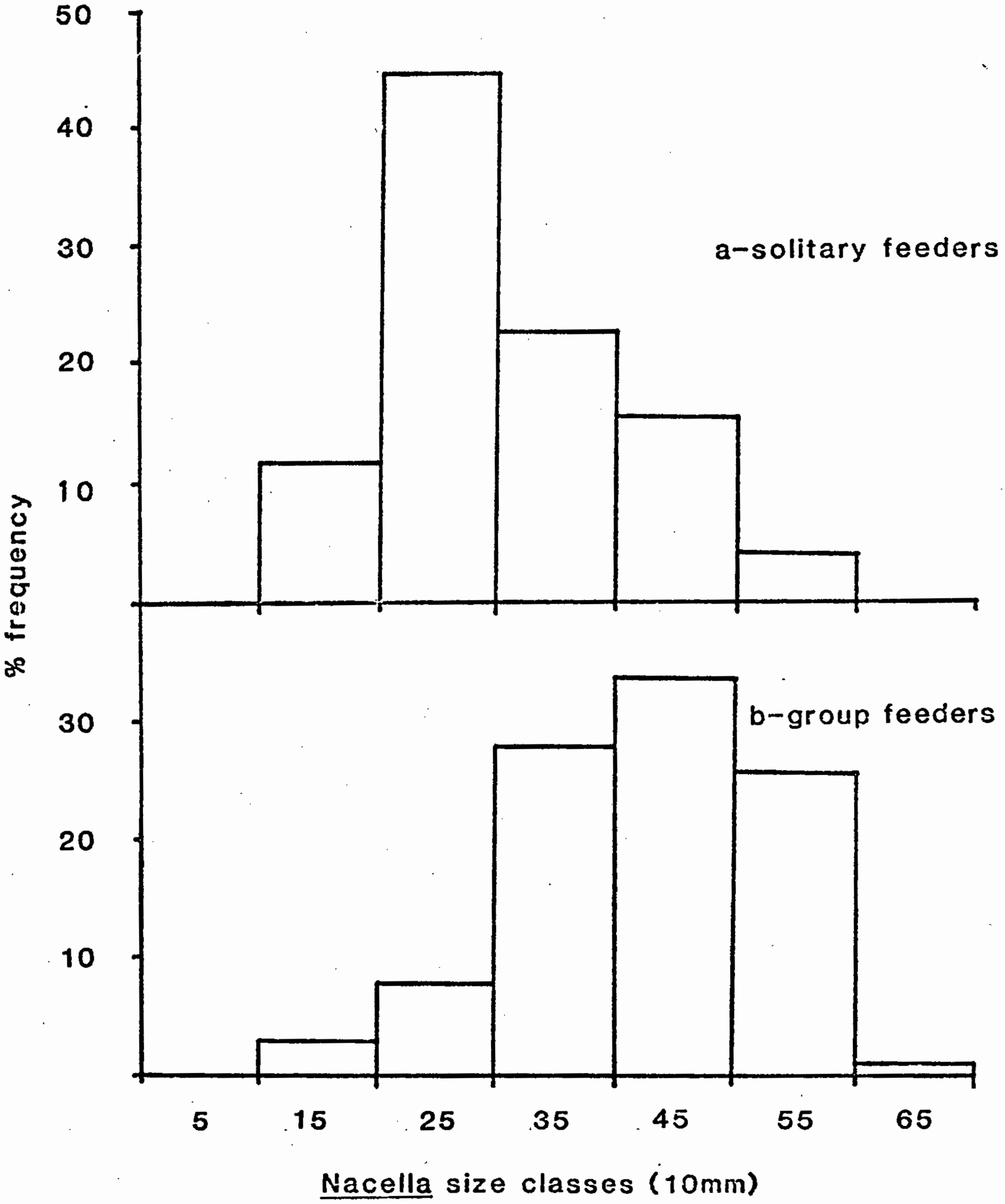

Fig. 2 A comparison of the size-frequences of *Nacella* eaten by (a) solitary *Anasterias*, and (b) clusters of the starfish. Solitary starfish fed on significantly smaller limpets than those feeding in groups ($t = 6,18$, $p < 0,001$).

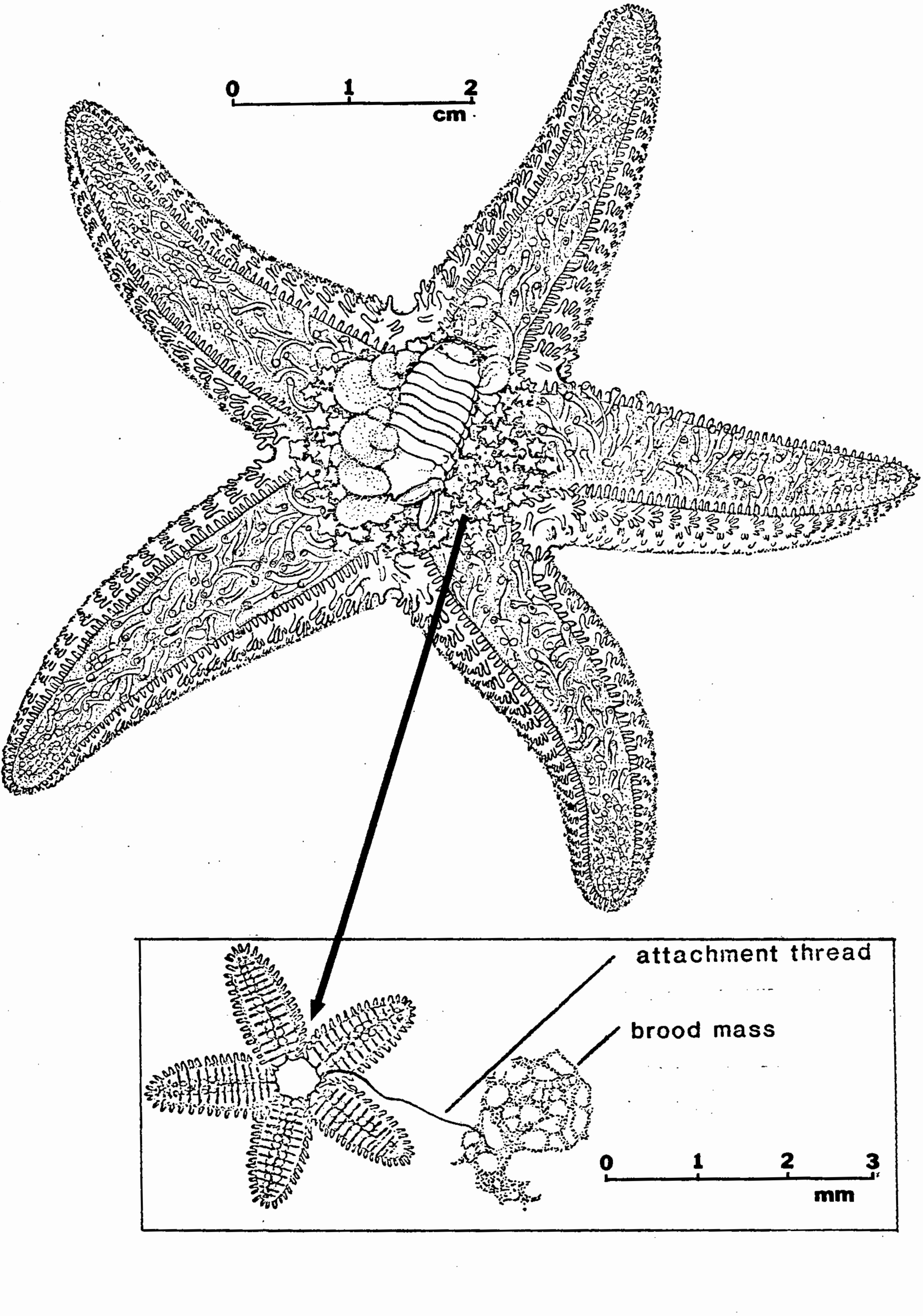

Fig. 3 Line drawing of a female starfish observed enveloping an isopod (*Dynamanella huttoni*) in her stomach whilst brooding her young. The six-month old young are at an advanced stage of development. Most have already left the mother, but those that remain are still connected to the brood sheath via attachment threads (see inset).

advancing towards a feeding clump pointed the tip of their approaching arm upwards and extended the terminal tube feet, supporting Sloan's (1980) suggestion that these tube feet are the major area of chemoreception.

This type of group cooperation in asteroids is remarkable enough but a second observation confirms the unusual sociability of *Anasterias*. Brooding of young is fairly well documented in asteroids although genuine brooding of eggs occurs mostly in cold-water starfish, particularly of the southern hemisphere (Hyman 1955). During June and July, *Anasterias* begins brooding, and carries up to 320 large yolky eggs, 1,6 mm in diameter. The eggs form a roughly spherical mass which is held under the stomach opening. By November, fully recognizable young starfish have developed and each has an attachment thread linking it to the mother. Young starfish begin leaving the brood in December, although even in April of the following year, female starfish can still be found harbouring a few remaining juveniles. An intriguing feature of this brooding relationship is that the females actively capture and feed on prey while carrying their young (Fig. 3). Observations of brooding females which were feeding were made in November, December and January, when the young were already well developed and starting to lose their attachment threads (Fig. 3 inset). Normally starfish do not feed whilst brooding (Hyman 1955; Landenberger 1966; Menge 1974), and the young are nourished on food reserves stored by the mother. In the case of *Anasterias*, however, the mother starfish supplements the nutrition of the young with fresh food from newly-captured prey. During the last stages of brooding, some of the young may break free from the attachment threads, but remain beneath the mother, where they may still derive nourishment by absorbing mulsh from the mother's digestive efforts. One brooding starfish with about 150 young was caged in the subtidal zone and over a period of 45 days, she devoured eight of the ten *Nacella* enclosed in the cage with her. During this time, the mean diameter of the juveniles increased from 3,0 mm to 3,6 mm, in spite of the fact that they had previously depleted all their yolk reserves, thus indicating that they must derive nutrition from the mother. Birkeland (1974) has suggested that in the period following metamorphosis, the first few meals of an asteroid may be critical to the recruitment potential of the individual but in the case of *Anasterias* this hazardous period is avoided because the female provides the first meals for the young. At a diameter of between 3 and 4 mm the young *Anasterias* break free of the mother and juveniles of 5 to 7 mm were found actively preying on tiny amphipods and bivalves (2 to 4 mm).

Thus *Anasterias* is not only unique in cooperatively hunting prey that would normally be too large to capture, but is also able to supply food directly to its brooded young.

## ACKNOWLEDGEMENTS

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# PART 4

# FEEDING ECOLOGY OF THREE INSHORE FISH SPECIES AT MARION ISLAND (SOUTHERN OCEAN)

## ABSTRACT

The diets, morphological features and habitats of the three inshore fish species *Notothenia coriiceps*, *N. macrocephala* and *Harpagifer georgianus* from Marion Island are described and compared on the basis of 258 specimens. Correspondence analysis of the three diets shows the existence of three clearly defined feeding niches despite the occurrence of some common prey species. Inter- and intraspecific similarities and differences in the diets of small and large size classes of each species are also compared by correspondence analysis. Size-limited predation by *N. coriiceps* on the limpet *Nacella delesserti* is described. Differences in the habitats occupied by the fish appear to be important in determining the species composition of their diets.

## INTRODUCTION

Three species of fish occur in the shallow inshore waters of Marion Island. *Notothenia macrocephala* Günther 1860 and *Notothenia coriiceps* Richardson 1844 are Antarctic cods of the family Nototheniidae. The third species, *Harpagifer georgianus* subsp.

*georgianus* Nybelin 1947, is a member of the plunder fish family Harpagiferidae.

While there are many studies on Antarctic fish (Holloway 1969; Everson 1970; Meier 1971; Permitin and Tarverdieva 1972; Richardson 1975; Targett 1981) few detailed reports on the feeding of sub-Antarctic fish exist except that of Hureau (1966) who examined the diet of *Notothenia macrocephala* and two other species of Nototheniidae at Kerguelen Island. De Villiers (1976) described the major prey of the three species of fish at Marion Island without providing any quantitative data. The aim of the present study was to provide baseline quantitative data on the diets and interrelationships of the three species mentioned above.

## MATERIALS AND METHODS

Specimens were obtained through numerous collections between May 1979 and May 1980, made at various sites in Transvaal Cove, a relatively sheltered bay close to the research station on the north-east coast of Marion Island. *Notothenia macrocephala* was captured on hook and line at depths ranging from 20 cm in the intertidal zone to 20 m at the base of the offshore *Macrocystis* belt. *Notothenia coriiceps* was caught mainly at depths of 1 - 4 m by using a hand-net whilst snorkelling, although a few specimens were obtained on hook and line in the shallow subtidal zone. *Harpagifer georgianus* was found under boulders and amongst rubble or algal turf in the intertidal and shallow subtidal zones, and all specimens were caught by hand.

Specimens were examined and dissected in the laboratory. The standard length of each fish was recorded to the nearest millimetre and mass measured to the nearest 0,1 or 1,0 gram. Stomachs were removed and the wet mass of contents recorded. Prey from each stomach was sorted to species level and then counted and weighed to the nearest 0,01 g. Lengths of selected prey species from each stomach were also recorded. Ingested seaweeds were classified as rhodophytes, chlorophytes or phaeophytes and wet mass recorded. Intestinal contents were examined although they were not used in the final analysis. All gut contents were preserved in 10 percent formalin. Stomach content data were pooled for each fish species and the contribution of each prey species compared by four methods:

1) as a percentage of the total wet mass of stomach contents (% mass);
2) as the percentage of stomachs in which it appeared (% occurrence);
3) the number of prey specimens (N);
4) the ranking index method recommended by Hobson (1974).

Ranking index (P.I.) values for each prey species were calculated from the formula:

$$\text{R.I.} = \%\ \text{mass} \times \frac{\%\ \text{occ}}{100}$$

and then expressed as a percentage of the sum of all R.I. values for each species of fish.

Diets of the three species were compared by correspondence analysis, a relatively recent technique developed by French statisticians. An early review of the technique is given by Benzécri *et al.* (1973). Greenacre (1978) provides a more recent description and Underhill (1981) describes the computer programme used. Correspondence analysis was used for inter- and intraspecific comparisons of the species composition of diets of small and large fish (which were defined as those fish less than or more than the median standard length for each species, respectively). The lengths of all shells of the limpet *Nacella delesserti* retrieved from the stomachs or intestines of *Notothenia coriiceps* were measured with vernier calipers to the nearest 0,1 mm.

## RESULTS

### Size, morphology and habitats

*Notothenia coriiceps* was the largest of the three fish and the 31 specimens studied had a mean standard length and standard deviation of 304 ± 60 mm. Maximum length and mass were 444 and 1800 g. Colour was always dark blue-black with a yellow to white ventral surface. Notable features were the squat head, wide mouth and fleshy pelvic fins (Fig. 1A). Solitary individuals were always seen lying on the bottom, between boulders or on rocky ledges, usually in association with the abundant limpet *Nacella delesserti*. The fish is a poor swimmer and specimens usually attempted to escape capture by moving into gaps between boulders rather than swimming away.

The 129 specimens of *Notothenia macrocephala* (Fig. 1B) had a mean standard length and standard deviation of 166 ± 60 mm. Maximum length and mass recorded were 294 mm and 546 g. Coloration patterns were varied, and younger specimens were usually dark red with white to orange bellies, whilst larger ones were dark brown dorsally, with orange and white ventral markings. Small specimens of *N. macrocephala* were regularly sighted underwater at depths of 1 - 4 m, either singly or in loose aggregations of up to 30 fish. Large specimens inhabit deeper water and were mostly caught in water 10 - 30 m deep.

