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Seasonality of feeding and nutritional status during the austral winter in the Antarctic sea urchin *Stereocaris neumayeri*

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Abstract The seasonal pattern of food intake and tissue energy status was measured over a 2 year period for two populations of the common Antarctic echinoid *Stereocaris neumayeri* living on contrasting substrata at Rothera Point, Adelaide Island, Antarctica. Food intake was estimated from faecal egestion, and both tissue mass and energy content assessed. Food availability was intensely seasonal, in that water column chlorophyll content and sediment pigment content varied markedly throughout the year. In response, both urchin populations showed an extremely seasonal cycle of faecal egestion, indicating a strong seasonality of feeding activity. Urchins from North Cove living on soft sediment fed at a considerably higher rate, and had a significantly larger Aristotle’s lantern, than those in South Cove, 1 km away, living on hard substrata and taking a more cosmopolitan diet. Faecal egestion in both populations was zero for a 7 month period in the austral winter of 1997, and again for a 4 month period in 1998. During the austral summer of 1997/1998, 84% of the total annual energy intake took place in the period January to March. Significant decrease in gut tissue mass provided energy for maintenance in early winter, although progressive reduction of both gonad energy content (but without a detectable change in gonad mass) and body wall organic mass provided energy during the late winter period. The mass of reproductive tissue showed large differences between the two sites, but there was no marked decrease associated with spawning. Tissue proximate composition was assessed stoichiometrically from elemental composition and also checked by direct assay; gonad tissue was richer in lipid than gut tissue, though both were dominated by protein and contained only small amounts of carbohydrate. These data suggest that the very strong seasonality of food intake does not pose a significant energetic challenge for this species.

Introduction

Changes in morphology as a response to variation in ecological conditions have been recorded for many members of the Echinodermata, and especially the Echinoidea. Such phenotypic changes have been suggested to enhance survival (Ebert 1996), and they include reduction of maximum body size, loss of mass in gonad and gut tissue and a relative increase in size of the Aristotle’s lantern under poor food conditions (Lawrence and Lane 1982; Marcus 1983; Ebert 1996). The Echinodermata are prominent members of the Antarctic marine fauna, and it has been suggested that such morphological changes have been important in adapting to the unique conditions of life in the Southern Ocean.

The nearshore Antarctic marine environment exhibits an extreme but predictable variability in food availability. As a consequence of the high latitude, the majority of autotrophic production takes place as a brief pulse at the height of the austral summer (Clarke et al. 1988; Clarke and Leakey 1996), leaving the remaining months of the year essentially devoid of energy input to the benthic community. Many species cease feeding during the austral winter (Gruzov 1977), and Clarke (1988) suggested that the effects of such starvation ought to be more heavily felt by suspension feeders and herbivores than by the omnivorous and carnivorous members of the benthic community, though this hypothesis has yet to be rigorously tested. Work by Barnes and Clarke (1994, 1995) based at Signy Island has shown that a marked heterogeneity is apparent between suspension-feeding taxa in the length of time for which feeding ceases during the polar winter, and that ability to feed for these groups appears to be related to size of phytoplankton taken. It is not however clear from these studies how any class of Antarctic benthic marine
invertebrate deals with winter starvation in physiological terms. Polar benthic invertebrates do not appear to lay down high-energy metabolic stores before the onset of the austral winter. This is in strong contrast to polar zooplankton many of which lay down extensive reserves, typically of lipid. It is likely that this is a response to the extra energetic costs associated with maintenance of position within the water column (Clarke and Peck 1991). For benthic Antarctic echinoderms biochemical compositions have been shown to be very similar to those from more temperate and tropical regions (McCIntock and Pearse 1987). Given the low metabolic rates reported for polar marine ectotherms (Clarke and Johnston 1999; Peck 1999), this may reflect a low demand for reserves to fuel overwinter survival. To date, there have been no published studies in which feeding activity, metabolic rate and biochemical composition have been measured throughout the year in a polar benthic marine invertebrate. We have therefore undertaken such a study to document the relationship between the non-feeding period of the austral winter and rate of depletion of energetic reserves.

