

Seasonality of respiration and ammonium excretion in the Antarctic echinoid *Sterechinus neumayeri*

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ABSTRACT: Oxygen consumption (MO_2) and ammonium excretion rates were recorded monthly over 2 yr for the regular Antarctic echinoid *Sterechinus neumayeri* to investigate metabolic activity in relation to seasonal food limitation (i.e. phytoplankton standing stock) at Adelaide Island ($67^\circ 34' \text{S}$, $68^\circ 07' \text{W}$). Phytoplankton standing stock showed a brief but intense summer bloom and extended winter minima characteristic of Antarctic nearshore localities. Metabolic data were expressed for a standard sea urchin of 24.4 mm horizontal test diameter (this was the mean size of urchins used in the study). Two geographically close populations were studied, and strong seasonality was observed in MO_2 at both sites. Mean austral winter minimal metabolic rates were 0.46 and 0.65 $\mu\text{mol O}_2$ standard ind. $^{-1} \text{h}^{-1}$ in 1997 and 1998 respectively at the main study site (North Cove). Mean winter oxygen-consumption rates at the second site (South Cove) were consistently lower throughout the study period (0.33 and 0.58 $\mu\text{mol O}_2$ standard ind. $^{-1} \text{h}^{-1}$ in 1997 and 1998 respectively), which coincided with reduced gonad mass in sea urchins from this site. The minimal winter metabolic rates persisted for 7 and 6 mo respectively. Changes in the organic mass (ash-free dry mass, AFDM) of a standard individual were also recorded mainly due to differences in reproductive condition, but also to seasonal accumulation and metabolic use of body reserves. Energy liberated by loss of AFDM in the winter period equated to a metabolic use of 64 to 432 J mo^{-1} , whereas winter MO_2 values indicated a metabolic use of 102 to 180 J mo^{-1} . Maximal summer MO_2 recorded was 1.44 and 1.62 $\mu\text{mol O}_2$ standard ind. $^{-1} \text{h}^{-1}$ in the 1997/98 and 1998/99 summers respectively, indicating a factorial increase over winter oxygen consumption rates of $\times 3.1$ and $\times 2.5$. Rapid metabolic increases occurred at the end of the winter, and were closely coincident with the onset of the phytoplankton bloom despite *S. neumayeri* being a deposit feeder. These MO_2 rates are amongst the lowest reported for echinoids. Ammonium excretion followed a similar seasonal cycle, with peak rates of 262 and 415 nmol NH_4^+ standard ind. $^{-1} \text{h}^{-1}$ during the 1997/98 and 1998/99 summer seasons, contrasting with winter minimum values of 81 and 72 nmol NH_4^+ standard ind. $^{-1} \text{h}^{-1}$ in 1997 and 1998. Echinoids are ammonotelic, and O:N ratios varied between 7 and 26 during the study period. Lowest values, indicating protein-based metabolism, were found at the immediate start of the austral summer. O:N ratios gradually increased during the summer and following winter, as lipid and carbohydrate became more important in fuelling metabolism. However, even at the highest ratios (~ 25), protein still accounted for 50% of the metabolic substrate. The strong metabolic seasonality indicated by these data suggest that the generalistic deposit-feeding strategy employed by *S. neumayeri* does not exempt this species from the intense seasonal cycle of food availability (i.e. chlorophyll standing stock) at Antarctic nearshore locations.