The 98 *Harpagifer georgianus* had a mean standard length and

TABLE 1 *Harpagifer georgianus* ,*Notothenia macrocephala* and *N. coriiceps*: Analysis of stomach contents

| | *H. georgianus* | | | | *N. macrocephala* | | | | *N. coriiceps* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % mass | % occ | N | % R.i. | % mass | % occ | N | % R.I. | % mass | % occ | N | % R.I. |
| Prey species | | | | | | | | | | | | |
| ALGAE | | | | | | | | | | | | |
| CHLOROPHYTA | | | | | | | | | | | | |
| small pieces (1-10 mm) | 00,5 | 4,1 | - | - | | | | | | | | |
| leafy pieces (up to 150 mm long) | | | | | 8,7 | 15,5 | - | 6,6 | 12,5 | 32,3 | - | 9,2 |
| RHODOPHYTA | | | | | | | | | | | | |
| leafy pieces | | | | | 16,1 | 22,5 | - | 16,0 | 41,9 | 54,8 | - | 52,9 |
| filamentous species | 1,9 | 16,3 | - | 0,7 | 4,4 | 9,3 | - | 1,9 | 0,8 | 16,1 | - | 0,2 |
| PHAEOPHYTA | | | | | | | | | | | | |
| *Durvillaea antarctica* | | | | | 0,2 | 1,6 | - | - | | | | |
| *Macrocystis pyrifera* | | | | | 3,2 | 1,6 | - | 0,5 | 1,4 | 6,5 | - | 0,2 |
| *Desmarestia rossii* | | | | | 3,7 | 1,6 | - | 0,5 | | | | |
| TOTALS | | | | 0,7 | | | | 25,5 | | | | 62,5 |
| INVERTEBRATA | | | | | | | | | | | | |
| CNIDARIA | | | | | | | | | | | | |
| Hydroida (unid.) | 0,3 | 1,0 | - | - | 0,1 | 3,1 | - | - | | | | |
| ANNELIDA | | | | | | | | | | | | |
| POLYCHAETA | | | | | | | | | | | | |
| *Platynereis australis* | 10,4 | 20,4 | 36 | 5,1 | 13,3 | 32,0 | 122 | 20,3 | 1,0 | 9,7 | 16 | 0,2 |
| *Romanchella perreiri* | 0,1 | 1,0 | 1 | - | - | 0,8 | 3 | - | | | | |
| Unidentified species | | | | | | | | | 0,2 | 6,5 | 7 | - |
| OLIGOCHAETA | | | | | | | | | | | | |
| *Lumbricillus* spp | 0,7 | 1,0 | 3 | - | 0,1 | 0,8 | 4 | - | | | | |
| TOTALS | | | | 5,1 | | | | 20,3 | | | | 0,2 |
| MOLLUSCA | | | | | | | | | | | | |
| GASTROPODA | | | | | | | | | | | | |
| *Nacella delesserti* | 0,5 | 1,0 | 1 | - | 3,1 | 7,0 | 11 | 1,0 | 27,1 | 51,6 | 56 | 32,2 |
| *Laevilitorina caliginosa* | - | 2,0 | 2 | - | 0,1 | 7,0 | 14 | - | - | 9,7 | 4 | - |
| POLYPLACOPHORA | | | | | | | | | | | | |
| *Hemiarthrum setulosum* | | | | | 0,1 | 3,9 | 8 | - | | | | |
| BIVALVIA | | | | | | | | | | | | |
| *Lasaea consanguinea* | 1,6 | 10,2 | 30 | 0,5 | 0,3 | 14,1 | 78 | 0,2 | | | | |
| *Kidderia bicolor* | - | 1,0 | 1 | - | | | | | | | | |
| *Gaimardia trapesina* | 0,1 | 1,0 | 1 | - | 4,6 | 12,5 | 103 | 2,7 | 0,3 | 6,5 | 18 | 0,1 |
| CEPHALOPODA | | | | | | | | | | | | |
| Unidentified squid | | | | | 0,8 | 0,8 | 1 | - | 0,1 | 3,2 | 1 | - |
| TOTALS | | | | 0,5 | | | | 3,9 | | | | 32,3 |

- continued

Table 1 (continued)

| | *H. georgianus* | | | | *N. macrocephala* | | | | *N. coriiceps* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % mass | % occ | N | % R.I. | % Mass | % occ | N | % R.I. | % mass | % occ | N | % R.I. |
| CRUSTACEA | | | | | | | | | | | | |
| COPEPODA | | | | | | | | | | | | |
| *Trigriopus angulatus* | 0,4 | 6,1 | 30 | 0,1 | | | | | | | | |
| TANAIDACEA | | | | | | | | | | | | |
| *Anatanais gracilis* | 0,4 | 4,1 | 5 | 0,1 | - | 3,9 | 7 | - | | | | |
| ISOPODA | | | | | | | | | | | | |
| *Antias bicornis* | 9,7 | 45,9 | 180 | 11,0 | | | | | | | | |
| *Munna instructa* | | | | | 0,1 | 5,5 | 20 | - | | | | |
| *Jaeropsis curvicornis* | | | | | - | 1,6 | 2 | - | | | | |
| *Dynamenella huttoni* | 4,4 | 18,4 | 34 | 2,0 | 12,8 | 46,1 | 338 | 27,8 | 1,1 | 45,2 | 112 | 1,2 |
| *Exosphaeroma gigas* | | | | | 0,9 | 4,7 | 14 | 0,2 | 1,7 | 25,8 | 17 | 0,9 |
| Unidentified | | | | | - | 0,8 | 1 | - | | | | |
| AMPHIPODA | | | | | | | | | | | | |
| *Jassa falcata* | 13,6 | 35,7 | 187 | 12,0 | 4,6 | 57,8 | 1336 | 12,3 | 0,3 | 41,9 | 114 | 0,2 |
| Eophiliantidae (unid.) | 2,6 | 22,5 | 41 | 1,5 | 0,1 | 14,0 | 61 | - | | | | |
| ?*Shakeltonia* sp | 28,6 | 65,3 | 415 | 45,7 | | | | | | | | |
| *Hyale* spp. | 19,0 | 40,8 | 146 | 19,1 | 1,4 | 24,2 | 202 | 1,6 | 0,1 | 9,7 | 13 | - |
| Eusiridae (unid.) | 4,6 | 20,4 | 41 | 2,2 | 3,5 | 37,5 | 312 | 6,1 | 1,2 | 35,5 | 292 | 0,9 |
| *Pontogeniella brevicornis* | | | | | 0,3 | 7,0 | 62 | 0,1 | 1,1 | 16,1 | 61 | 0,5 |
| Unidentified | | | | | 0,1 | 1,6 | 17 | - | | | | |
| EUPHAUSIACEA | | | | | | | | | | | | |
| Unidentified | | | | | 0,1 | 2,3 | 3 | - | | | | |
| NATANTIA | | | | | | | | | | | | |
| *Nauticavis marionis* | | | | | 4,2 | 4,7 | 59 | 0,9 | | | | |
| BRACHYURA | | | | | | | | | | | | |
| Unidentified | | | | | 1,5 | 3,9 | 5 | 0,3 | | | | |
| TOTALS | | | | 93,7 | | | | 49,3 | | | | 3,7 |
| CHELICERATA | | | | | | | | | | | | |
| ACARINA | | | | | | | | | | | | |
| *Halozetes* sp. | 0,2 | 3,1 | 3 | - | | | | | | | | |
| PYCNOGONIDA | | | | | | | | | | | | |
| *Tanyetylum cavidorsus* | | | | | - | 2,3 | 3 | - | | | | |
| INSECTA | | | | | | | | | | | | |
| *Ectemnorrhinis similis* | 0,2 | 1,0 | 1 | - | - | 3,1 | 6 | - | | | | |
| ECHINODERMATA | | | | | | | | | | | | |
| *Anasterias rupicola* | | | | | - | 0,8 | 1 | - | | | | |
| CHORDATA | | | | | | | | | | | | |
| PISCES | | | | | | | | | | | | |
| *Harpagifer georgianus* | | | | | 5,4 | 3,1 | 9 | 0,8 | 0,9 | 9,7 | 3 | 0,2 |
| *Notothenia macrocephala* | | | | | 2,4 | 0,8 | 1 | 0,1 | 6,6 | 6,5 | 2 | 1,0 |
| Unidentified | | | | | 3,3 | 0,8 | 3 | 0,1 | 1,0 | 3,2 | 3 | 0,1 |
| TOTALS | | | | | | | | 1,0 | | | | 1,3 |
| Unidentified objects | | | | | - | 2,3 | 14 | - | | | | |
| INORGANIC MATTER | | | | | | | | | | | | |
| Gravel | 0,1 | 4,1 | 5 | | 0,3 | 9,4 | 12 | 0,1 | - | 3,2 | 2 | - |

standard deviation of 48 ± 8 mm. Maximum length and mass were 69 mm and 6,5 g. Colours were cryptic and specimens were usually mottled brown and red with pale ochre undersurfaces. Notable features were the two pairs of defensive opercular spines, forward directed eyes and sharply pointed jaw (Fig. 1C). The species was abundant in the intertidal zone and many specimens were found in residual pools of water under boulders at low tide. A few individuals were encountered amongst algal turf at depths of 2 - 3 m. Like *N. coriiceps*, this species also spends much of its time lying motionless on the bottom. Up to three *H. georgianus* could be found in close proximity to one another although most specimens were found singly.

## Diets

*Notothenia macrocephala* stomachs contained the widest range of prey types of which *Dynamenella huttoni*, *Platynereis australis* and rhodophyte algae had the highest percentage R.I. values of 27,8%, 20,3% and 17,9% respectively (Table 1). Algae, isopods, polychaetes and amphipods formed the bulk of the diet. *Notothenia coriiceps* stomachs contained mostly rhodophytes (53,1%) and the limpet *Nacella delesserti* (32,2%). Chlorophyte algae, isopods and other fish were also eaten (Table 1). *Harpagifer georgianus*, the smallest of the three fish, was the most carnivorous species and algae had a low percentage R.I. value of 0,7 percent. The three amphipods *Shakeltonia* sp., *Hyale hirtipalma* and *Jassa falcata* formed 76,1% of the diet but isopods and polychaetes were also preyed on.

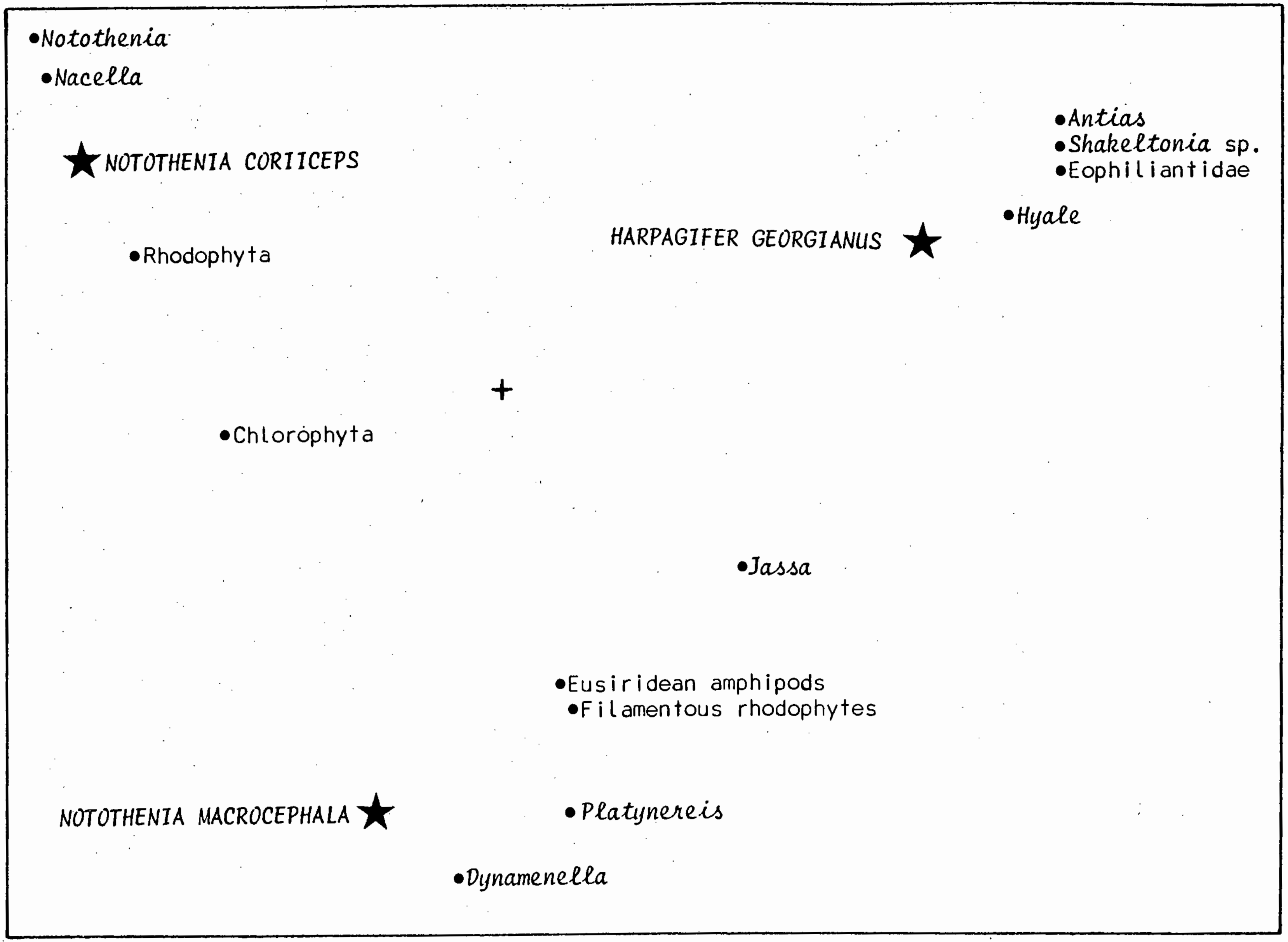

Fig. 2 Correspondence analysis of the diets of the three fish. Data for the analysis were percentage R.I. values.

★ = fish species; ● = prey species + = origin

Table 1 shows that only a few prey species were consumed in significant numbers by all three species of fish (e.g. *Dynamenella huttoni*, *Jassa falcata* and *Platynereis australis*) but that there are overlaps in the diets of any two species compared against one another. Correspondence analysis was a useful technique for displaying these feeding relationships graphically. As shown in Fig. 2, the computer-generated plot of each prey species graphically places it closest to the fish that consumes it. A prey that is consumed almost exclusively by one species of fish will be furthest from the origin. A prey that is shared between two species of fish will be drawn towards both fish species and consequently will lie between them. A prey shared between all three species would lie close to the origin. Figure 2 reveals that the most exclusive prey of *N. coriiceps* is the fish *N. macrocephala* and the limpet *Nacella delesserti* while *N. coriiceps* and *N. macrocephala* both consume Chlorophytes and *N. macrocephala* and *H. georgianus* share *Jassa falcata*. The equal distribution of the three fish around the origin indicates that the species composition of their diets is very different so that competition for common prey species is unlikely. *Notothenia coriiceps* and *N. macrocephala* lie closest together because of their common consumption of algae (mostly *Ulva*, *Porphyra* and *Rhodymenia*) whilst the distance between *N. coriiceps* and *H. georgianus* is largest since amphipods contribute little to the diet of *N. coriiceps* compared to *H. georgianus*

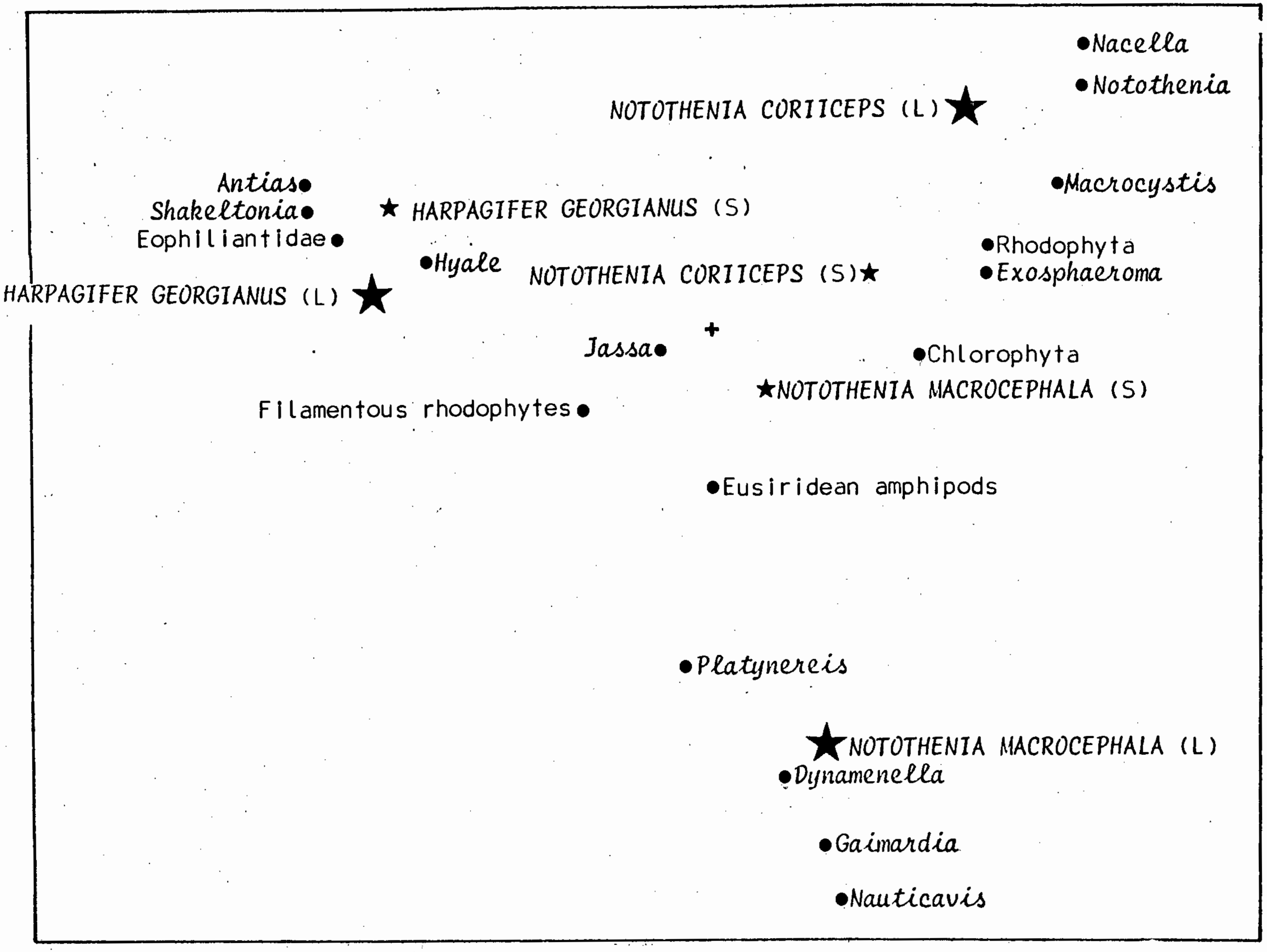

Figure 3 Correspondence analysis of diets of small and large size classes of the three species of fish.

