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Ecology of the starfish *Anasterias rupicola* at Marion Island (Southern Ocean)

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ABSTRACT: The starfish *Anasterias rupicola* (Verrill) is the most conspicuous littoral macro-invertebrate predator at Marion Island; it has a mean density of 17.5 individuals m^{-2} in the intertidal and infratidal zones. *A. rupicola* 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*. Two other important prey are the polychaete *Platynereis australis* and the isopod *Dynamenella huttoni*. *A. rupicola* 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. *A. rupicola* 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 *A. rupicola* population feeding at any one time. Starfish confined with *N. delesserti* 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 *A. rupicola*. It is estimated from calculations that the starfish removes 31.0 *N. delesserti* m^{-2} yr^{-1}. The only discernible growth was recorded in brooded juveniles which showed an overall increment in diameter of 1.26 mm in 6 to 8 mo. It is suggested that *A. rupicola* takes at least 39 yr to attain its maximum diameter of 110 mm. Intertidal *A. rupicola* are preyed on by the lesser sheathbill *Chionis minor* and the kelp gull *Larus dominicanus*. *A. rupicola* is a key predator of littoral organisms at Marion Island; its cooperative 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 marine communities have been noted in the tropics (Endean and Stablum 1973), on temperate rocky shores (Paine, 1969; Menge, 1972) and in the Antarctic (Dayton et al., 1974). At Marion Island in the sub-Antarctic (46°56′ 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; otherwise, little is known of the habits of this southern asteroid genus. Blankley and Grindley (in press) show that the total energy requirements of the 7 main predators of littoral organisms at Marion Island is in the region of 8.44 kJ d^{-1} m^{-2} and that *A. rupicola* is responsible for 3.9 kJ of this amount. *A. rupicola* displays an unusual degree of social cooperation in the capture and digestion of large prey; this is described in more detail by Blankley (1982) and Blankley and Branch (in prep.).

The main aim of the present study was to describe the feeding habits of *Anasterias rupicola* at Marion Island, especially in relation to its major prey *N. delesserti*. Other aspects of the ecology of *A. rupicola* – including 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 was carried out from May 1979 to May 1980 at Transvaal Cove, a rocky boulder beach on the north-east coast of Marion Island (Southern Ocean). *Anasterias rupicola* was observed in pools and amongst boulders at low tide and subtidally to depths of 4 m. Conditions ranged from very calm to days when 3 to 5 m waves

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swept the entire beach. 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.

Biomass and population structure. Anasterias rupicola densities were recorded from 184 random quadrats (0.1 m^2) in the intertidal and infratidal zones. The maximum diameter of each starfish was measured to the nearest mm and its wet mass was recorded to the nearest 0.1 g.

Diet. Anasterias rupicola that were feeding usually were conspicuously humped, but failing this indication, starfish were turned over and their stomachs examined for prey. Both prey and starfish were collected and *A. rupicola* diameter and prey length were measured to the nearest mm. Wet masses of prey and starfish were recorded to the nearest 0.01 g. Dry masses of *A. rupicola* 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 to 40 m stretch of beach was carefully searched and all 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 rupicola* were fed with *Nacella delesserti* to determine feeding rates. Cages were constructed from cylindrical PVC 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 to *Durvillaea antarctica* holdfasts in a sheltered gulley. Between 1 and 19 *A. rupicola* were measured and placed in each of these cages and 10 to 15 *N. delesserti* of known shell lengths were confined with them. After 1 mo limpets that had been eaten were replaced with fresh specimens. At the end of about 2 mo (59 to 65 d) the experiment was terminated, although one cage was monitored for 5 mo. A reliable regression equation relating *N. delesserti* shell length to dry body mass was calculated and used to determine the mass of flesh consumed by *A. rupicola* from the limpets they had killed. Two control cages – one containing only *A. rupicola,* the other only *N. delesserti* – were monitored for 110 and 94 d respectively; they provided data on mortality rates of *N. delesserti* in cages (negligible) and on growth of *A. rupicola* 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 caging experiments were pooled and the number and shell-free dry mass of limpets eaten by the 71 *A. rupicola* in 2 mo were calculated. Calorific content of dry limpet flesh was determined from representative samples using a Gentry diabatic micro-bomb calorimeter. The average daily intake of limpet flesh by the starfish in each cage was plotted against the total dry mass of the caged starfish, thus showing the energy requirements for a given biomass of *A. rupicola.*