KEY WORDS: Aerobic scope · Metabolic rate · Nitrogen excretion · O:N ratio · Oxygen consumption · Sea urchin · Polar winter

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INTRODUCTION

Antarctic marine ectotherms live at low but fairly stable temperatures (annual variation typically less than 3°C). Several studies of individual taxa have shown that they exhibit low resting metabolic rates (White 1975, Peck et al. 1987, Davenport 1988, Peck 1989, 1996, Chappelle & Peck 1995, Ahn & Shim 1998). Comparative studies indicate a positive relationship between water temperature and resting metabolic rate (Luxmoore 1984, Clarke 1991, Peck & Conway 2000). Clarke & Johnston (1999) showed that a typical tropical fish at 30°C requires approximately 6 times as much oxygen for resting metabolism as does a polar fish at 0°C ($Q_{10} = 1.83$). The lowered metabolic rate of these Antarctic ectotherms has been suggested to be a consequence of reduced basal costs, of which protein turnover appears to be a major component (Clarke 1998). Such reduced costs could influence the relative growth efficiencies of polar species and may also be significant for the survival of polar benthos during the energy-limited austral winter.

A consequence of reduced resting metabolic rates may, however, be a diminished capacity for power generation (aerobic scope) in polar species. The maximum level of activity attained by an organism is linked factorially to its resting metabolic rate, and for sessile or slow moving ectotherms it is usually in the range of $\times 2$ to $\times 4$ (Peck 1998). Because of the underlying effect of temperature on resting metabolic rate, the same factorial increase will result in a greatly reduced absolute metabolic rise for a cold-water species compared with a similar species from warmer water. In this context, seasonal variations in the metabolism of polar marine invertebrate populations are of interest.

Food availability to the benthic community (as estimated by autotrophic biomass) varies strongly with season in Antarctic nearshore locations because of the sharp reduction in solar insolation in winter months at high latitudes (Clarke 1998, Clarke et al. 1988, Karl et al. 1991, Clarke & Leakey 1996). The austral winter is therefore an energy-limited period, and some (though not all) benthic species cease feeding for varying lengths of time (Barnes & Clarke 1994, 1995). Brockington et al. (2001) showed that *Sterechinus neumayeri* ceased feeding for between 4 and 7 mo during the austral winter at Rothera Point, Adelaide Island, and that 84 % of the total annual faecal egestion took place during the pelagic bloom period in the austral summer. During winter, polar species must therefore survive on body reserves, a strategy which is possible because of the low metabolic rates exhibited by polar benthos (Clarke & Peck 1991). However the period of reduced food availability may be lengthy, and data are not available to relate observed metabolic energy demand under starvation to body-mass loss for any benthic Antarctic ectotherms.

The aim of this study was to document seasonal variation in oxygen consumption ($\text{MO}_2 \mu\text{mol h}^{-1}$) for the common Antarctic sea urchin *Sterechinus neumayeri* over a 2 yr period. This enabled comparison with echinoid oxygen-consumption rates from temperate and tropical latitudes, and also provided a field-derived factorial and seasonal aerobic scope. Oxygen consumption was compared with loss of standard individual mass during the period of winter starvation via an oxycaloric coefficient. Rates of ammonium excretion ($\text{NH}_4^+ \mu\text{mol h}^{-1}$) were also determined over the same period, and comparisons of atomic oxygen:nitrogen (O:N) ratios were used to give an indication of metabolic substrate utilised.

METHODS

Fieldwork for this study was carried out in the Bonner Laboratory at the British Antarctic Survey's Rothera Research Station on Adelaide Island (67° 34' S, 68° 07' W) between February 1997 and January 1999 (Fig. 1). *Sterechinus neumayeri* is particularly abundant near Rothera Station, reaching maximal densities of 223 ind. m^{-2} (Brockington unpubl. data). Two geographically close sites were contrasted because sea urchins from each location differed markedly in reproductive