★= large size classes ; ★= small size classes ; ● = prey species; + = origin.

## Size relationships

The three fish differed widely in size and shape yet managed to share a few common prey species. However, these common prey usually had different mean sizes for the three species of fish. Thus the mean wet mass of *Platynereis* consumed by *H. georgianus* was 0,02 g compared to 0,21 and 0,29 g for *N. macrocephala* and *N. coriiceps* respectively. Similarly the mean mass of *Nacella* consumed by *N. macrocephala* was 0,54 g compared to 2,25 g for *N. coriiceps* and the mean mass of *Dynamenella* taken by *H. georgianus* was 0,008 g compared to 0,073 g for *N. macrocephala*. The mean mass of the 1163 animals in the stomachs of *H. georgianus* was 0,005 g compared to 0,04 g for the 2850 found in *N. macrocephala* and 0,28 g for the 721 recovered from *N. coriiceps*.

The correspondence analysis of feeding relationships between small and large size classes of the three species of fish is shown in Fig. 3. The relatively short distance between the small and large classes of *H. georgianus* indicates that size makes little difference to diet in this species. Small and large *N. macrocephala* showed the greatest difference in prey species composition because smaller individuals consumed more *Jassa falcata* and seaweeds than larger specimens which fed more on *Platynereis* and *Dynamenella*. Larger *N. coriiceps* ate more *Nacella* than smaller ones. Small *N. macrocephala* and small *N. coriiceps* showed the greatest interspecific similarity in diet, based on their corresponding reliance on rhodophytes, chlorophytes and *Jassa falcata*. The diet of large

*H. georgianus* showed a far closer similarity to the diets of the small classes of the other two fish species than to the large size classes.

## Predation of *Nacella* by *Notothenia coriiceps*

A total of 136 *Nacella* shells were recovered from the stomachs and intestines of 22 of the 31 *N. coriiceps* specimens examined. The majority of limpet shells was found far back in the intestine so that it seems likely that shells are voided with faeces although they were not encased in mucoid capsules as reported by Stobbs (1980) for the giant clingfish *Chorisochismus dentex* which feeds on patellid limpets. Even the largest *Nacella* were easily removed from rocks by hand and did not appear to cling to surfaces with the great forces recorded by Branch and Marsh (1978) for some South African limpets so that *N. coriiceps* is easily able to dislodge *Nacella* with its strong mouth while the limpets are moving around with their shells elevated. This was seen on two occasions whilst snorkelling. Figure 4 shows that there is a wide variation in the sizes of *Nacella* preyed on (9,0 - 55,0 mm), particularly by large fish. Nevertheless a significant correlation ($r = 0{,}6$; $p < 0{,}01$) exists between the standard lengths of the individual fish and the lengths of *Nacella* shells found in their guts. Figure 4 shows that larger *N. coriiceps* were able to consume larger limpets but data are insufficient to conclude whether they prefer larger to smaller limpets or whether

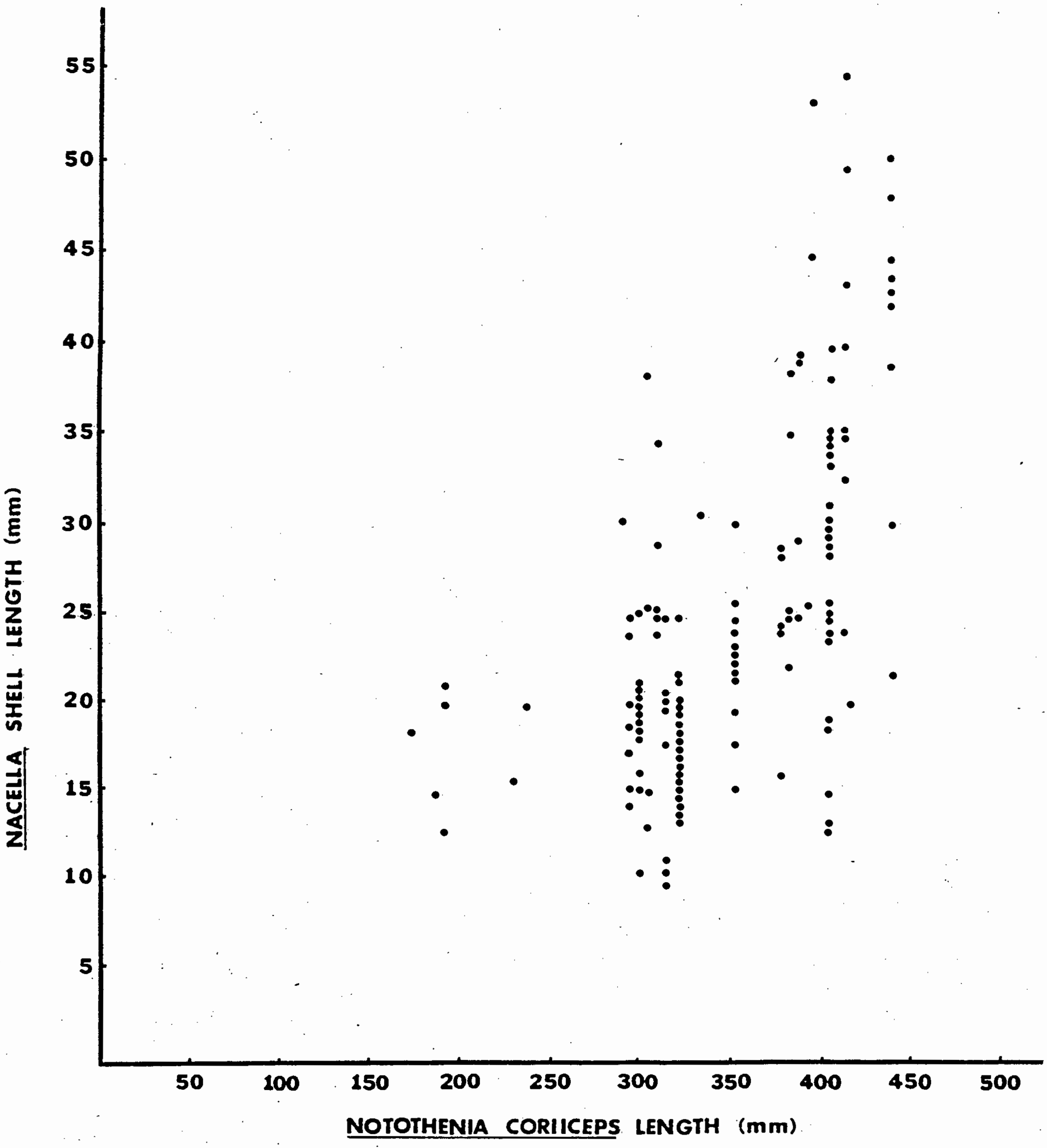

Figure 4 *Notothenia coriiceps* predation of *Nacella delesserti*; lengths of shells from fish guts compared to the size of the fish predator.

they simply feed randomly on limpets up to the size they can handle. Relatively few limpets with shell lengths greater than 45 mm were preyed on by the fish so that *Nacella*, which has a maximum size of 65 mm, has a refuge in size from predation by *N. coriiceps*.

## DISCUSSION

Antarctic fish communities are comparatively simple and the level of interspecific overlap in food resources is low compared to that in temperate and tropical regions (Targett 1981). The presence of only three inshore species of fish at Marion Island reflects the low diversity of the isolated and relatively youthful marine community to which they belong. The oldest Marion Island lavae are less than 300 000 years old (McDougall 1971). The results of this study show that the three species have distinct differences in morphological characteristics, life habits and diet, and hence competition for food resources is virtually non-existent.

The carnivorous plunder fish, *Harpagifer georgianus*, has the most specialised diet of the three species with five species of amphipods and two isopod species forming 93,5 percent of its food, so that it is clearly dependent on small crustaceans as its prey. *Harpagifer* is preyed on by the other two species of fish and heavy predation by the imperial cormorant *Phalocrocorax atriceps* and sometimes the gull *Larus dominicanus* also occurs on it (Blankley 1981 & Part 2).

*Harpagifer georgianus* thus forms an important link in the marine food web of Marion Island. Other studies confirm the reliance of *H. georgianus* on crustaceans as food, and Meier (1971), Richardson (1975), Duarte and Morano (1981) and Targett (1981) all found that amphipods formed more than 95 percent of the diet of *Harpagifer* species.

The diet of *Notothenia macrocephala* is likely to be far more complex than described here since this species has pelagic and not demersal eggs, as found in the other two species (unpublished data) and is therefore likely to spend part of the year at sea. *N. macrocephala* is omnivorous and feeds mostly on seaweeds and its major prey (isopods, amphipods and polychaetes) are species found in association with algal turf. Hureau (1966) found that *N. macrocephala* at Kerguelen Island mainly ate the isopod *Glyptonotus antarcticus*, bivalve *Hiatella antarctica*, amphipods, small fish and algae. The mean mass of animal prey eaten by *N. macrocephala* at Kerguelen Island can be derived from Hureau's (1966) data as 0,25 g which is close to the figure of 0,28 g recorded in the present study. However Hureau (1966) found that algae formed only 20% of the total mass of *N. macrocephala* stomach contents compared to 57% in this study. Further studies on the distribution and life habits of this species would be useful. No other studies on this species are recorded in the literature. Further studies on its distribution and life habits would be useful.

*Notothenia coriiceps* is a widely distributed species found around most of the Antarctic continent and at most sub-Antarctic islands (Biomass Scientific Series, 1977). Shabika (1971) recorded that *N. coriiceps* consumes the limpet *Patinigera polaris* at Palmer Station, Antarctica. Richardson (1975) found thtat the stomach contents of *N. coriiceps neglecta* at Signey Island, South Orkney Islands consisted mostly of algae, amphipods, anthozoans and molluscs, of which the limpet *Nacella concinna* was found in 35 percent of the stomachs examined. Targett (1981) found that *N. coriiceps* at South Sandwich Islands fed mostly on amphipods and some isopods, but his samples were taken 3,5 km offshore at depths of 15 - 70 m. In the present study *N. coriiceps* was found to be mostly herbivorous, although the limpet *Nacella delesserti* is likely to provide it with more energy since seaweeds were voided in a fairly undigested state.

Each of the three species appeared to occupy a clearly defined feeding niche in this study, although some similarities in the diets of *H. georgianus* and the smaller size classes of *cephala* and *N. coriiceps* are shown in Fig. 3. These similarities are likely to be the result of overlap in habitat occupation since the smaller *N. macrocephala* and *N. coriiceps* were caught close inshore only a metre or two deeper than the sites where most of the *Harpagifer* were found in the intertidal zone: as Targett (1981) has stated "habitat separation is important more often than either within-habitat prey separation or temporal separation in avoiding food resource overlap" based on Schoener's (1974) findings. Thus large *N. macrocephala* which inhabited deep (15 - 20 m) water and large *N. coriiceps* which were found on the bottom in water 2 - 5 m deep showed clear-cut differences in diet between one another and to the intertidal population of *H. georgianus*, because the habitats they occupy offer different species as prey.

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# PART 5

# ECOLOGY OF THE LIMPET
# *NACELLA (PATINIGERA) DELESSERTI* (PHILIPPI)
# AT MARION ISLAND (SOUTHERN OCEAN)

## ABSTRACT

The ecology of the Marion Island limpet *Nacella (Patinigera) delesserti* (Philippi) is described from studies of its biomass, habitats, feeding, growth and its value as a central prey species.

*N. delesserti* is the most abundant macro-invertebrate on the shores of Marion Island and is the major prey of the starfish *Anasterias rupicola*, kelp gull *Larus dominicanus* and cod *Notothenia coriiceps*. Mean densities of *Nacella* in the intertidal and subtidal zones are 75,1 and 93,2 m$^{-2}$ respectively. Extraordinarily high numbers of 319,9 *Nacella* m$^{-2}$ are recorded from the subtidal of Prince Edward Island. *Nacella* form stacks or towers in the subtidal and up to 42 *Nacella* were found piled one on top of another. Generally *Nacella* is common in areas where the predatory starfish *Anasterias* is rare. The main diet of *Nacella* is algal spores and sporelings, although loose fronds of the kelp *Durvilleaea antarctica* are readily grazed. Limpets which were held in cages and fed on kelp fronds provided data on grazing rates, growth and assimilation efficiency. The growth of free ranging, labelled *Nacella* was also monitored and provided data for use in Ford-Walford plots. The relationship between length and age was

determined by use of the Van Bertalanffy growth equation. Growth is fairly rapid in the early stages of life and *Nacella* attains a length of 50 - 60 mm after five years and lives for a maximum of 8 years. *Nacella* production is 40,77 g dry flesh weight or 798,3 kJ $m^{-2}$ $y^{-1}$ giving it a production biomass ratio of 0,65 which, according to its longevity, indicates a comparatively moderate rate of turnover. Size-specific predation of *Nacella* by fish, starfish and gulls is an important cause of mortality and affects population structure accordingly. *Nacella* with shell length exceeding 50 mm attain a relative refuge in size from predation.

## INTRODUCTION

*Nacella (Patinigera) delesserti* (Philippi) is the most conspicuous macro-invertebrate on the shores of Marion Island. De Villiers (1976) noted the predominance of *Nacella* and the variety of habitats occupied by this species which occurs in the intertidal and subtidal zones. *Nacella* plays an important rôle in the inshore food web and provides 90% of the diet of the starfish *Anasterias rupicola* (Part 2), about 50% of the prey of the kelp gull *Larus dominicanus* (Blankley 1981 and Part 1) and 27% of the food of the cod *Notothenia coriiceps* (Part 4). *Nacella* is also the dominant macro-herbivore of the eulittoral zone and probably has an important influence on the distribution and abundance of marine algae. For these reasons a study of *Nacella* is of central importance for any comprehensive account of the marine ecology of Marion Island.

Few quantitative studies have been undertaken on limpets from other sub-Antarctic islands, although Simpson (1976) described aspects of the littoral ecology of molluscs on Macquarie Island and also investigated reproduction in *Nacella (Patinigera) macquariensis* (Simpson, 1982). On the other hand the biology of the Antarctic limpet *Nacella (Patinigera) concinna* (earlier described as *Patinigera polaris*) is better known and has been studied by workers such as Walker (1972), Berry and Rudge (1973), Shabica (1976), Ralph & Maxwell (1977) and Picken (1980).

The aim of the present study was to provide quantitative data on the biomass, production and grazing rates of *Nacella* at Marion Island and to relate these data to its rôle as a secondary producer and a major prey of tertiary inshore predators.

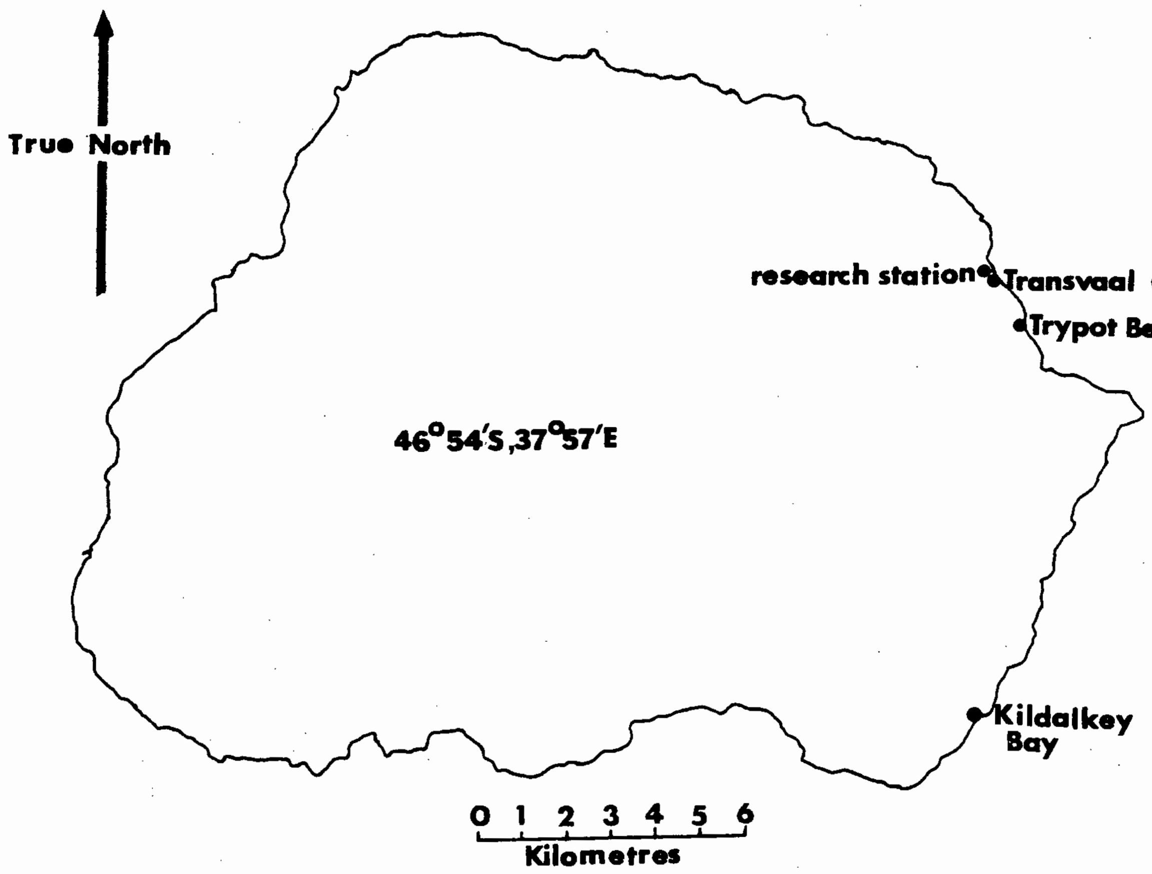

Fig. 1 An outline map of Marion Island, showing the location of Transvaal Cove.