The amount of time required by starfish to digest a meal of limpet was recorded in the field. Estimates of the number of limpets removed by the starfish $m^{-2}\ yr^{-1}$ were calculated firstly from biomass of *Anasterias rupicola* combined with the feeding rates of caged *A. rupicola,* and secondly from the formula given by Menge (1972), modified to suit the needs of the present study:

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

where: A = average proportion of starfish observed feeding; B = proportion of limpets in the diet; C = number of foraging hours available per day (assumed to be 12 for the intertidal population); D = time (h) spent consuming an average limpet; E = 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 rupicola* were tagged with numbered fish tags threaded with 8 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 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 3 wk. 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 rupicola* were collected between June 1979 and May 1980, and the mean sizes of juveniles in the broods were compared every 2 mo to calculate the growth rate of juveniles. Mean sizes were calculated from the diameters of ca. 20 individuals from each of the broods.

RESULTS

Biomass, habitats and population structure

Mean density of *Anasterias rupicola* was 17.5 ± S.D.

43.2 individuals m^{-2}. In terms of biomass, the mean dry mass of *A. rupicola* was 15.7 ± 6.8 g m^{-2} (= 117.5 ± 47.9 kJ m^{-2}). Of the 184 quadrats sampled 126 contained no starfish but in the remaining quadrats *A. rupicola* had a mean density of 57.5 ± 64.0 m^{-2} and the 10 densest quadrats (each 0.1 m^2) contained a total of 171 starfish. *A. rupicola* 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 *A. rupicola*, 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 *A. rupicola* (< 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 *A. rupicola* were found in less cryptic habitats on horizontal rocky surfaces, usually in areas close to stands of the abundant limpet *Nacella delesserti*. Very few *A. rupicola* were found in thick layers of algal turf (e.g. *Rhodymenia* and *Corallina* spp.) or amongst small unstable boulders. Live *A. rupicola* were rarely encountered above the water level at low tide, except when engaged in a struggle with its main prey, *N. delesserti*, or when cast up on to the higher shore by heavy seas. Relatively few *A. rupicola* were encountered at depths exceeding 5 m and densities of the starfish were greatest just below the intertidal zone and at depths of 1 to 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. The largest starfish had a diameter of 110 mm and a wet mass of 34.2 g.

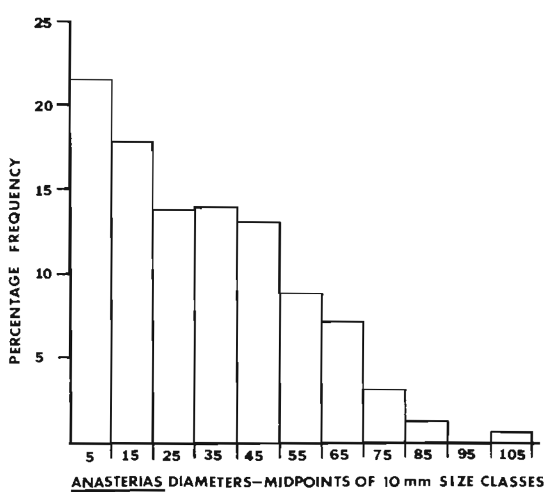

Fig. 1. *Anasterias rupicola*. Size class frequency distributions of starfish sampled from the biomass study (N = 322)

Diet, prey capture and size relations

Anasterias rupicola is exclusively carnivorous and even very young individuals (4 to 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 starfish predation occurred on *N. delesserti*, in terms of dry mass the limpet comprised 90 % of the diet. Two other important prey were the polychaete *Platynereis australis* and the isopod *Dynamenella huttoni*. *A. rupicola* uses its tube feet and arms to capture most prey, which are digested externally by evagination of the cardiac stomach; 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 animals such as amphipods and isopods were often noted to seek shelter under *A. rupicola* where, instead, they ended up as a meal for the starfish.