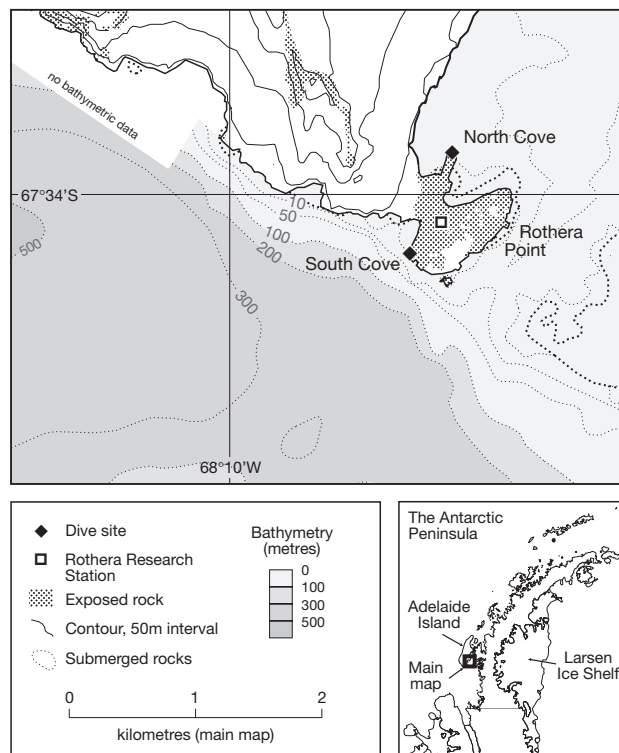


Fig. 1. Map of Rothera Point, Adelaide Island, showing locations of North and South Cove sampling sites in relation to the British Antarctic Survey Research Station

condition throughout the study period. The first sampling site (North Cove) was at 30 m depth in North Cove on a sediment substratum. The second site (South Cove) was 1 km to the south at 6 to 10 m depth on hard rock at Honeybucket Island. Sea urchins were collected using SCUBA, with access from the shore in summer and through holes cut in the sea-ice during winter. After collection, specimens were returned quickly to the Bonner Laboratory, where they were carefully sorted and any adherent material removed. They were held in gently running seawater overnight in a flow-through aquarium to allow time for recovery from handling before metabolic measures were taken. Oxygen consumption (MO_2) and ammonium excretion rates were measured simultaneously on the same individuals to allow calculation of O:N ratios. The non-feeding period, based on gut-content analysis, for this species for each austral winter was between May and December 1997 and between May and September 1998 (Brockington et al. 2001). Specimens returned to the laboratory during this time showed very low locomotor activity.

Measurements of both MO_2 and ammonium excretion were conducted monthly, using 24 individuals from North Cove (the main study site), and 8 from South Cove. A wide size range of sea urchins was assessed each month and the overall study size range was 3.8 to 59.9 mm. After respiration and ammonium excretion measurements were completed, the test diameter of each individual was measured in 3 horizontal directions and a mean value calculated. Dry mass was then determined for whole sea urchins using the entire body including gut contents, after drying to a constant mass at 60°C; ash-free dry mass (AFDM) was obtained by difference following ignition of the entire body (and gut contents) at 465°C for 22 h. The biomass to diameter relationship (using AFDM for biomass due to the large percentage of inorganic material present in echinoids) was then calculated for each site for each month.

Couloximetric measurement of MO_2 . MO_2 values were assessed using closed-chamber respirometry techniques similar to those described by Chapelle & Peck (1995), and individual MO_2 was obtained by comparisons with control chambers (no sea urchin). Three sizes of respirometer (60, 80 or 180 ml) were used, and incubation times were adjusted to allow for variations in MO_2 arising from body size and time of year. The MO_2 rate of *Sterechinus neumayeri* is independent of falling environmental oxygen concentration down to a tension of 50 mm Hg, indicating that closed-chamber respirometry methods are fully appropriate for this species (Brockington unpubl. data). The oxygen tension in the chambers was not allowed to fall below 100 mm Hg during this study. Two replicate measures were made from each respirometer, and MO_2 was

calculated after a correction of the respirometer volume for water displaced by the urchin.

Chambers were inverted carefully 3 times at the end of each trial to ensure adequate mixing, and replicate 25 μ l samples of water were withdrawn using a gas-tight syringe through a septum, and injected into a coulometer (Peck & Uglow 1990) to measure oxygen content. The small sample method used here has an advantage over traditional polarographic systems which require animals to be held in relatively large volumes of seawater; this has important implications for the measurement of the very low MO_2 rates often exhibited by polar benthic invertebrates.