## MATERIALS AND METHODS

The major study site for work on *Nacella* was Transvaal Cove, a relatively sheltered bay on the north-east coast of Marion Island (Fig. 1). Field work was initiated in May 1979 and continued until May 1980. A brief survey was also conducted at neighbouring Prince Edward Island during May 1980.

### Density and biomass

The density of intertidal *Nacella* was determined from 184 0,1m$^2$ quadrats. Quadrat sites were chosen by randomly throwing the quadrat frame on the shore and all limpets were collected from the area it enclosed. Limpets were counted and weighed in the laboratory and their shell lengths measured.

Subtidal *Nacella* were studied by means of underwater photography. Sites for photographs were chosen by randomly throwing a weighted five-metre rope in the shallow subtidal region (1 - 4 m depth). The rope was then stretched across the area where it landed and colour photographs were taken at 50 cm intervals along its length from a height of 1,0 - 1,5 m. Over 500 slides were obtained in this manner but only 107 were eventually chosen for analysis. Criteria for the choice of slides were clarity of focus, lack of parallax and placement of the marked rope. Slides were printed as postcard-sized prints and the area shown was calculated from the dimensions of the rope. All

*Nacella* visible in the central portion of the print, representing an area of 0,25 $m^2$ (Marion Island) or 0,5 $m^2$ (Prince Edward Island), were then counted.

A regression of dry flesh weight on shell length was calculated to allow subsequent conversions of shell length to dry body mass. The energy content of *Nacella* flesh (kJ $g^{-1}$) was determined from representative samples on an AMPC micro-bomb calorimeter.

## Growth and grazing rates

Growth rates were determined for free-living animals in the field as well as for limpets maintained in cages. Free-living limpets were labelled with Dymotape labels stuck to the shell with Araldite glue. After shell length and body mass had been recorded in the laboratory the limpets were returned to the sea in the vicinity of a subtidal site marked with an anchored buoy. On subsequent dives during the next eight months any tagged limpets seen were collected, re-measured and returned to the station. A total of 260 limpets was tagged and the recovery of animals at the end of eight months was about 20%.

The growth of *Nacella* was also determined from monthly measurements of limpets which were maintained in cages and fed on fronds of the kelp *Durvillaea antarctica*.

Cages to house limpets were constructed from cylindrical P.V.C.

piping, 250 mm long and 80 mm in diameter. The ends of the cages were closed off with stainless steel mesh (mesh size 1 mm$^2$) and the cages were tied with strong nylon twine to *Durvillaea antarctica* holdfasts in a sheltered gulley. Groups of 15 - 49 *Nacella* were confined in five of these cages for periods of 3 - 7 months. Limpets in four of these cages were supplied with kelp each month whilst a control group of 49 *Nacella* was deprived of food for nearly three months. Different numbers of limpets, covering different sizes, were housed in each of the cages used in the feeding experiments. Two cages contained small *Nacella* ($<$ 43 mm) whilst the limpets in the other two cages had shell lengths ranging between 11 and 62 mm. The shell lengths of the limpets kept in each cage were measured with vernier calipers and ranked according to size. Rank orderings of subsequent monthly measurements allowed the growth of each limpet to be monitored. A shell length - dry mass regression curve which was determined for the limpets at the termination of the caging experiments showed no significant departure from regressions obtained for the normal population and hence increments in shell length could be converted directly to increments in dry body mass.

## Consumption rates

Freshly cut *Durvillaea* fronds were weighed and put in each of the four experimental cages each month and any remaining kelp from the previous month was removed. A control cage, containing only kelp, was also monitored each month to assess the loss of kelp in cages due to abrasion, amphipod and isopod grazing, and bacterial breakdown. Laboratory controls of the kelp were also kept to assess the effect of prolonged immersion in sea water on wet-dry mass conversion ratios.

Kelp remaining in the cages at the end of each month was dried to constant mass of 80°C and the amount of dry kelp consumed in each cage per month (A) was calculated from the following formula:

$$A = (B \times C) - D \times C - E$$

where:

B = original wet mass of kelp provided
C = ratio of dry:wet kelp
D = wet mass of kelp lost in the control cages via abrasion and micro-grazers
E = dry mass of kelp remaining in the cage.

Growth rate obtained by the above methods were first plotted as a Ford-Walford plot - the regression of length at time (t + 1) on length at time t - using the equation:

$$L_{t+1} = m L_t + i \qquad (1)$$

where:

m is the slope of the line, and
i is the vertical intercept (Ford, 1933; Walford, 1946).

Constants obtained from the Ford-Walford plots were used to determine length and age relationships of the limpet in the Von Bertalanffy growth equation:

$$L_t = L \quad (l-e^{-K\ (t\ -\ t_o)} \qquad (2)$$

where:

$L$ is the asymptotic length,

$K$ is the growth coefficient, and

$t_o$ is the theoretical age at length zero (the start of settled growth).

## Production

*Nacella* production was expressed as the annual increment in dry soft body mass $m^{-2}$ and was calculated using the following formula:

$$\text{Production } m^{-2}\ y^{-1} = \sum_{i=1}^{n} (F \times G \times H)$$

where:

F = mean density $m^{-2}$

G = the proportion of the *Nacella* population in each size class

H = the predicted production of an average limpet in each size class (from the growth data)

n = the number of 5 mm size classes.

This assessment of production excludes losses due to mortality which have not yet been determined.

TABLE 1 Densities of *Nacella delesserti* at Marion and Prince Edward Islands

| Site and Method | No. & size of quadrats | Density (Mean ± S.E.) |
|---|---|---|
| Marion intertidal (quadrat counts) | 184 x 0,1 $m^2$ | 75,05 ± 9,2 $m^{-2}$ |
| Marion subtidal (photo-quadrats) | 107 x 0,25 $m^2$ | 93,2 ± 11,3 $m^{-2}$ |
| Prince Edward subtidal (photo-quadrats) | 15 x 0,50 $m^2$ | 319,9 ± 53,9 $m^{-2}$ |

## RESULTS

### Density and biomass

Mean density of *Nacella* in the Marion Island intertidal zone was 75,05 ± S.E. 9,2 $m^{-2}$ (Table 1). Density in the subtidal zone was slightly higher (93,2 ± 11,3 $m^{-2}$) but substantially less than the extraordinarily high numbers recorded for the subtidal population of *Nacella* at Prince Edward Island (319,9 ± 53,9 $m^{-2}$). Mean biomass of intertidal *Nacella* at Marion Island was 62,23 g dry flesh mass $m^{-2}$ (= 1292 kJ $m^{-2}$). Biomass of the subtidal population was estimated to be much greater than this ($\simeq$ 115,6 g $m^{-2}$) partly because of higher densities and partly because of the fact that it was only possible to count large *Nacella* ( > 25 mm) in the photographs. Some areas in the subtidal zone, especially at Prince Edward Island, were so densely occupied by layers of *Nacella* that the substratum was obscured from view. Under these circumstances *Nacella* usually formed stacks or towers, and up to 42 *Nacella* were found piled one on top of another. Thirty two percent of the limpets counted in the subtidal photoquadrats occurred at Marion Island in such stacks.

### Habitats

Intertidal *Nacella* occurred mostly on vertical surfaces and extended up to the high water level. Large *Nacella* (40 - 60 mm) were plentiful amongst stable boulders in the higher regions of the intertidal zone, whilst smaller *Nacella* (10 - 30 mm) were most common on exposed *Lithothamnion* encrusted ledges in the swash zone, a habitat they shared with the chiton *Hemiarthrum setulosum*. Generally *Nacella* was common in areas where the predatory starfish *Anasterias rupicola* was rare. *Anasterias* has a density of 17,5 ± S.D. 43,2 $m^{-2}$ in the intertidal zone (Blankley, unpub.) but 64,6% of the *Nacella* sampled came from quadrats where *Anasterias* was absent. Subtidal *Nacella* mostly formed dense aggregations and towers on the sides and tops of large boulders where starfish were unable to reach them. Most *Nacella* occurred at depths of 2 - 4 m and relatively few limpets were sighted at depths greater than 5 m. *Nacella* was rarely found amongst dense beds of subtidal coralline algae but was fairly plentiful amongst holdfasts of the domiant kelp *Durvillaea antarctica* and in stands of *Rhodymenia* sp.

## Diet

*Nacella* appeared to feed mostly on algal spores and sporelings and surfaces on which the limpets were very abundant were noticeably free of new algal growth. *Durvillaea antarctica* is readily grazed by *Nacella* and the limpets converge on loose fronds: up to 50 *Nacella* were found holding down and grazing a piece of kelp. In the intertidal zone *Nacella* radula marks were noted on *Ulothrix* sp., *Rhodymenia* sp. and on *Durvillaea antarctica* holdfasts, stipes and fronds. *Nacella* thus has a generalised diet on Marion Island where it grazes on all suitable algae and has no competition from any other similar herbivores.

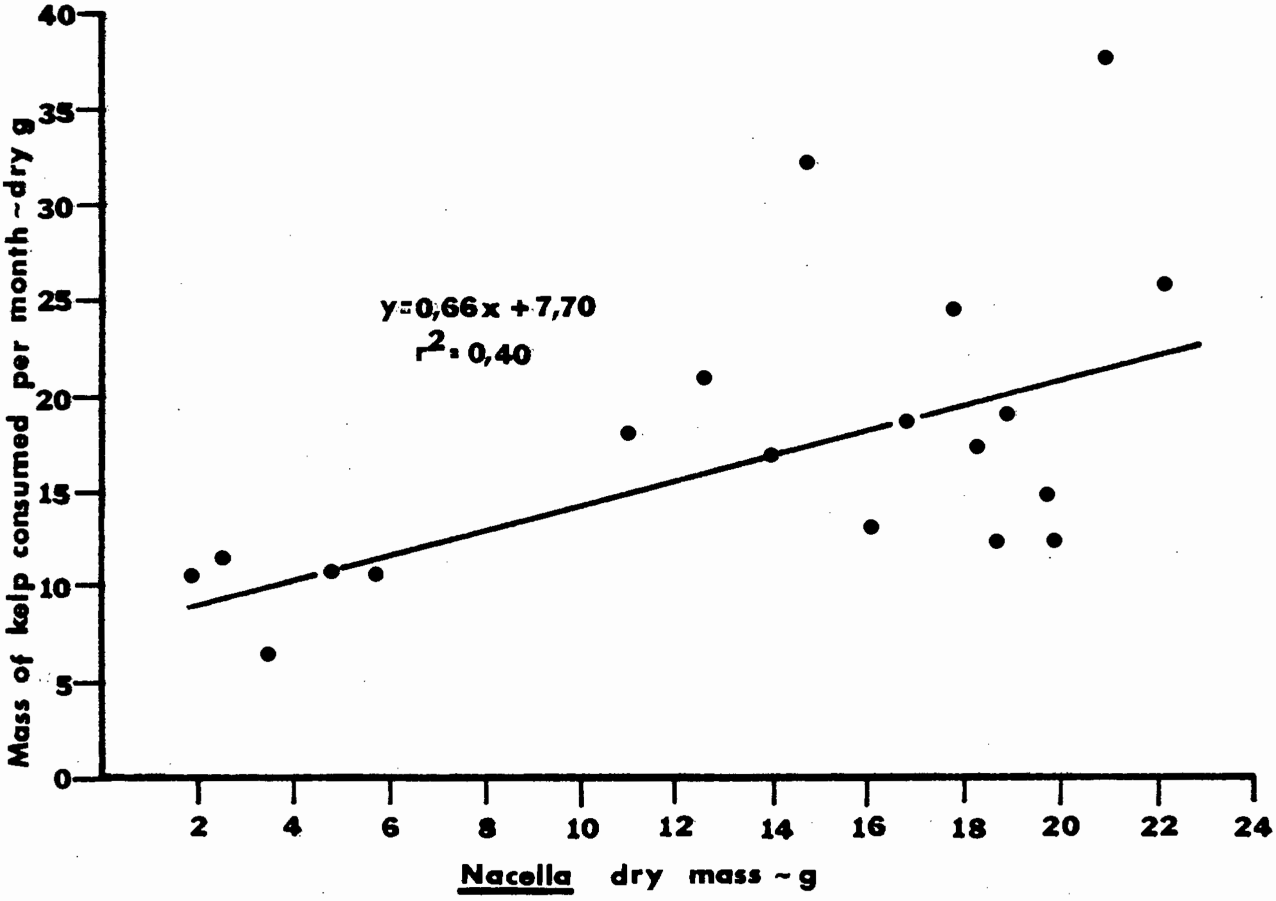

Fig. 2 Monthly consumption of kelp by caged *Nacella*. The mass of kelp grazed per month is plotted against the total mass of limpets in each cage.

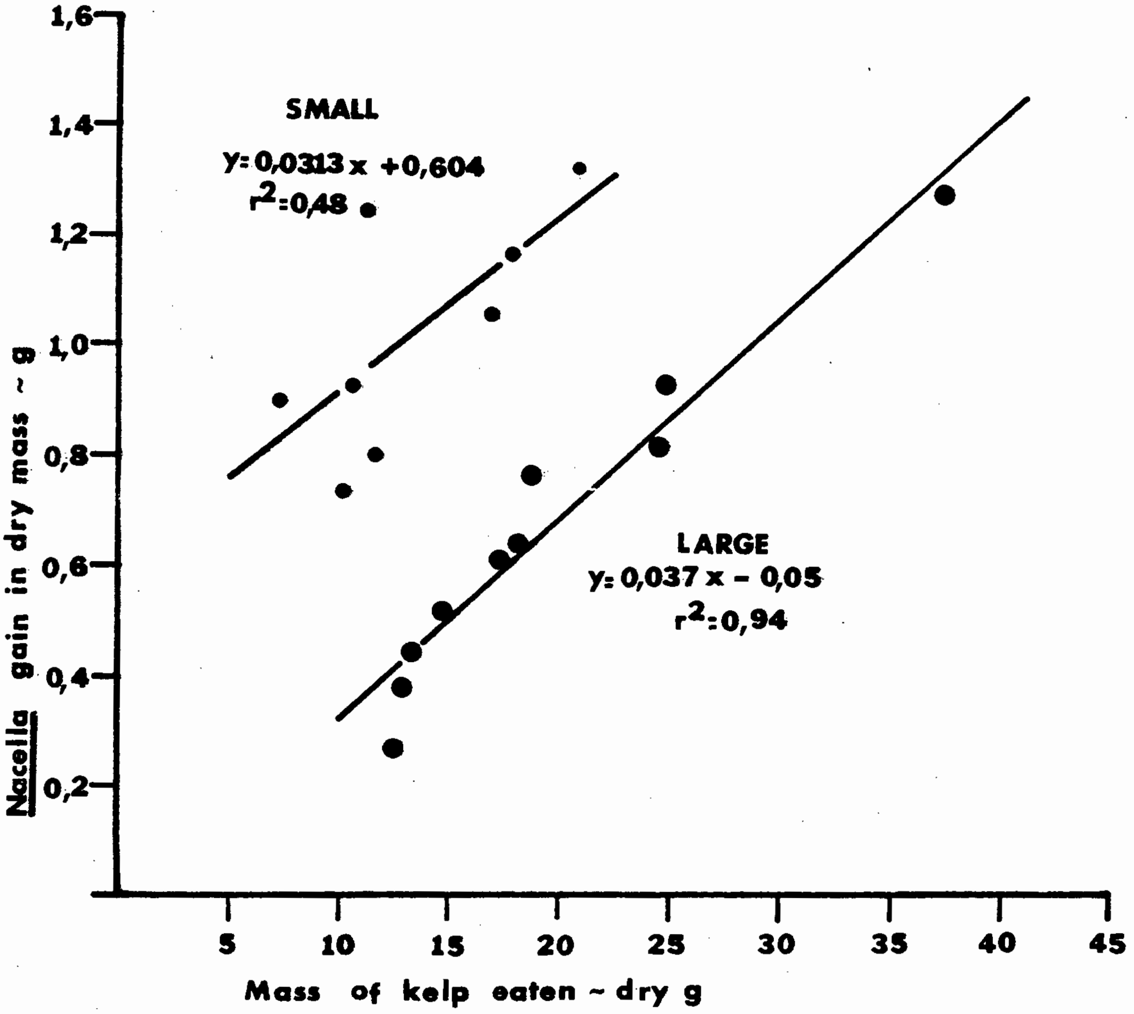

Fig. 3 Assimilation of kelp by caged *Nacella*. Gain in mass of *Nacella* as a function of the mass of kelp grazed is different for small ( < 43 mm) and large limpets.