Anasterias rupicola 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

Table 1. Species composition of the diet of *Anasterias rupicola* at Marion Island recorded as % number of feeding observations on each species and % 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	*Shackletonia* sp., amphipod	1	<1
	Others (18 species)	11	5
	Totals: 29 prey	n = 404	169 g

Table 2. Details of *Anasterias rupicola* cluster-feeding on its main prey species, showing the relations between % incidence of cluster-feeding, dry mass of prey, and 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 ± 0.9	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	–	–
Shackletonia sp.	0.0	1.8	–	–

suggests that predation by *A. rupicola* is size-limited, large starfish being able to capture large prey, while smaller individuals are restricted to small prey. The smallest starfish (4 to 40 mm diameter) fed almost exclusively on prey less than 10 mm in length, such as amphipods, pelecypods and chitons. Larger *A. rupicola* (20 to 60 mm) fed more on larger animals such as polychaetes and isopods, whilst the largest starfish (40 to 80 mm) fed mostly on the limpet *Nacella delesserti.*

This size-limited feeding relation is complicated, however, by the phenomenon of cluster-feeding on larger prey, for 2 to 14 *Anasterias rupicola* could be found clustered around and feeding on a single prey item. In the case of the limpet *Nacella delesserti,* groups of *A. rupicola* actually cooperatively capture large limpets which they would not be able to deal with individually (Blankley, 1982; Blankley and Branch, in prep.).

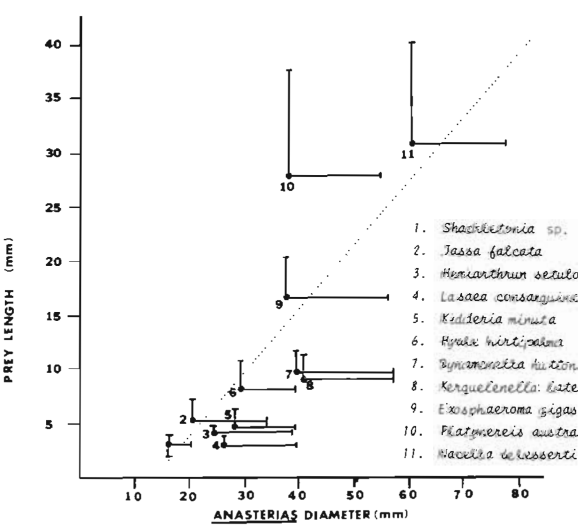

Fig. 2. *Anasterias rupicola.* Size-limited predation on its major prey species. Mean diameter (+ 1 S.D.) of *A. rupicola* found feeding on each prey species is plotted against the mean length (+ 1 S.D.) of the prey. A significant linear regression ($y = 0.65\,x - 10.39$; $r^2 = 0.67$) fits the data (shown by dotted line)

Table 2 shows that cluster feeding only occurs on the 5 largest prey species, and that there is a significant correlation ($r = 0.84$; $p < 0.01$) between incidence of cluster-feeding and mean soft dry mass of prey. The mean number of *Anasterias rupicola* in feeding clusters also increases with increasing mean prey mass and the largest cluster (14 starfish) occurred on a *Nacella delesserti.*

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 rupicola* population feeding at any one time, although this figure is only a rough estimate as various factors affecting feeding rates were not taken into account (e.g. seasonality and prey availability).

Pooled data from the results of the 10 caging experiments, where 71 *Anasterias rupicola* (totalling 86.5 g dry flesh mass) were enclosed with a total of 188 limpets, revealed that the starfish consumed 78 limpets (63.6 dry g) in 2 mo. Despite the artificial nature of the cages and the fact that overall densities of *A. rupicola* ($118\ m^{-2}$) and *Nacella delesserti* ($113\ m^{-2}$) in the cages were fairly high, the experiments provided useful data on the rates of starfish consumption of limpets. The total dry mass of starfish in each of the 10 experimental cages was plotted against their respective average daily consumption of limpet 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 *A. rupicola* (Fig. 3).

Using the mean biomass values obtained for *Anas-*

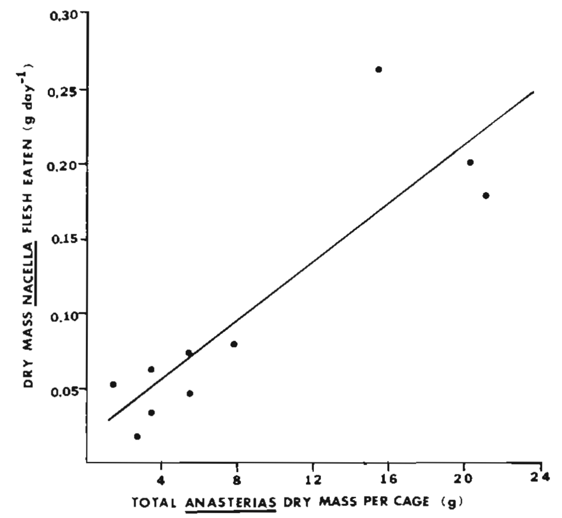

Fig. 3. Relation between total dry mass of *Anasterias rupicola* in each of the experimental feeding cages and their corresponding daily intake of *Nacella delesserti* flesh. A significant linear regression fits the data ($y = 0.0098x + 0.0158$; $r^2 = 0.77$) and was used to determine consumption rates for a given biomass of *A. rupicola*