Ammonium excretion. Immediately after oxygen measurements were completed, the respirometer lid was removed and 10 ml aliquots of water were transferred to duplicate teflon tubes (i.e. 2 tubes each containing 10 ml) for ammonium analysis. Ammonium levels in the seawater were determined spectrophotometrically using the phenol hypochlorite method of Solórzano (1969) as modified by Liddicoat et al. (1975) and Clarke et al. (1994). The incubation stage of the assay was also modified according to Catalano (1987) by using teflon tubes and tungsten illumination. The assay was calibrated by spiking seawater with ammonium sulphate, and the background ammonium concentration in seawater controls was subtracted from the experimental values. As for MO_2 , ammonium excretion rates were calculated after correction of chamber volume for the displacement of the sea urchin.

Chlorophyll standing stock. Seawater chlorophyll standing stock was measured weekly as part of a long-term monitoring programme at Rothera Station. Water samples were collected from 15 m depth using a hand-held plastic water corer, and returned to the laboratory in polythene bottles. After gentle agitation the samples were fractionated using a succession of filters (20 to 0.2 μ m) under gravity and in the dark. Chlorophyll was extracted from the retained particulate matter with a mixture of 2:1 chloroform:methanol, and subsequently assayed fluorometrically using a Turner fluorometer calibrated against a chlorophyll standard extracted from *Anacystis nidulans* (Sigma-Aldrich).

Statistical analysis of data. Data were analysed using multiple regression and ANOVA, performed using Statistical Analysis Software, Version 6.12 for Windows (SAS Institute Inc. 1998).

RESULTS

Autotrophic standing stock

The strong seasonality of phytoplankton standing stock recorded at Rothera (Fig. 2) is likely to have

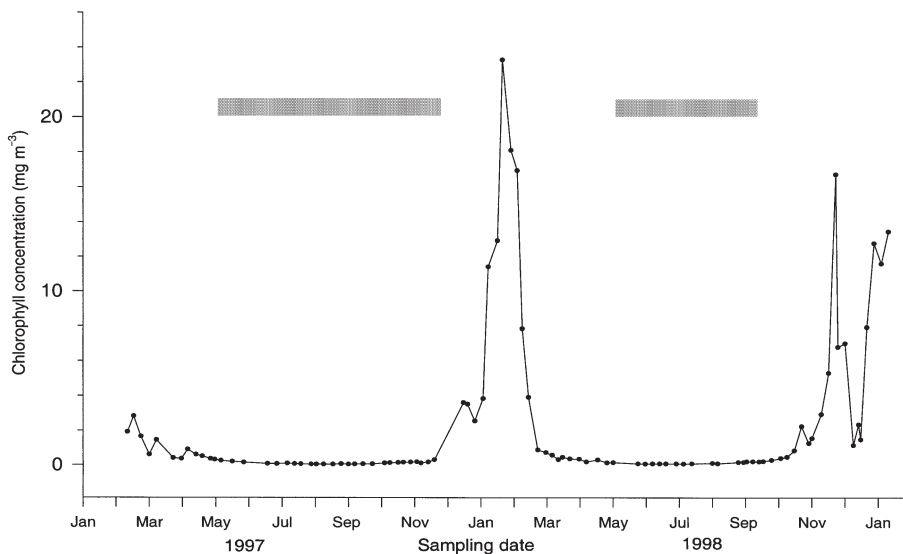


Fig. 2. Seasonal variations in total water-column chlorophyll *a* near Rothera Research Station between February 1997 and January 1999. Water samples were collected from 15 m depth in Ryder Bay, and each point is the mean of 3 separate measurements from a single bottle sample (data from Rothera Time Series monitoring programme). Shaded bars represent *Stereochinus neumayeri*'s non-feeding period determined by Brockington et al. (2001)