## Grazing rates

The design of the caging experiments prevented calculation of grazing rates for different size classes of *Nacella* but did allow a linear regression to be calculated which could be used to predict the monthly food intake of a given biomass of *Nacella* (Fig. 2). Since both the growth and kelp intake of the caged limpets were monitored on a monthly basis the assimilation efficiency of *Nacella* could also be calculated. The total gain in mass of each set of caged *Nacella* plotted against the dry mass of kelp eaten each month gave a mean conversion ratio (of g kelp to g flesh) of 0,1454 for the small limpets ($<$ 30 mm) and 0,0658 for the larger animals (Fig. 3).

In the control cage where 50 limpets ranging in size from 12,25 - 48,25 mm were deprived of food for 88 days only three of the smaller limpets died. A slight but negligible increment in mean shell length of 0,16 mm was recorded, mean wet mass also increased by 0,15 g, and the surviving limpets appeared to be normally healthy and lively at the end of the experiment.

## Growth rates

Growth of both experimentally-fed limpets and free-range animals was plotted as the regression of length at time (t + 1) on length of time (t) using equation 1 (p.84). For the caged limpets the values of $L_t$ were the mean shell lengths of limpets in each 5 mm size class at the start of the caging experiments and $L_{t+l}$ for each size class

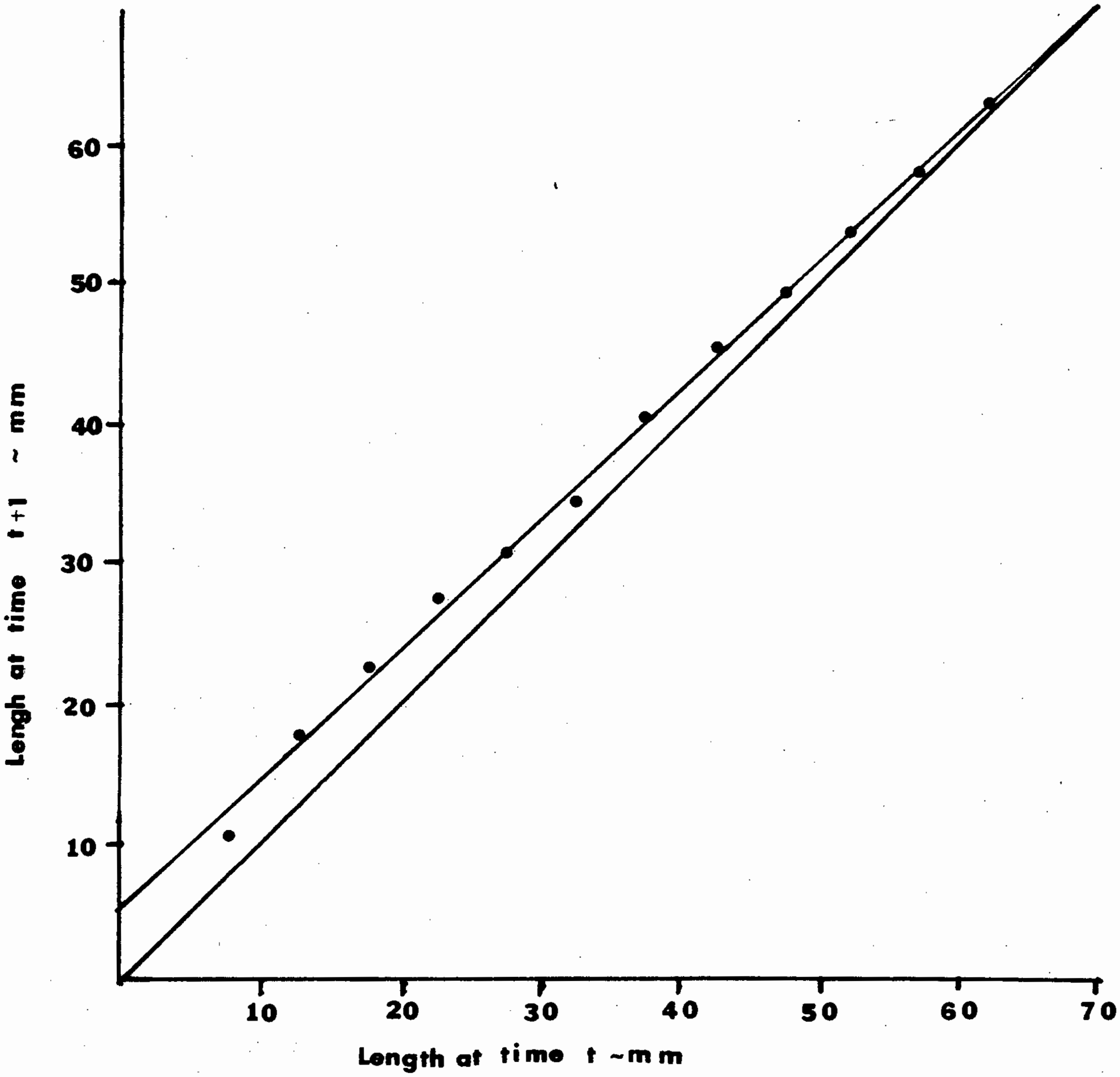

Fig. 4A Ford Walford plot of growth data for mean increment values of caged *Nacella*.

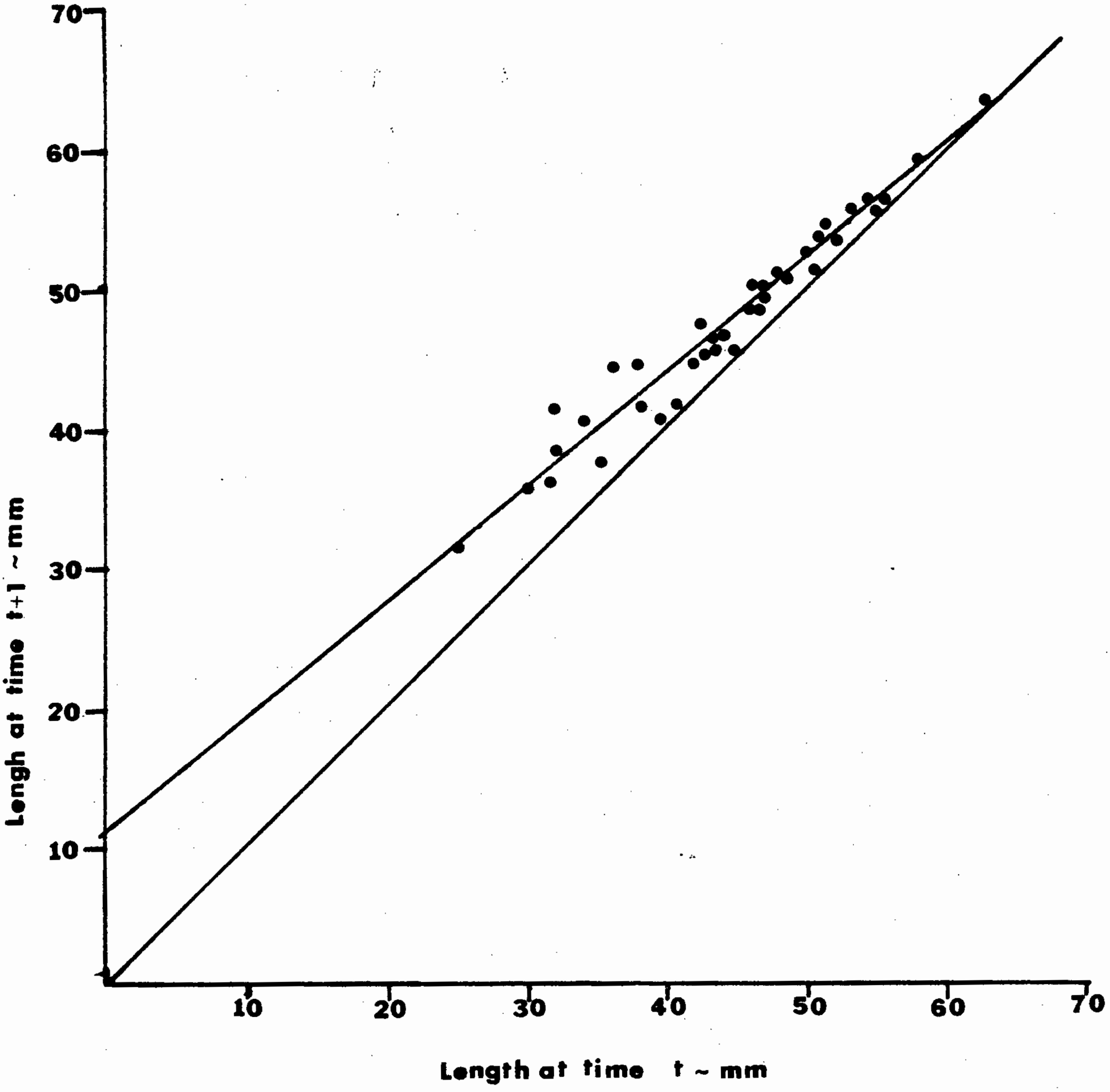

Fig. 4B Ford Walford plot of growth data for absolute values for free-ranging *Nacella*. Not all 69 values are shown.

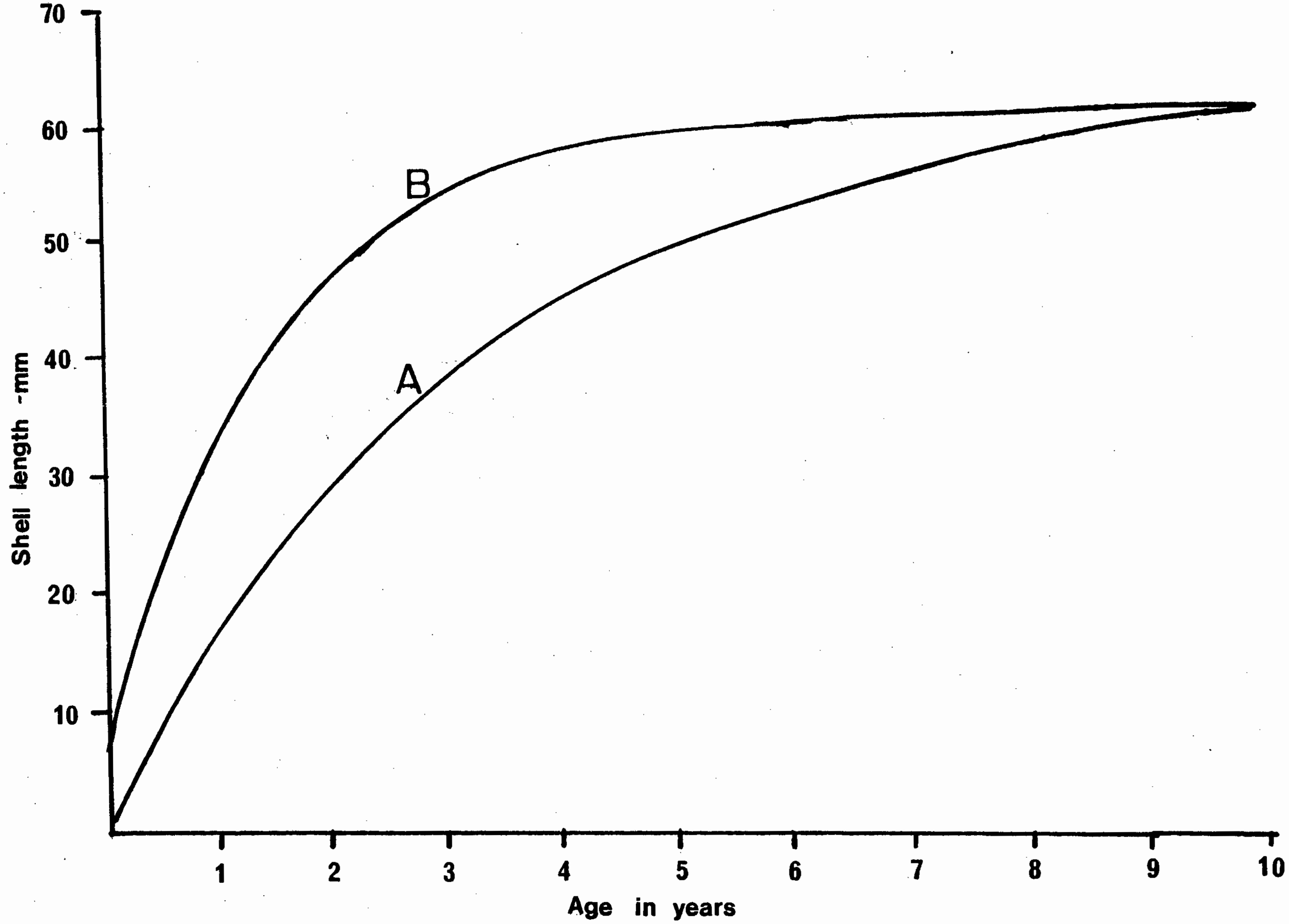

Fig. 5 Von Bertalanffy relationships between shell length and age of (A) caged, and (B) free-range *Nacella delesserti.*

was obtained by adding the mean increment in shell length after three months to $L_t$. For the free-range sample $L_t$ was initial shell length and $L_{t+1}$ was the shell length at recapture, standardised for a period of three months. The constants m and i were calculated by the method of least squares and these were found to be 0,9006 and 6,4454 respectively for the caged limpets and 0,82211 and 10,89 for the free-range animals. Ford-Walford plots of $L_{t+1}$ on $L_t$ are shown in Fig. 4a (caged limpets) and Fig. 4b (free-range animals).

The parameters L (asymptotic length) and K (growth constant) can be obtained as $L = i/(l - m)$ and $K = (- \log_e m)$. For the experimentally fed limpets L = 64,87 and K = 0,0738 and for the free-range animals L = 64,00 and K = 0,1971. The last parameter necessary for calculation of the Von Bertalanffy growth equation is $t_o$, the theoretical age at length zero. Simpson (1982) found that *Nacella macquariensis* at Marion Island produced fully developed trochophores 50 h after fertilization and suggested that it was unlikely that the larvae feed in the plankton so that $t_o$ in the closely related *N. delesserti* can be assumed to be negligible although it could also be negative. Using the Von Bertalanffy growth equation approximate relationships between length and age for the two groups of limpets were determined and are shown in Fig. 5.

Since no limpets with shell lengths < 25 mm were recaptured in the free-range study the resultant growth curve lacks support for the smaller size classes. The growth curve of the caged limpets is more reliable although growth in the smaller size classes was slower than

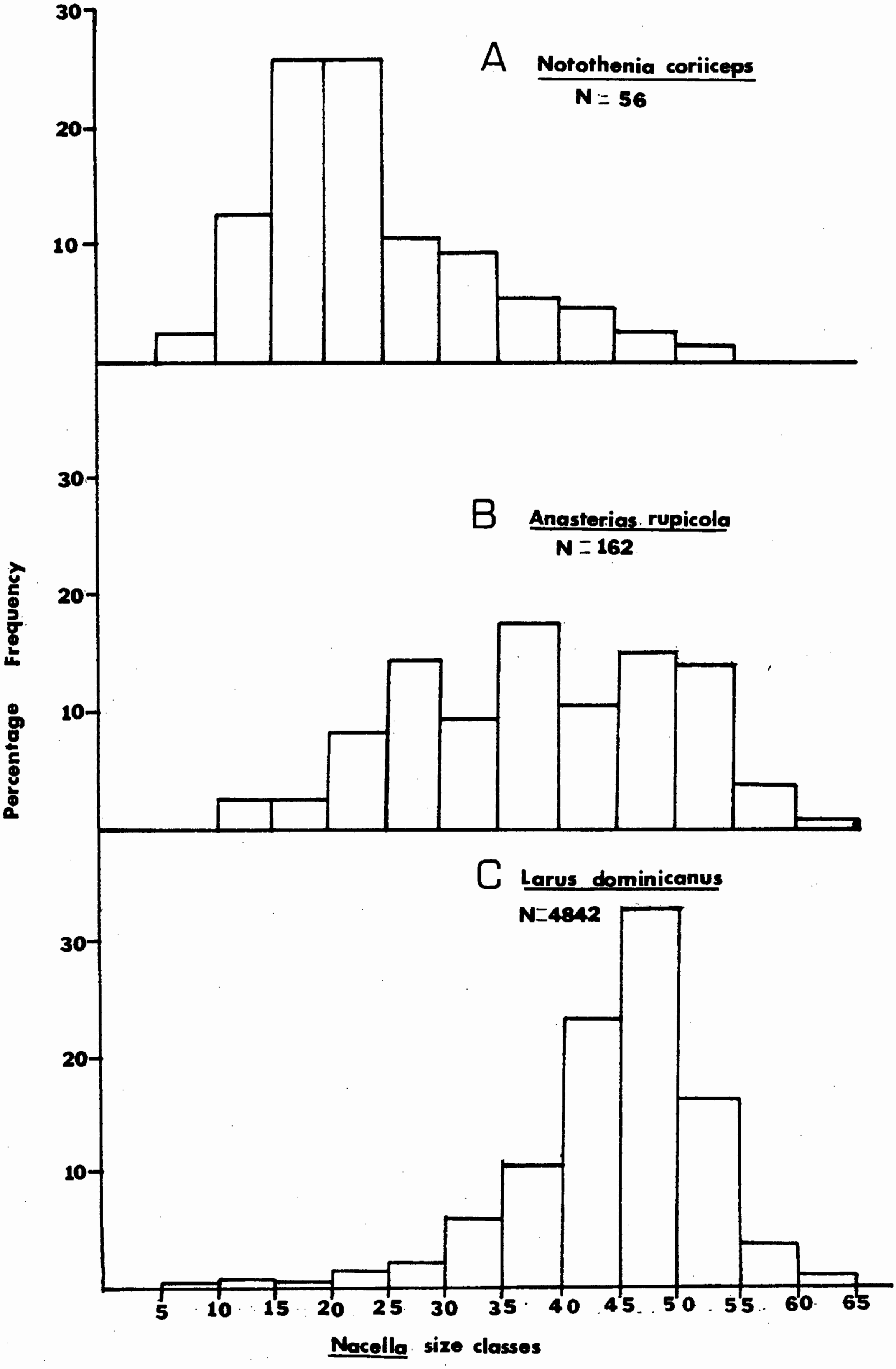

Fig. 6 Size-frequency distribution for *Nacella* preyed upon by:

(A) *Notothenia coriiceps*

(B) *Anasterias rupicola*

(C) *Larus dominicanus*

under natural conditions. Evaluating both curves simultaneously, growth in *Nacella* is fairly rapid in the early stages of life and limpets attain a length of 50 - 60 mm after five years. *Nacella* lives for a maximum of 8 - 10 years and attains a maximum size of about 65 mm. Normal life span is probably in the vicinity of 3 - 5 years.