terias rupicola and energy values of *Nacella delesserti* flesh it can be calculated from the above data that *A. rupicola* consumes the equivalent of 3.9 kJ of limpet $m^{-2}\ d^{-1}$. From this it can be tentatively derived that *A. rupicola* consumes the equivalent of 1424 kJ of limpet $m^{-2}\ yr^{-1}$ or 84 averaged-sized limpet $m^{-2}\ yr^{-1}$. These feeding rates are obviously maximal and only apply to areas where there are abundant supplies of *N. delesserti*.

On 6 occasions solitary starfish were supplied with a 40 to 45 mm limpet to record the time taken to digest a single limpet. The original starfish was soon joined by others and feeding clusters consisting of 8 to 14 *Anasterias rupicola* were formed. These seeded clusters took a mean of 79.2 ± S.D. 10.7 h to digest the limpets completely.

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

$$\frac{0.117 \times 0.4 \times 12}{79.2} (17.5)\ (250) = 31.0\ \textit{Nacella}\ m^{-2}\ yr^{-1}$$

Growth rates

Free-range growth experiments had to be abandoned because the tagged *Anasterias rupicola* pulled out the nylon filaments bearing their tags. *A. rupicola* held in cages for the feeding experiments showed inconsistent increases and decreases in both diameter and wet mass after 2 mo (Fig. 4) and no reliable pattern

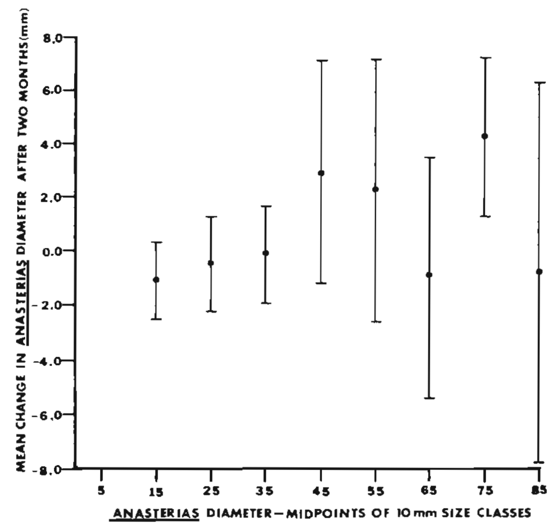

Fig. 4. *Anasterias rupicola*. Growth of starfish maintained in cages and fed on *Nacella delesserti* for 2 mo. Mean changes in starfish diameter (± 1 S.D.) for each 10 mm size class show no general trend

of growth could be found, even in the cage monitored for 5 mo. Similarly, starfish confined without food for 110 d in the control cage suffered no mortality and showed no general trend of decrease in mass or diameter. These findings suggest that *A. rupicola* 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 rupicola* 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 rates fruitless.

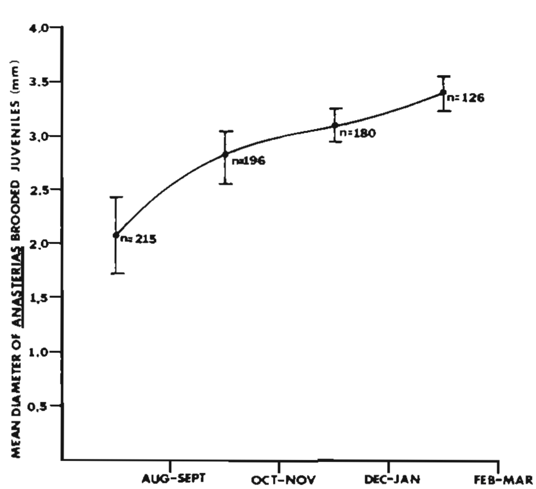

Fig. 5. *Anasterias rupicola*. Mean diameters of juveniles sampled from broods collected every 2 mo during the 8 to 10 mo brooding cycle (n = number of representative juveniles measured)

Brooding

Anasterias rupicola is a synchronous brooder and females larger than 21 mm in diameter appear to raise young once every 2 yr (unpubl. own data). Brooders found in June and July carried up to 320 large yolky eggs 1.6 mm in diameter. Fig. 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 3.42 mm in February-March of the following year, giving an overall increment of 1.26 mm in 6 to 8 mo.