important implications for benthic suspension feeders and, via vertical flux, also for generalists and deposit feeders. A single intense bloom was recorded at the start of the 1997/98 austral summer which developed in early January, the onset coinciding with the break-out time of the winter fast-ice. At its peak, this bloom reached a chlorophyll concentration of over 24 mg m^{-3} , which contrasted with the less intense early and late summer blooms (15 to 20 mg m^{-3}) in 1998/99. The development of fast-ice during the 1998 winter was on a considerably smaller scale than that in 1997, and it is likely that the extra light penetrating the water column in 1998 allowed for the earlier development of the phytoplankton bloom in November. Low winter chlorophyll concentrations (in the range 0.05 to 0.2 mg m^{-3}) persisted for 142 d in 1997 and 159 d in 1998.

Echinoid AFDM

A total of 723 measurements of the AFDM of *Stereochinus neumayeri* were made during the 25 mo study period, over a total size range of 3.8 to 59.9 mm test diameter (mean = 24.4 mm, SD = 8.6 mm). Data were

expressed for a standard individual of 24.4 mm test diameter, which was the mean size of the sea urchins used. Standard individual values were obtained following double \log_e -transformed regressions of AFDM versus test diameter (Fig. 3).

Multiple regression and ANOVA provided a good fit to both the North and South Cove data (overall fits: North Cove $F = 2653$, $p < 0.0001$; South Cove $F = 1468$, $p < 0.0001$) and indicated that echinoid AFDM was higher in 1998 than 1997 at both sites (North Cove $F = 4.086$, $p = 0.044$, South Cove $F = 4.194$, $p = 0.042$). The same technique also indicated that the North Cove sea urchins had a significantly greater AFDM in both years than the South Cove sea urchins ($F = 26.89$, $p < 0.0001$).

Changes in echinoid AFDM during the non-feeding period were estimated from the multiple regression and ANOVA model. In May 1997 the AFDM of a standard 24.4 mm test-diameter individual at North Cove was 0.362 g, which had decreased to 0.345 g by December (a drop of 0.003 g mo^{-1} over the winter non-feeding period). For 1998 (North Cove), the decrease between May and

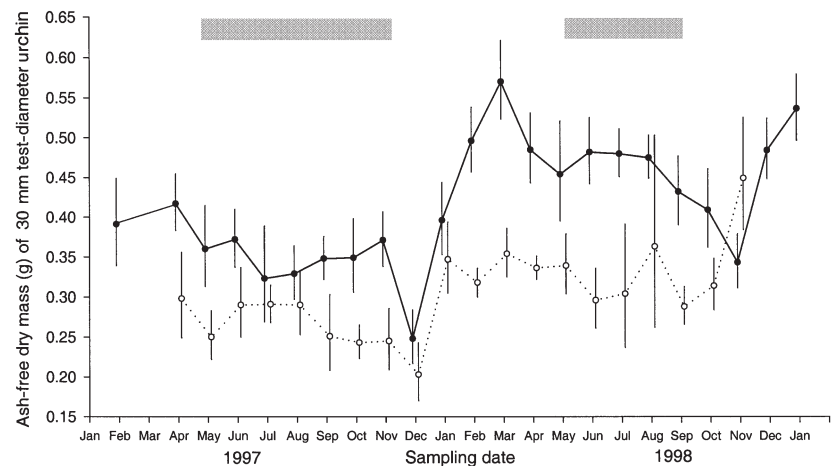


Fig. 3. *Stereochinus neumayeri*. Organic mass (ash-free dry mass) of a standard 30 mm test-diameter sea urchin plotted for the duration of the study period for samples from 30 m depth on sediment substratum at North Cove (●) and 6 to 10 m depth on a rock substratum at South Cove (○). Plotted results are from regressions of \log_e -transformed data for mass against test diameter ($n = 24 \text{ mo}^{-1}$ for North Cove, and $n = 8 \text{ mo}^{-1}$ for South Cove). Error bars represent 95% confidence intervals of the regressions, larger positive intervals are due to the use of logarithmic transformations. Shaded bars represent *S. neumayeri*'s non-feeding period determined by Brockington et al. (2001)

September was from 0.508 to 0.433 g for the same test-diameter individual (0.019 g mo^{-1}). For South Cove, the decrease in mass over the same periods was 0.006 and 0.011 g mo^{-1} for 1997 and 1998 respectively (Table 1).