The net production of *Nacella* was estimated from the formula given in the Methods section using data from the present study. From these calculations *Nacella* production was found to be 40,77 g dry flesh weight or 798,3 kJ $m^{-2}y^{-1}$.

## Population structure and predation

The size class distributions of *Nacella* consumed by the fish *Notothenia coriiceps*, the starfish *Anasterias rupicola* and the kelp gull *Larus dominicanus* are shown in Figs 6a, 6b, 6c respectively.

*Notothenia coriiceps* swallows limpets whole and passes the shells out with faeces (Part 4), and hence is restricted to eating relatively small *Nacella* of 10 - 30 mm. *Larus dominicanus* mainly catches large *Nacella* (35 - 55 mm) in shallow water and devours the soft parts of the limpets on the shore (Blankley, 1981). A few small *Nacella* are, however, swallowed whole by the gulls and the shells regurgitated later. *Anasterias rupicola* preys extensively on *Nacella* and its habit of grouping to co-operatively hunt and digest limpets allows it to exploit even the largest *Nacella* (Part 3).

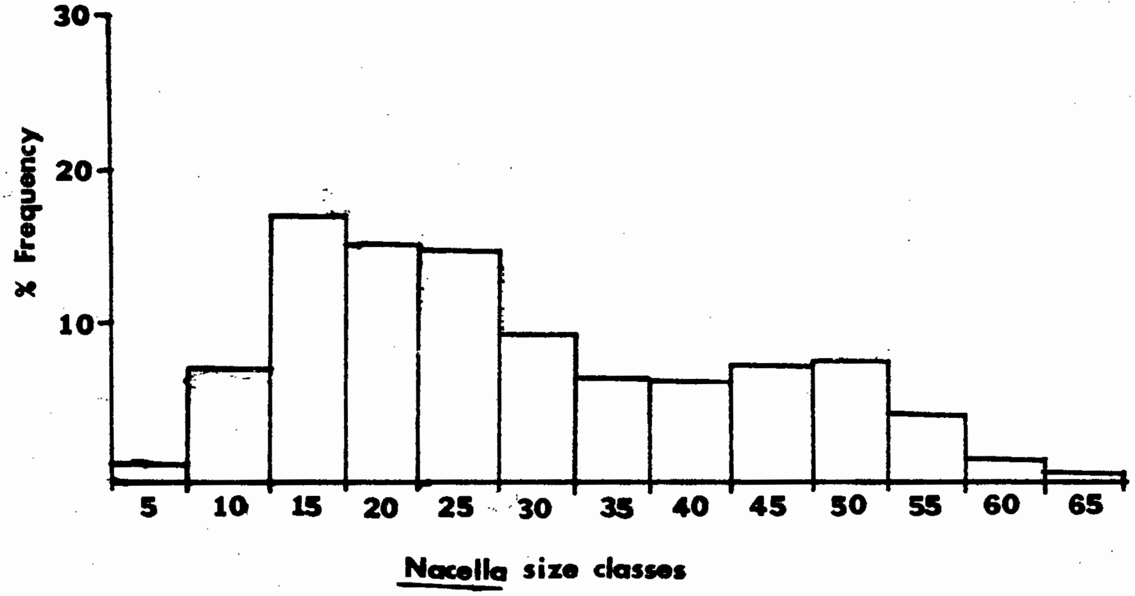

Fig. 7 Size-frequency distribution for *Nacella delesserti* (n = 1367).

Figure 6B shows that *Anasterias* eats *Nacella* throughout most of its size range, although most of its prey are limpets between 20 - 55 mm.

The size class distribution of *Nacella*, obtained from the biomass samples is shown in Fig. 7. The small proportion of animals less than 10 mm in length indicates that very small limpets could have been overlooked. On the other hand growth in the first year of life is very rapid (Fig. 5) and relatively few *Nacella* remain in the smallest size classes for any significant length of time. Otherwise the structure of the population appears to be fairly normal with the bulk of individuals between 15 - 30 mm and a decline in the numbers of limpets over 50 mm long.

Although the data presented here are insufficient for the calculation of accurate mortality rates and survivorship curves it seems reasonable to assume that the above predation affects the population structure of *Nacella*. *Notothenia coriiceps* mostly consumes *Nacella* which are less than a year old (< 30 mm). *Anasterias rupicola* is likely to be responsible for the drop in abundance of limpets 26 - 42 mm long (1 - 2 years old). The effect of *Larus dominicanus* on the abundance of larger *Nacella* is limited to a narrow belt in the intertidal and shallow subtidal zones where the gull is able to reach them.

The slight rise in abundance of limpets 42 - 54 mm long suggests that these larger individuals have a refuge in size from predation.

Mortality from old age appears to occur after a shell length of 64 mm has been attained.

## DISCUSSION

The mean density of *Nacella* at Marion Island (84 $m^{-2}$) is greater than the maximum density of 41 $m^{-2}$ of *Nacella macquariensis* recorded by Simpson (1976) at Macquarie Island, but less than Picken's (1980) estimate of 123,7 ± 21,2 $m^{-2}$ for *Nacella (Patinigera) concinna* at Signey Islands. In the present study, however, maximum quadrat density of *Nacella* was 463 $m^{-2}$ at Marion Island and 500 $m^{-2}$ at Prince Edward Island whilst the maximum density recorded by Picken (1980) was 372 $m^{-2}$. Considering that *N. delesserti* reach a maximum size of 65 mm compared to 40 mm for *N. concinna* in Picken's (1980) study, *N. delesserti* must have a much higher mean biomass than other sub-Antarctic and Antarctic limpets. *Nacella* has no serious grazing competitor in the Prince Edward Island group and its numbers reflect this. Growth of the population is checked only by limited availability of suitable habitats, the physical destruction caused by tumbling boulders and macrophytes in storms, and predation by starfish, fish and gulls. The population structure of *Nacella* (Fig. 7) indicates that mortality is heaviest during the second and third years of life after a shell length of 25 - 30 mm has been reached. *Notothenia coriiceps, Anasterias rupicola* and *Larus dominicanus* prey on *Nacella* with modal shell lengths of 25 mm, 45 mm and 47 mm respectively, and the feeding activities of these predators are likely to be the greatest cause of the limpet's mortality.

Picken (1980), working in the sublittoral of Signey Island, also found that *N. concinna* formed stacks or towers consisting of 2 - 6 limpets. He related the occurrence of these stacks to annual spawning synchrony of *N. concinna* in the austral summer (in November and December). On Marion Island, however, much larger towers consisting of 2 - 42 *Nacella* were observed all year round. Although reproduction was not investigated in the present study it is suggested that the towers simply reflect the gregarious nature of *Nacella* under crowded conditions. At Prince Edward Island many large areas (20 x 20 m) were examined, and in each case they could certainly not have contained all the *Nacella* present if the limpets had formed a single layer.

Whilst *Nacella* occurs at high densities at Marion Island a reasonably fast rate of growth was shown by the free-range animals, suggesting that ample grazing is available for the limpet, although at Prince Edward Island relatively few *Nacella* were found with shell lengths exceeding 45 mm, indicating that food supply becomes limiting under very crowded conditions. At Marion Island a cork buoy (surface area = 0,023 $m^2$), which was out of the reach of the limpets, was used to mark a subtidal station and during three months was rapidly colonised by a dense growth (3,4 g dry weight) of young algae (*Durvillaea, Rhodymenia, Ulva* and unidentified filamentous species). Relatively few *Nacella* have dense algal growth on their shells (apart from a layer of pink *Lithothamnion*), especially in areas densely populated by *Nacella*, so presumably algal settlement on the shells is grazed off by other *Nacella*.

Few records of rates of food consumption by limpets are available, and Branch (1981) describes the difficulty of quantifying this part of the energy budget. Given that the mean biomass of intertidal *Nacella* is 62,23 g $m^{-2}$ (1292 kJ $m^{-2}$) and using the rate of consumption shown in Fig. 2, it can be deduced that *Nacella* grazes the equivalent of 784 dry g kelp (8804 kJ) $m^{-2}$ $y^{-1}$. Since the caged animals grew more slowly than the free-range sample (Fig. 5) this estimate is likely to be conservative. Wright and Hartnoll (1981) estimated that at the Isle of Man *Patella vulgata* has an average biomass of 346 kJ $m^{-2}$ and annual consumption rate of 1605 kJ $m^{-2}$.

Picken (1980) records an annual production of 2,9 g $m^{-2}$ for *N. concinna*. The considerably higher estimate of production obtained for *N. delesserti* in the present study is 40,77 g or 798,3 kJ $m^{-2}$ $y^{-1}$ is also a conservative estimate, since the annual rate of production for limpets less than 30 mm in length had to be calculated from the growth of caged limpets, since no data were obtained for free-living animals of this size. The input of juvenile recruitment is also not included so that the production of *Nacella* is probably much higher than the given estimate. *Nacella* certainly needs such a high rate of production to sustain its numbers under the heavy predation inflicted on it by its three main predators. *Anasterias rupicola* removes 31 *Nacella* $m^{-2}$ $y^{-1}$ (Part 2). *Larus dominicanus* was found to deposit a

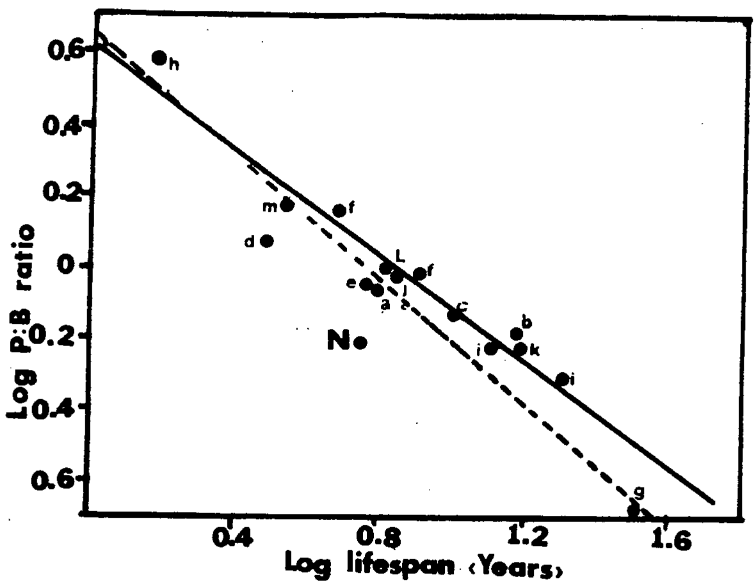

Fig.8 Relationship between log (Production:Biomass, log P/B) and log (lifespan): a, *Cellana tramoserica*; b, *Notoacmea petterdi*; c, *Patelloida alticostata*; d, *Siphonaria diemenensis*; e, *Patella peroni*; f. *Collisella scabra*; g, *Nacella concinna*; h, *Fissurella barbadensis*; i, *Patella cochlear*; j, *P. granularis*; k, *P. longicosta*; l, *P. granatina*; m, *P. oculus* (all from Branch, 1981): n, *Nacella delesserti* (this study): the dotted line is Robertson's (1979) generalized line for invertebrates.

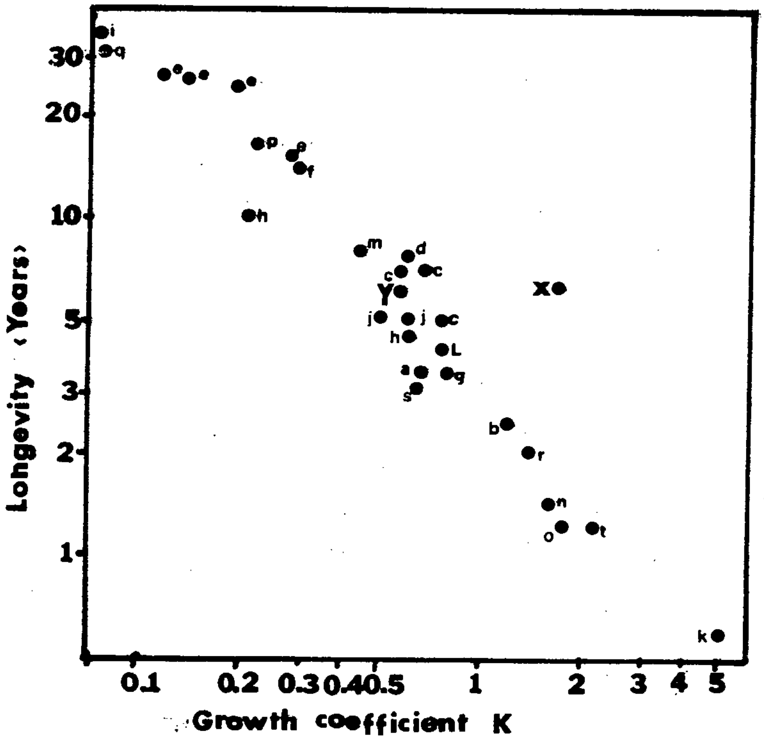

Fig.9 Correlation between longevity and growth coefficient in patellacean limpets: a, *Patella compressa*; b, *P. barbara*; c, *P. granularis*; d, *P. granatina*; e, *P. cochlear*; f, *P. longicosta*; g, *P. oculus*; h, *P. vulgata*; i, *Nacella concinna*; j, *Collisella digitalis*; k, *Notoacmea insessa*; l, *C. strigatella*; m, *Notoacmea persona*; n, *Patelloida mimula*; o, *P. insignis*; P. *P. alticostata*; q, *Notoacmea petterdi*; r, *Cellana radiata*, s, *C. tramoserica*; t, *Helcion pellucidus* (all from Branch, 1981): x, Free range *Nacella delesserti* (this study); y, Caged *Nacella delesserti* (this study).

monthly mean (± S.D.) of 441 ± 236 *Nacella* shells on the 150 m long study beach (Blankley, 1981) and a total of 56 *Nacella* were recovered from the stomachs of 31 specimens of the abundant cod *Notothenia coriiceps* (Part 4).

The negative correlation between production (P):biomass (B) ratios and longevity (Robertson, 1979) demonstrates "strategies" of low or high turnover in different invertebrate species. Branch (1981) updated this relationship with the addition of new data for limpet species and the position of *Nacella*, from data obtained in the present study, shows it has a moderate rate of turnover (Fig. 8). Branch (1981) also clearly demonstrates the inverse correlation between the growth coefficient (K) and longevity for many limpet species (Fig. 9) and concludes that different species display different growth patterns as adaptations to particular circumstances. Hence Picken (1980) relates the very low growth rate of *Nacella concinna* as an adaptation to the low availability of food in the Antarctic. Likewise *Patella longicosta* and *P. cochlear* are territorial species and their comparatively slow growth is related to their dependable but limited local supply of algae which they cannot overgraze (Branch, 1981). *Nacella delesserti* also grows comparatively slowly but the free-range animals (x) had a considerably higher growth coefficient than the caged limpets (*y*). Intraspecific competition for food amongst the dense population of *Nacella* at Marion Island could be a major factor limiting their growth rate. Whilst it was initially thought that the caged limpets would exhibit maximal growth rates because they had unlimited access to food the converse occurred and this suggests that although the kelp *Durvillaea antarctica* is obviously palatable to the limpets it is not as stimulatory to growth as their natural diet.