DISCUSSION

Although *Anasterias rupicola* exploits a wide range of prey species at Marion Island, the limpet *Nacella delesserti* is its major source of food. Even the smallest *A. rupicola* is able to feed on large, energetically rewarding *N. delesserti* by joining other starfish in the digestion and sometimes capture of a limpet (Blankley, 1982; Blankley and Branch, in prep.). At Macquarie Island, Simpson (1976) also noted that *A. directa* and *A. mawsoni* formed feeding clusters on their 2 largest species of molluscan prey (25 to 35 mm) despite the fact that starfish densities there were only in the region of 1 to 2 m^{-2}. As seen in Fig. 2, there are clearly limitations on the size of prey that solitary *A. rupicola* can capture; cooperative behaviour thus appears to be a succesful strategy allowing them to exploit large prey.

Mean densities of *Anasterias rupicola* recorded in the present study (17.5 ind. or 15.7 dry g m^{-2}) are fairly high, especially when compared to the density of 1 to 2 starfish m^{-2} recorded by Simpson (1976). The high density of *A. rupicola* is reflected in the estimates of its food consumption from caging experiments (84 starfish or 1424 kJ m^{-2} yr^{-1}) or from Menge's (1972) formula (31 limpets or 525.5 kJ m^{-2} yr^{-1}). Since the *A. rupicola* in cages had unlimited access to *Nacella delesserti*, their consumption rate is likely to be a maximum limit and the latter estimate is probably more accurate for the natural population. *N. delesserti* 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}) in the intertidal and subtidal zones (Blankley, 1982). This figure for limpet production does not include the input of juvenile recruits in the population and is thus a conservative estimate.

The tendency of *Anasterias rupicola* to form aggregations is not unusual for a starfish, and Sloan (1980) lists 18 asteroid species known to form aggregations, mostly in response to food resources. Aggregations of *A. rupicola* occurred predominantly in sheltered areas with relatively high prey densities; the most noticeable aggregations were usually found on horizontal surfaces directly below dense clumps of *Nacella delesserti* living on vertical surfaces. The starfish presumably exploit these stands of limpets whenever possible – for instance during exceptionally calm conditions when they can move safely on vertical surfaces or when limpets move downwards into starfish territory. Starfish predation on limpets 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.

The major reason for failure to show growth appears to be its slow rate in *Anasterias rupicola*, undetectable in the short study period. Barker (1979) found that juvenile *Stichaster australis* reached a diameter of 8 mm in 7 to 8 mo after metamorphosis and take a further 11 mo to attain a size of 24 mm. According to Chia (1966), another brooding starfish, *Leptasterias hexactis*, broods eggs to the stage when young starfish metamorphose after 2 mo, and Menge (1975) found that the same starfish lives 10.2 yr after maturity. The 1.26 mm increment in diameter after 6 to 8 mo shown by brooded *A. rupicola* juveniles in the present study is thus suggestive of very slow growth; 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 bimonthly increment in diameter (0.47 mm) of well-fed caged *A. rupicola* is at all reliable, then *A. rupicola* takes at least 39 yr to attain a maximum size of 110 mm; considering the admittedly sparse evidence it may live even longer than this.

Few predatory starfish are preyed upon by other predators, but at Marion Island the lesser sheathbill *Chionis minor* and kelp gull *Larus dominicanus* regularly eat intertidal *Anasterias rupicola* (Blankley, 1981).

The Marion Island intertidal and subtidal community is characterized by relatively low species diversity on account of the geological youth and isolation of the Prince Edward Island system. There are only 7 main predators (*Anasterias rupicola*, 3 resident avian species, 3 species of fish) in the littoral community and *A. rupicola* is the dominant predator in terms of both biomass and consumption rates. Blankley and Grindley (in press) calculated the biomass and energy requirements of each of the predators in relation to their respective foraging areas. In terms of fresh mass *A. rupicola* has a mean biomass of 63.6 g m^{-2} of foraging area compared to 53.3 g m^{-2} for the other 6 predators combined. The energy requirement of *A. rupicola* is 46.2 % of the total energy requirements of all the predators. These results clearly indicate that *A. rupicola* is a key predator of littoral organisms at

Marion Island. Furthermore, its cooperative feeding behaviour, brooding habit and slow growth make it an interesting species which merits further study.

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