Seasonal MO_2

Standard individual MO_2 rates rose rapidly at the end of the austral winter period, coinciding exactly with the onset of the phytoplankton bloom. They then remained high during the feeding period described by Brockington et al. (2001) in both years (Fig. 4). Rates of MO_2 decreased after the summer peak as feeding activity and phytoplankton standing stock also de-

creased, and minimum winter MO_2 values (non-feeding state) were recorded for 7 mo in the 1997 winter and 6 mo in 1998 between May and November. As for echinoid biomass, MO_2 was adequately described by a model using multiple linear regression and ANOVA on \log_e -transformed data ($F = 737.2$, $p < 0.0001$). Overall MO_2 was significantly lower at South Cove than at North Cove ($F = 42.41$, $p < 0.0001$). For North Cove, the highest recorded standard individual values were $1.44 \mu\text{mol O}_2 \text{ h}^{-1}$ in February 1998, and $1.62 \mu\text{mol O}_2 \text{ h}^{-1}$ in February 1999. Mean winter MO_2 values were estimated by calculating the mean of the standard individual values for the months between May and December in 1997 and May to November in 1998: North Cove = $0.46 \mu\text{mol O}_2 \text{ h}^{-1}$ in winter 1997, and $0.65 \mu\text{mol O}_2 \text{ h}^{-1}$ in winter 1998. Thus the factorial increase in metabolic rate between winter and summer was $\times 3.1$ for 1997, and $\times 2.5$ for 1998 at North Cove. Factorial increases for South Cove calculated in the same way are of similar magnitude; $\times 3.6$ for 1997 and $\times 2.6$ for 1998.

Table 1. *Sterechinus neumayeri*. Comparison of energy available from loss of standard individual ash-free dry mass (AFDM) during non-feeding period of austral winter with metabolic energy use (calculated via an oxy-caloric coefficient from winter respiration rate). Energy liberated per month is in broad agreement with heat dissipated

Year, Site	Non-feeding period ^a (mo)	Reduction in AFDM (g mo^{-1})	Energy liberated (J mo^{-1})	Mean molar oxygen consumption (winter) ($\mu\text{mol mo}^{-1}$)	Heat dissipated (J mo^{-1})
1997					
North	6	0.003	64	336	145
South	6	0.006	138	236	102
1998					
North	4	0.019	432	471	204
South	4	0.011	242	418	181

^aData from Brockington et al. (2001)