Results of this study show that *Nacella delesserti* is an important species in the littoral community of Marion Island and plays a keystone role in the organisation of community structure there. Its large population, which forms dense carpets at placed, undoubtably takes a heavy toll of seaweed settlement and probably influences the major pattern of algal community structure. In its role as the dominant secondary producer on the shores *Nacella* provides the major portion of the diets of three tertiary predators whilst maintaining a plentiful population.

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# PART 6

# INTERTIDAL AND SUBTIDAL PREDATORS, PREY, AND ENERGY FLOW AT MARION ISLAND

## ABSTRACT

Quantitative data are provided on the abundance of seven predatory species and the densities and biomass of the 18 species of major littoral prey utilised by these predators. The abundance of predators is given from field data (fish and starfish) and estimates available in the literature (birds). Biomass of littoral prey species is estimated from 118 random 0,1 $m^2$ quadrats. The three species of resident predatory birds are the Imperial Cormorant (285 breeding pairs), the Kelp Gull (923 resident) and the Lesser Sheathbill (3500 resident). The three species of predatory fish are estimated to occur at the following densities: *Notothenia coriiceps* (0,04 $m^{-2}$), *Notothenia macrocephala* (0,1 $m^{-2}$), and *Harpagifer georgianus* (1,0 $m^{-2}$). The carnivorous starfish *Anasterias rupicola* occurs at densities of 17,5 per $m^2$. The limpet *Nacella delesserti* is the most conspicuous and important prey species and has a mean density of 75 per $m^2$. Maximum densities, mean densities and biomass (dry mass and kJ per $m^2$) are given for six species of amphipods, three isopod species, two bivalve and other prey species. All prey investigated form at least 1% (by mass) of the diet of one or more predators. Estimates of the predators' energy requirements per $m^2$ of foraging zone are also given. Data are finally presented in the form of a quantitative food web showing the major trophic links in terms of kJ consumed $m^{-2}$ $day^{-1}$. It is unlikely that competition for common food resources occurs in the higher trophic levels.

## INTRODUCTION

Compared to the many quantitative studies which have been published on the terrestrial biota and migratory birds and mammals of Marion Island (Siegfried *et al.* 1979) our knowledge of the abundance and interactions of littoral organisms is rather sparse. In addition no studies of energy flow in the intertidal and subtidal zones of other sub-Antarctic islands have been reported. De Villiers (1976) described the major zonation patterns and species-composition of the Marion Island littoral community without providing quantitative data and although he recorded 94 species of littoral animals not all of these species are important from an ecological point of view.

Studies of the diets of the seven obvious predators of littoral prey on the island have now been undertaken to establish the relative importance of the various prey species (Parts 1 - 4). In addition the ecology of the most important prey species, the limpet *Nacella delesserti*, has also been studied (Part 5). The aims of the present study were to provide quantitative information on the biomass of the various predators and their prey and also to estimate the energy requirements of the different predators in relation to the standing crop energy values of the major prey species.

## MATERIALS AND METHODS

The main study site was Transvaal Cove, a relatively sheltered rocky and boulder beach on the north east coast of Marion Island (see p. 80)

Estimates of the numbers of resident birds on Marion Island are provided by Burger (1978) and Siegfried *et al.* (1978) whilst Williams (unpublished) provides data on the mean mass of each avian species on the island. These data were used to calculate the biomass of the three species of birds considered here. The foraging areas available to the three species of birds were estimated from personal observations of feeding activities and shore topography around Marion Island's 77 km coastline.

The numbers of fish were estimated from counts made along subtidal transects. The mean mass of each species of fish multiplied by the number $m^{-2}$ provided an estimate of biomass. The density, biomass and energy requirements of the starfish *Anasterias rupicola* are given in Part 2. Energy requirements of the bird species were calculated from the Existence Metabolism (E.M.) equation provided by Kendeigh *et al.* (1977) where E.M. (k cal $day^{-1}$) = 4,142 $W^{0,5444}$ and W = fresh mass in grams. The energy requirements of each species per m² was calculated by dividing the total population's energy requirements by the area (m²) of foraging zone utilised. The figure so obtained was further reduced, in proportion to the percentage of the diet consisting of marine organisms to provide an estimate of energy obtained from marine sources. The energy requirements of the predatory fish species were calculated in a similar fashion but the general equation used here was that provided by Winberg (1956) where Q = 35,8 $W^{0,81}$ cal $day^{-1}$. Where Q = the resting metabolic rate per individual in calories per day and W is the fresh mass of the individual in grams. All energy requirement values were converted to kJ $day^{-1}$ $m^{-2}$ for ease of comparison.

The densities and biomass of prey and associated non-prey species on the shore were estimated from 118 random 0,1 $m^{-2}$ quadrats sampled between September 1979 and May 1980. Three zones were sampled in the quadrat surveys. The spray and splash zones were treated as a single zone which was recognised as the belt extending up to three metres above sea-level where wave and wind action, as opposed to tidal flux, dampened the boulders, ledges and cliffs. The intertidal zone was a narrow belt (tidal range = 70 cm) and the upper limit was easily recognised in the field as the uppermost limit of the common encrusting pink ***Lithothamnion*** spp. The subtidal zone was sampled in a depth of four metres. All organisms were scraped from the substratum and removed from each quadrat, and were either analysed as fresh material in the laboratory or preserved in 10% formalin for later analysis. Animals were sorted to species level and then counted, dabbed dry and wet-weighed to the nearest 0,01 g. Representative samples of at least 100 animals of the larger species and 1000 specimens of smaller species were dried at 60°C to constant mass for the determination of dry mass values. Shells were removed from molluscan species to provide shell-free dry mass values.

The maximum density of each species was calculated from the five quadrats in which the species occurred at the highest densities. The energy content of the commonest species was determined from representative samples of dried, powdered flesh which were bombed in an AMPC micro-bomb calorimeter. For the remaining species, all of which were rare or contributed little to the overall biomass, energy values were estimated from values given for related taxa by Field *et al.* (1980). From the above data the mean standing stock of each prey and non-prey species was calculated in terms of kJ $m^{-2}$ for each of the three zones sampled.

## RESULTS

Table 1 shows that there are a substantial number of predators which exploit marine prey at Marion Island. ***Chionis minor***, the Lesser Sheathbill, feeds highest on the shore and although only 10% of its diet consists of marine organisms, it obtains 1,25 kJ $day^{-1}$ $m^{-2}$ of shore from the seaweeds and small invertebrates it consumes. The

TABLE 1 Biomass, foraging zones and estimated energy requirements of the seven main predators of littoral organisms at Marion Island

| Predators | Foraging zone | Numbers on Marion Island (birds) or density m$^{-2}$ | Biomass/total foraging area (g fresh mass m$^{-2}$) | % of diet biomass consisting of marine organisms | Energy requirements kJ day$^{-1}$ m$^{-2}$ shore |
|---|---|---|---|---|---|
| AVES | | | | | |
| *Phalacrocorax atriceps*<br>Imperial cormorant | Shallow and deep subtidal zones (1-15 m depth and 1-50 m off shore) | 570 | 1425 kg/38,5x10$^{5}$m$^{2}$<br>(0,37 g m$^{-2}$) | 100 | 0,18 |
| *Larus dominicanus*<br>Kelp gull | Intertidal and offshore *Macrocystis* surface canopy | 923 | 831 kg/4,62x10$^{5}$m$^{2}$<br>(1,80 g m$^{-2}$) | 66 | 0,93 |
| *Chionis minor*<br>Lesser sheathbill | Spray/splash zone and intertidal | 3500 | 1575 kg/1,54x10$^{5}$m$^{2}$<br>(10,23 g m$^{-2}$) | 10 | 1,25 |
| PISCES | | | | | |
| *Notothenia coriiceps* | Benthic subtidal | ? 0,04 m$^{-2}$ | ? 28,0 g m$^{-2}$ | 100 | ? 1,21 |
| *Notothenia macrocephala* | Subtidal - midwater and benthic | ? 0,1 m$^{-2}$ | ? 10,0 g m$^{-2}$ | 100 | ? 0,61 |
| *Harpagifer georgianus* | Benthic intertidal and subtidal | ? 1 m$^{-2}$ | ? 2,9 g m$^{-2}$ | 100 | ? 0,36 |
| ECHINODERMATA | | | | | |
| *Anasterias rupicola* | Benthic intertidal and subtidal | 17,5 m$^{-2}$ | 63,6 g m$^{-2}$ | 100 | 3,9 |

starfish *Anasterias rupicola* is the heaviest consumer of intertidal and subtidal organisms (3,9 kJ day$^{-1}$ m$^{-2}$) and preys mostly on the limpet *Nacella delesserti.* The three species of fish exploit three different feeding niches in the intertidal and subtidal zones (Part 4) and their total impact is in the region of 2,18 kJ day$^{-1}$ m$^{-2}$. The Kelp Gull *Larus dominicanus* feeds on *Nacella delesserti* in the intertidal and shallow subtidal zones and also on the bivalve *Caimardia trapesina* from the offshore *Macrocystis* canopy and removes a total of 0,93 kJ day$^{-1}$ m$^{-2}$. The Imperial Cormorant, *Phalacrocorax atriceps,* hunts fish and crustaceans in the inshore waters and consumes approximately 0,18 kJ day$^{-1}$ m$^{-2}$.

Table 2 shows the biomass and standing crop energy values of the main organisms which occur in the three zones sampled. The biomass of algae is higher than that of animal biomass in each of the zones and total biomass is greatest in the subtidal zone and lowest in the spray and splash zone. In the spray and splash zone 25,9% of the total standing stock (kJ m$^{-2}$) consists of non-prey species whilst this value is only 8% in the intertidal zone and 3% in the subtidal zone. In the spray and splash zone the amphipod *Hyale grandicornis* is the most important prey species (31,8 kJ m$^{-2}$) although the small bivalve *Lasaea consonguinea* occurs at very high densities. *Nacella delesserti* forms over 90% of the standing stock of available food in the intertidal and subtidal zones and, in terms of space occupation and biomass, dominates the system. Significantly, it is also the most heavily exploited prey species (Table 3) and occurs to some extent in the diets of six of the seven predators. The polychaete *Platynereis*

TABLE 2 Density and biomass of littoral prey and associated (non prey) organisms at Marion Island

| | Description | Density $m^{-2}$ (mean ± S.E.) | Maximum density $m^{-2}$ | Dry mass ($g\ m^{-2}$) | $kJ\ m^{-2}$ | Energy content $kJ\ g^{-1}$ dry mass |
|---|---|---|---|---|---|---|
| SPRAY AND SPLASH ZONES | | | | | | |
| Prey species | | | | | | |
| *Hyale grandicornis* | amphipod | 463 ± 194 | 3 316 | 2,04 | 31,8 | 15,59 |
| *Lasaea consanguinea* | bivalve | 1037 ± 631 | 8 846 | 0,51 | 8,7 | 17,06 * |
| *Kerguelenella lateralis* | siphonariid | 57 ± 2 | 458 | 0,28 | 4,5 | 16,07 * |
| Insecta | weevils, coleopteran larvae, kelp flies | 49 ± 24 | 396 | 0,07 | 1,3 | 18,57 * |
| *Kidderia minuta* | bivalve | 24 ± 14 | 220 | 0,01 | 0,2 | 16,52 * |
| *Hemiarthrum setulosum* | chiton | 4 ± 3 | 57 | 0,01 | 0,1 | 10,00 * |
| Total | | | | 2,92 | 46,6 | |
| Associated fauna | | | | | | |
| *Lumbricillus* spp. | oligochaetes | 694 ± 420 | 5 712 | 0,77 | 13,6 | 17,66 * |
| Planarians | unidentified | 38 ± 19 | 342 | 0,10 | 1,1 | 11,00 * |
| *Anatanais gracilis* | tanaid | 41 ± 38 | 610 | 0,09 | 0,9 | 10,00 * |
| *Trigriopus angulatus* | copepod | 353 ± 307 | 5 300 | 0,03 | 0,3 | 10,00 * |
| *Halozetes* spp. | mites | 261 ± 2552 | 23 378 | 0,01 | 0,1 | 10,00 * |
| Others | 13 species | - | - | 0,02 | 0,3 | 15,00 * |
| Total | | | | 1,02 | 16,3 | |
| Algae (*Porphyra*, *Bostrychia*, *Rama*) and lichens | | - | - | 77,0 | 1095,7 | 14,22 * |
| INTERTIDAL ZONE | | | | | | |
| Prey species | | | | | | |
| *Nacella delesserti* | limpet | 75 ± 9 | 380 | 62,23 | 1292,0 | 20,76 |
| *Kidderia minuta* | bivalve | 2048 ± 816 | 16 394 | 2,70 | 44,6 | 16,52 * |
| *Platynereis australis* | polychaete | 29 ± 12 | 248 | 1,30 | 25,7 | 19,76 |
| *Lasaea consanguinea* | bivalve | 1634 ± 1146 | 16 534 | 0,80 | 13,6 | 17,00 * |
| *Dynamenella huttoni* | isopod | 184 ± 99 | 1 398 | 1,08 | 12,0 | 11,11 |
| *Hyale hirtipalma* | amphipod | 406 ± 225 | 2 973 | 0,63 | 9,8 | 15,56 * |
| *Hemiarthrum setulosum* | chiton | 188 ± 126 | 1 553 | 0,47 | 6,6 | 14,04 * |
| *Exosphaeroma gigas* | isopod | 46 ± 38 | 472 | 0,53 | 5,5 | 10,38 |
| *Jassa falcata* | amphipod | 70 ± 37 | 632 | 0,14 | 2,2 | 16,00 * |
| *Shakeltonia* sp. | amphipod | 99 ± 62 | 1 014 | 0,09 | 1,3 | 14,44 * |
| *Antias bicornis* | isopod | 588 ± 588 | 15 000 | 0,07 | 0,8 | 11,43 * |
| Eophiliantidae | amphipod | 488 ± 290 | 4 728 | 0,04 | 0,6 | 15,00 * |
| Eusiridae | amphipod | 9 ± 7 | 150 | 0,01 | 0,2 | 20,00 * |
| Total | | | | 70,09 | 1414,9 | |
| Associated fauna | | | | | | |
| *Romanchella* spp. | tube worms | 531 ± 337 | 5 420 | 1,28 | 28,2 | 22,03 * |
| *Pseudocnus laevigatus* | holothuroid | 8 ± 4 | 84 | 1,20 | 11,3 | 9,41 * |
| *Lumbricillus* spp. | oligochaetes | 512 ± 389 | 4 396 | 0,57 | 10,0 | 17,54 * |
| Nematodes | unidentified | 758 ± 744 | 7 632 | 0,08 | 1,2 | 15,00 * |
| Others | 16 species | - | - | 6,03 | 72,4 | 12,00 * |
| Total | | | | 9,16 | 123,1 | |
| Algae (*Rhodymenia*, *Ulva*, *Lithothamnion* etc.) | not counting *Durvillaea* | - | - | 124,4 | 1769,5 | 14,22 * |

- continued

* = estimates

Table 2 (contd.) Density and biomass of littoral prey and associated (non prey) organisms at Marion Island

| | Description | Density m$^{-2}$ (mean ± S.E.) | Maximum density m$^{-2}$ | Dry mass (g m$^{-2}$) | kJ m$^{-2}$ | Energy content kJ g$^{-1}$ dry mass |
|---|---|---|---|---|---|---|
| SUBTIDAL ZONE | | | | | | |
| Prey species | | | | | | |
| *Nacella delesserti* | limpet | 93 ± 11 | 463 | 115,60 | 2400,1 | 20,76 |
| *Platynereis australis* | polychaete | 114 ± 41 | 354 | 5,11 | 100,9 | 19,76 |
| *Hyale hirtipalma* | amphipod | 2183 ± 2131 | 7858 | 3,38 | 52,6 | 15,56 * |
| *Jassa falcata* | amphipod | 1383 ± 993 | 4978 | 2,77 | 44,3 | 16,00 * |
| *Dynamenella huttoni* | isopod | 298 ± 182 | 1086 | 1,75 | 19,5 | 11,11 |
| *Gaimardia trapesina* | bivalve (juveniles) | 156 ± 133 | 562 | 0,67 | 11,1 | 16,60 |
| *Kidderia minuta* | bivalve | 226 ± 178 | 812 | 0,30 | 4,9 | 16,33 * |
| Eusiridae | amphipod | 44 ± 28 | 263 | 0,05 | 0,8 | 16,00 * |
| Euphiliantidae | amphipod | 314 ± 204 | 1810 | 0,03 | 0,4 | 13,33 * |
| *Lasaea consanguinea* | bivalve | 26 ± 26 | 92 | 0,01 | 0,2 | 20,00 * |
| Total | | | | 129,67 | 2634,8 | |
| Associated fauna | | | | | | |
| *Pseudocnus laevigatus* | holothuroid | 47 ± 12 | 54 | 3,76 | 35,3 | 9,41 * |
| Polychaetes | unidentified | 19 ± 10 | 68 | 0,68 | 12,2 | 17,94 * |
| Ophiuroidea | brittle stars | 18 ± 10 | 64 | 0,76 | 2,2 | 2,89 * |
| Unidentified | ascidian | 433 ± 359 | 1560 | 0,18 | 1,2 | 6,66 * |
| *Apseudes* sp | tanaid | 5 ± 2 | 18 | 0,03 | 0,3 | 10,00 * |
| *Tanystylum cavidorsum* | pycnogonid | 5 ± 2 | 14 | 0,01 | 0,2 | 20,00 * |
| Others | 10 species | | | 2,53 | 30,4 | 12,02 * |
| Total | | | | 7,95 | 81,8 | |
| Algae (*Lithothamnion*, *Ulva*, mixed reds) | | | | 336,0 | 4781,0 | |
| DEEP WATER AND OFFSHORE | | | | | | |
| Prey species | | | | | | |
| *Gaimardia trapesina* (on *Macrocystis pyrifera*) | bivalve | ? | ?2000 | ? | ? | 16,60 |
| *Nauticavis marionis* | shrimp | ? | ? | ? | ? | |
| Cephalapoda | squid | ? | ? | ? | ? | |