_stereochinus neumayeri_ (Meissner, 1909) is a regular echinoid which is endemic to the Antarctic, has a circumpolar distribution and is present in great abundance at Rothera Point (Brockington 1998). It has been described as a generalist feeder by McClintock (1994), and such a strategy has been suggested to increase fitness by allowing feeding over a much longer period (Dell 1972). Brand (1976) demonstrated a reduced occurrence of amphipods in the gut contents of _s. neumayeri_ at Anvers Island (64°33'S; 63°35'W) during the winter months in comparison to two more specialised feeders that were able to maintain amphipod feeding rates at this time. Here we document the feeding period for _s. neumayeri_ in relation to water column and sediment autotrophic standing stock, and secondly we record seasonal changes in body morphology and energy content between two geographically close sites. This work forms part of a much larger investigation into the ecology and physiology of this species in relation to the effects of the polar winter; data on the seasonal variations in respiration and ammonia excretion of _s. neumayeri_ will be reported elsewhere (Brockington, in preparation).

**Materials and methods**

Fieldwork for this study was carried out in the environs of the British Antarctic Survey Research Station at Rothera Point, Antarctica (67°34'S; 68°07'W) between February 1997 and January 1999 (Fig. 1). Experimental and analytical work took place at the newly constructed Bonner Laboratory facility. Animals were obtained using SCUBA from two sites, by diving from the shore or inflatable boats in summer, and through holes cut in the sea-ice during winter periods. Two sites were compared because of large ecological differences between two geographically close populations (Brockington 1998). The first site at North Cove was a sediment substratum (30 m depth) at the northernmost outreach of the Rothera Station runway. At the second site, 1 km to the south (South Cove), urchins (_stereochinus neumayeri_) were collected from between 6 and 10 m on a hard rock substratum. Collection took place on a monthly basis from each site, with divers being careful to select animals of a standard size (30 mm test diameter). Specimens were returned to the Bonner Laboratory immediately after collection and carefully sorted to remove attached debris. Faecal egestion, organ mass and energetic content were measured monthly on urchins from both sites according to protocols outlined below.

**Chlorophyll standing stock**

Water column associated primary production has important implications for the benthic community through downward flux to secondary consumers. Seawater chlorophyll standing stock was measured at weekly intervals as part of a long-term monitoring programme. Water samples were collected from a depth of 15 m using a NIO type sampler and returned to the laboratory in polycarbonate bottles. After gentle agitation the samples were fractionated using a succession of filters (smallest pore size 0.2 μm) under gravity and in the dark. The chlorophyll was extracted from the ash-free particulate matter with a mixture of 2:1 chloroform:methanol, and subsequently assayed fluorometrically using a Turner fluorometer calibrated against a chlorophyll standard (Anacystis nidulans; Sigma). Records of sea-ice formation and thickness were also taken at weekly intervals during the winter periods.

Benthic chlorophyll standing stock at the North Cove site was estimated by a series of sediment cores as a measure of in situ food availability. Ten replicate cores of 26 mm diameter were taken on a roughly monthly basis by SCUBA divers, from the area where _s. neumayeri_ were collected for the feeding study. The end of the core was pushed into the sediment to a depth of approximately 30–60 mm and sealed at the protruding end with a bung. The core was then lifted clear of the sediment and the other end sealed with a second bung. The cores were transported to the surface and back to the laboratory in a vertical position and were subsequently frozen at −20°C. The frozen core was then loosened from the holder by running briefly under hot water and breaking away the frozen seawater at the top of the core (any residual ice being removed with a razor blade). The top 5 mm were then sectioned from each of the ten replicate cores. Five of the replicates were dried to constant mass at 65°C, and organic content subsequently determined (as ash-free dry mass, AFDM) by difference following ignition at 465°C for 22 h. The remaining five of the top core sections were placed in test tubes containing 2:1 by volume chloroform:methanol and left overnight at ± 5°C in the dark to extract chlorophyll and phaeopigments (Wood 1985). After incubation the supernatant was filtered, diluted and chlorophyll assayed fluorometrically as described above. The data were expressed as mass of chlorophyll per square metre of seafloor, this measure combining benthic in situ standing stock with material transported by vertical flux and advection from the water column.

**Faecal egestion**

The direct measurement of feeding rate in free-living marine invertebrates is technically very difficult. In this study faecal production was measured each month from material egested over a 24 h incubation period from freshly collected animals [a technique developed by Hargrave (1972) and Calow (1975) and subsequently adapted for polar marine invertebrates by Clarke (1990)]. A total of 16 animals of as near as possible to a test diameter of 30 mm were divided into four groups of four and placed in 5 l beakers of clean seawater. The total amount of material egested over the period by each of the four groups was then collected and sorted to remove any extraneous debris (broken spines, etc) before being carefully washed with fresh water and dried to constant mass at 65°C. The total dry mass of all the four animals in each group was also determined, and excretion of faecal material per total weight of urchin dry mass in each of the four replicates calculated for the 24 h period.