* = estimates

TABLE 3 The relative compositions of the marine portions of the diets of seven predators of intertidal and subtidal organisms at Marion Island

| Prey | *Harpigifer georgianus* % mass (N) | *Notothenia macrocephala* % mass (N) | *Notothenia coriiceps* % mass (N) | *Anasterias rupicola* % mass (N) | *Larus dominicanus* % mass (N) | *Chionis minor* % mass (N) | *Phalacrocorax atriceps* % mass (N) |
|---|---|---|---|---|---|---|---|
| ALGAE | | | | | | | |
| *Ulva*, *Rhodymbia*, *Porphyra*, *Durvillaea*, *Macrocystis* etc. | 2,4 | 35,3 | 57,6 | - | - | 90 | - |
| INVERTEBRATA | | | | | | | |
| Polychaeta | | | | | | | |
| *Platynereis australis* | 10,4 (36) | 13,3 (12,2) | 1,0 (16) | 1,8 (42) | - | 1 (0,5) | - |
| Unidentified species | * | * | 0,2 (7) | * | | | 10 (1) |
| Gastropoda | | | | | | | |
| *Nacella delesserti* | 0,5 (1) | 3,1 (11) | 2,71 (56) | 90,2 (161) | 45 (1-6) | 1 (1) | - |
| *Laevilitorina caliginosa* | * | * | * | 0,1 (4) | - | * | - |
| *Kerguelenella lateralis* | - | - | - | 0,5 (20) | - | 1 (1-5) | - |
| Polyplacophora | | | | | | | |
| *Hemiarthrum setulosum* | - | 0,1 (8) | - | 0,1 (10) | - | * | - |
| Bivalvia | | | | | | | |
| *Lasaea consanguinea* | 1,6 (30) | 0,3 (78) | - | 9,1 (26) | - | * | - |
| *Gaimardia trapesina* | 0,1 (1) | 4,6 (103) | 0,3 (18) | 0,1 (3) | 45 (6-10) | * | - |
| *Kidderia minuta* | * | * | - | 0,1 (13) | - | * | - |
| Cephalopoda | | | | | | | |
| Unidentified squid | - | 0,8 (1) | 0,1 (1) | - | - | - | ?(3) |
| Isopoda | | | | | | | |
| *Antias bicornis* | 9,7 (180) | - | - | * | - | - | - |
| *Dynamenella huttoni* | 4,4 (34) | 12,8 (338) | 1,1 (112) | 1,2 (40) | - | * | - |
| *Exosphaeroma gigas* | = | 0,9 (14) | 1,7 (17) | 1,2 (16) | - | * | - |

- continued -

Table 3 (contd.) The relative compositions of the marine portions of the diets of seven predators of intertidal and subtidal organisms at Marion Island.

| Prey | *Harpigifer georgianus* | *Notothenia macrocephala* | *Notothenia coriiceps* | *Anasterias rupicola* | *Larus dominicanus* | *Chionis minor* | *Phalacrocorax atriceps* |
|---|---|---|---|---|---|---|---|
| | % mass (N) | % mass (N) | % mass (N) | % mass (N) | % mass (N) | % mass (N) | % mass (N) |
| INVERTEBRATA (contd) | | | | | | | |
| Amphipoda | | | | | | | |
| *Jassa falcata* | 13,6 (187) | 4,6 (1336) | 0,3 (114) | 0,1 (15) | - | 1 (2) | - |
| Eophiliantidae (unid.) | 2,6 (4,1) | 0,1 (61) | - | - | - | - | - |
| *Shakeltonia* sp. | 28,6 (415) | - | - | 0,1 (5) | - | * | - |
| *Hyale* spp. | 19,0 (146) | 1,4 (202) | 0,1 (13) | 0,1 (12) | - | 2 (20) | - |
| Eusiridae (unid.) | 4,6 (41) | 3,5 (312) | 1,2 (292) | * (3) | - | * | - |
| *Pontogeniella brevicornis* | - | 0,2 (18) | 1,1 (61) | * | - | - | - |
| Natantia | | | | | | | |
| *Nauticavis marionis* | - | 4,2 (59) | - | * | - | - | 10 (10) |
| Brachyura | | | | | | | |
| Unidentified crab | - | 1,5 (5) | * | * | - | - | - |
| Insecta | | | | | | | |
| weevils, coleopteron larvae, kelp flies | 0,2 (1) | * | - | * | * | 1 (5) | - |
| Echinodermata | | | | | | | |
| *Anasterias rupicola* | - | * | * | * | 2,0 (0,1) | 1 (0,5) | - |
| CHORDATA | | | | | | | |
| Pisces | | | | | | | |
| *Harpagifer georgianus* | - | 5,4 (9) | 0,9 (3) | - | * | * | 22 (4) |
| *Notothenia macrocephala* | - | 2,4 (1) | 6,6 (2) | * | * | - | 56 (1) |
| Unidentified fish | - | 3,3 (3) | 1,0 (3) | - | - | - | * |
| Other prey species | 2,3 | 2,2 | - | 4,3 | ? 8,0 | 2,0 | ? 2,0 |
| Source of data | Stomach contents | | | Prey items | Observations<br>Beach cast, regurgitations | faeces | regurgitations |
| Number of samples | 98 | 129 | 31 | 404 | N = rough estimates of number of prey consumed per day | | |

* = slight predation occurs

\- = never observed as prey

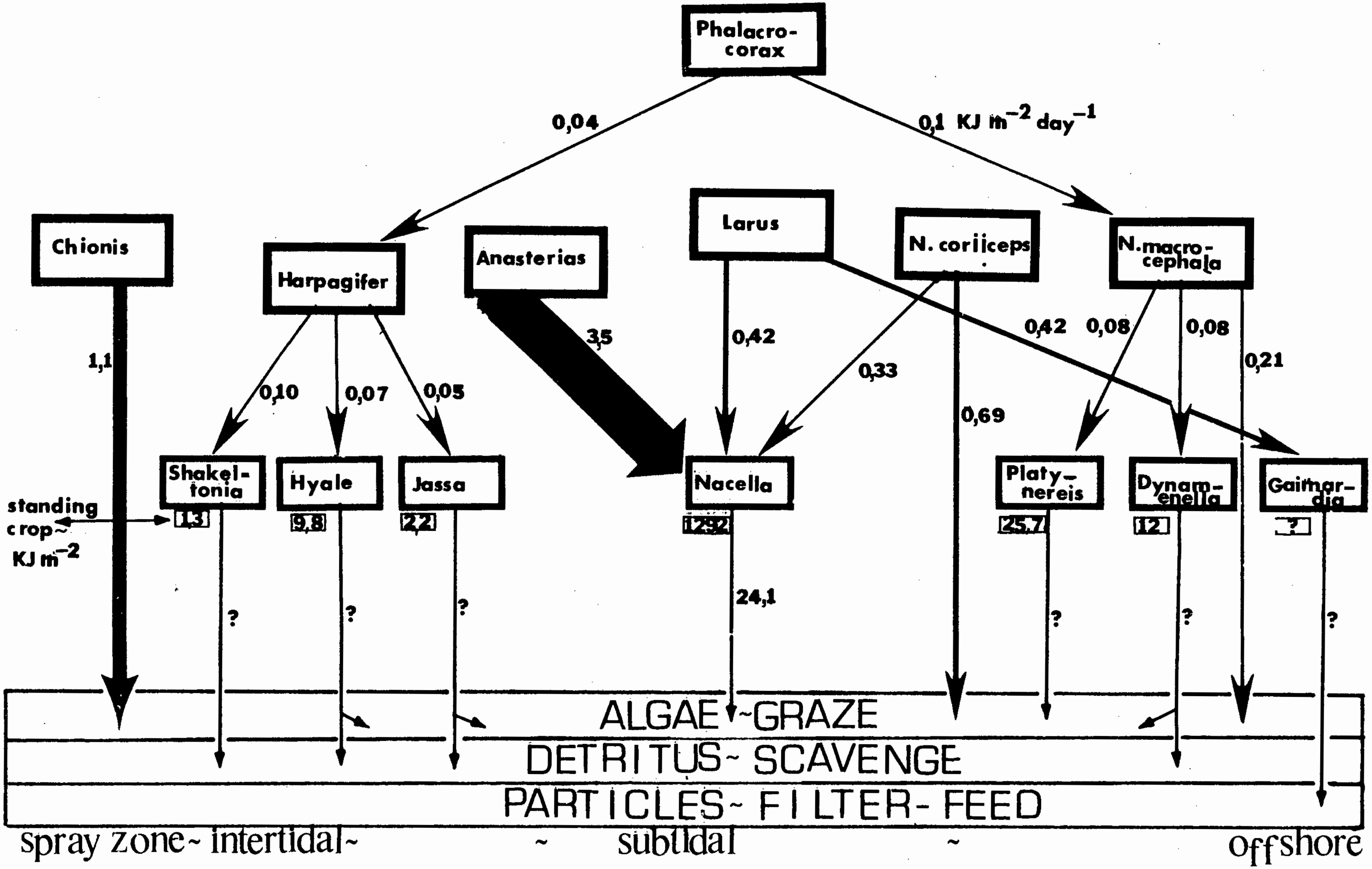

Fig. 1 Food web showing the main predator-prey interactions in the Marion Island intertidal and shallow subtidal zones. Arrows are directed from predator to prey and values shown are the daily consumption rates of each prey by the predator concerned given in kJ m$^{-2}$ day$^{-1}$. Standing crop energy values of the prey species are also shown (kJ m$^{-2}$). Animals found highest on the shore are shown on the left, offshore species on the right.

*australis*, isopod *Dynamenella huttoni* and various amphipod species are also widely used as prey and algae are an important source of food for the two species of nototheniid fish and also for the Lesser Sheathbill.

Figure 1 shows the main paths of energy flow in the system. Values of prey consumption are all expressed as a fraction of the daily energy intakes of each predator per m² of shore. For reference the mean standing crop energy values of the prey species are also provided. The food web presented here is obviously simplistic and connectance (i.e. number of connections amongst the component species) appears to be low as only the very strongest trophic links between species are shown, compared to Table 3 where minor feeding links are also quantified. The limpet *Nacella delesserti* stands out as the key species of prey as the total energy it supplies for the predators (4,25 kJ day$^{-1}$ m$^{-2}$) is greater than that provided by all other prey species combined. *Nacella* is also the major source of energy in the diets of three predators (*Anasterias rupicola, Larus dominicanus* and *Notothenia coriiceps*) whilst each of the other prey species only features significantly in the diet of one of the predators.

## DISCUSSION

Food webs are common topics in the ecological literature, e.g. Paine (1966, 1980), May (1973), De Angelis (1975), Cohen (1978) and their importance stems from their value in providing a description of community structure and interactions. The significance of studying food webs is often shown in studies of pollution where the problem of bioaccumulation of pollutants such as heavy metals in the top levels of the food web is a serious one. On the other hand it is a difficult task to provide a comprehensive, quantitative account of all the interactions which occur at the different levels in a reasonably complex food web even when basic structure may be fairly readily described. Cohen (1978) reviews over 30 food webs and it is not difficult to find faults of incompleteness in any one of these. Food webs vary seasonally and geographically (Paine 1980) and long-term, broad-based studies on any system are necessary before valid interpretations can be made. Nevertheless, intense, short-term studies of food webs (such as the present one) provide much useful information from which community structure can be described. Although straight-forward biomass and production studies provide useable and relevant information they tend to lack vitality and do not transmit more than a superficial view of the community as a whole compared to interaction-based studies.

An important aspect ignored in many food web studies is the influence of body size on predator-prey interactions. Although this is a popular topic in many predation studies (e.g. Brooks & Dodson 1965; Paine 1976; Griffiths & Seiderer 1980) it is largely omitted in most studies of predation in whole communities, probably on account of the further complexity it introduces. In the Marion Island system both the starfish *Anasterias rupicola* and the fish *Notothenia coriiceps* were found to be limited by size restrictions in their predation of the limpet *Nacella delesserti* so that only larger members of the populations are able to actively capture limpets (Parts 3 & 4). Similarly, differences in the diets of small and large size classes of the three species of fish were also recorded (Part 4). Food webs should thus not be seen just as simple systems consisting of one-to-one trophic links between species but also as sequences of dynamic interactions between predators and prey which grow at different rates and alter the interaction between them as they do so. Thus, although adult *Anasterias* are essentially monophagous on *Nacella*, the juveniles ( <30mm) are only able to reach a size where they are able to prey on *Nacella* by feeding on smaller prey such as amphipods and isopods, or by joining larger starfish for a meal of *Nacella*. This latter activity is a unique habit which allows the starfish to circumvent the restrictions of size-limited predation.

Since the Marion Island system is less than 300 000 years old (McDougall, 1971) it should not be expected to house a very complex marine assemblage. Macquarie Island is a far older system which has a more complex assemblage of molluscs and echinoderms (Simpson 1976; 1982) and about 64% of the Macquarie Island molluscan species are endemic (Dell, 1964). The kelp bed communities of the Cape Peninsula, South Africa, are dominated by algae and filter feeders (Field *et al*, 1980), but McQuaid (1980) found that on rocky shores biomass is dominated by algae on sheltered shores and by filter feeders on exposed shores. On Marion Island, algae had the highest biomass on the shores (Table 2) and although filter feeders are exceptionally numerous they are mostly small bivalves with a low biomass compared to the dense populations of the herbivorous limpet *Nacella*. However the relative turnover-rates of different species have not yet been determined and the many small species of amphipods and bivalves are likely to have higher rates of turnover compared to *Nacella*. Molluscs and echinoderms have received the most attention in studies of inshore marine organisms of the Antarctic and sub-Antarctic which is not surprising since limpets and starfish in particular appear to dominate the littoral systems of sub-Antarctic islands (Simpson, 1976; Brand 1980; Picken, 1980). The presence of fish is largely ignored by most authors except those working directly on fish species, such as Hureau (1966) and Targett (1981). In the present study an attempt has been made to investigate all members of the inshore community to allow a more comprehensive picture of the community to be presented than could have been obtained from a study of only the benthic community.

Table 3 and Fig. 1 show that although the species diversity of the diets of the seven predators is fairly high, only one or two species form the major portion of the diet of any one predator. Brand (1980) found that food web connectance was very high in the Antarctic shallow water benthic community of Arthur Harbour, due to the diverse diets of most organisms. He suggested that this results in high niche overlap, implying that competition for trophic resources is severe but suggests that the community remains stable by "de-coupling" processes which avoid trophic stress. Methods of de-coupling include switching of food preferences to include more abundant food items, changing feeding behaviour so that a different method of food procurement is used at different times and lowering the rate of metabolism when food is scarce. Although such processes could well be operative in the Marion Island system there appears to be an abundant supply of food in the system throughout the year although algae are more prominent in summer than in winter. This contrasts with Antarctica where winter depletion of food resources is severe.

The large *Nacella* population on Marion Island appears to take a heavy toll on algal sporeling settlement however (requiring 24,1kJ day$^{-1}$ m$^{-2}$ : Part 5) and although algal biomass dominates the inshore system the availability of suitable algae which can be eaten by *Nacella* could be limiting to growth of the limpets. Evidence for this was supplied by a survey of the extremely plentiful subtidal *Nacella* population at Prince Edward Island where the mean size of limpets was much smaller than those of the less crowded Marion Island subtidal (Part 5 and unpublished data).

Generally the intertidal and subtidal community of Marion Island forms a relatively simple system. Indeed if the system was more complex it would not have been possible to describe the food web as succinctly as it has been here. Sub-Antarctic marine communities generally tend to follow patterns of organization described for the Antarctic although the fact that the sub-Antarctic consists of a number of discrete and often youthful islands introduces many problems when one is making generalizations for the sub-Antarctic as a whole. Brand (1980) records the shallow water benthic community of the Antarctic Peninsula as consisting predominantly of generalist species which have a flexible repertoire of ecological behaviour allowing them to constantly adjust to the changes in their relatively unstable physical and biological environment. Similarly, the animals investigated in the present study were all found to be generalists (with wide feeding niches) rather than specialists relying on a single specific feeding technique or particular species of prey for their survival. In view of the relative youth and paucity of endemic species in the Marion Island system (van Zinderen Bakker, 1971) the shallow water marine community may thus be seen as a composite of loosely interacting, opportunistic colonising species and as such, represents a late pioneer stage in the evolution of a sub-Antarctic community.

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