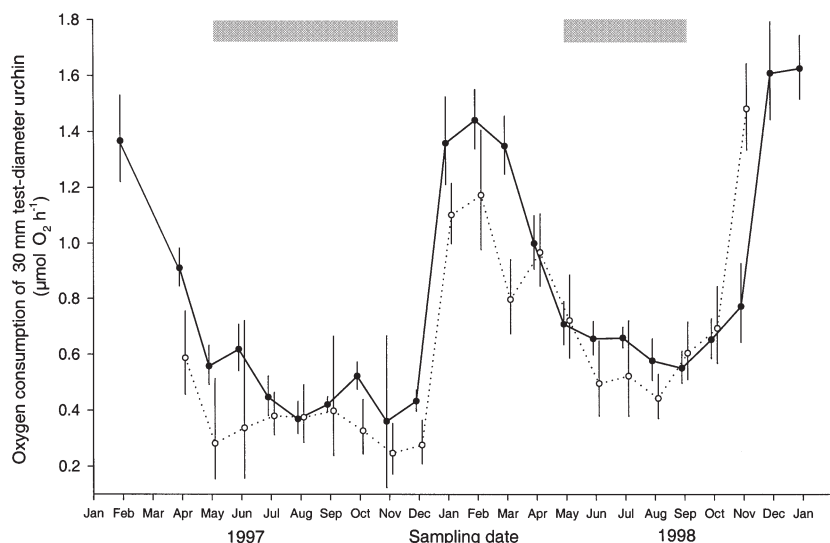


Fig. 4. *Sterechinus neumayeri*. Molar oxygen consumption (MO_2) rates for a standard 30 mm test-diameter sea urchin from North (●) and South Cove (○). Plotted results are from \log_e -transformed data for MO_2 against test diameter ($n = 24 \text{ mo}^{-1}$ for North Cove, and $n = 8 \text{ mo}^{-1}$ for South Cove). Further details as in legend to Fig. 3

Seasonal ammonium excretion and oxygen:nitrogen (O:N) ratio

Strong seasonal and interannual variation also occurred in ammonium excretion (Fig. 5). The multiple regression and ANOVA model again provided a good fit to the data ($F = 280.6$, $p < 0.0001$), but indicated no differences between sites ($F = 0.328$, $p = 0.567$). Large between-year differences were evident in the magnitudes of the summer maxima recorded ($262 \text{ nmol NH}_4^+ \text{ standard ind.}^{-1} \text{ h}^{-1}$ in the 1997/98 summer, and $415 \text{ nmol NH}_4^+ \text{ standard ind.}^{-1} \text{ h}^{-1}$ in the 1998/99 summer). Winter excretion levels were very similar for both years (mean = $76.6 \text{ nmol NH}_4^+ \text{ standard ind.}^{-1} \text{ h}^{-1}$).

Regressions of O:N ratio against echinoid diameter were not significant for any of the months investigated. The O:N ratio was always in the range of 5 to 26 (Fig. 6). The peak in ammonium excretion at the end of the austral winter period took place before the peak in MO_2 , and hence

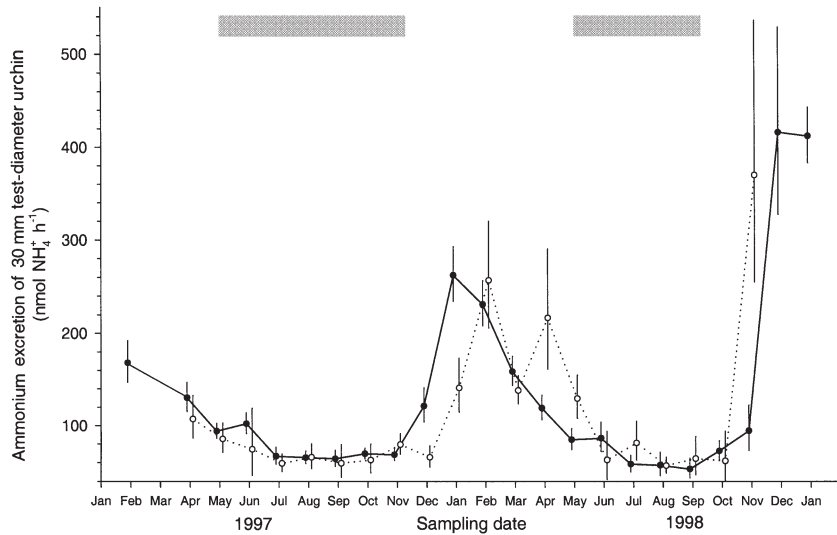


Fig. 5. *Sterechinus neumayeri*. Ammonium excretion rates for a standard 30 mm test-diameter sea urchin from 2 sites. Values were calculated from regressions of \log_e -transformed data and are presented as for Fig. 4. Further details as in legend to Fig. 3

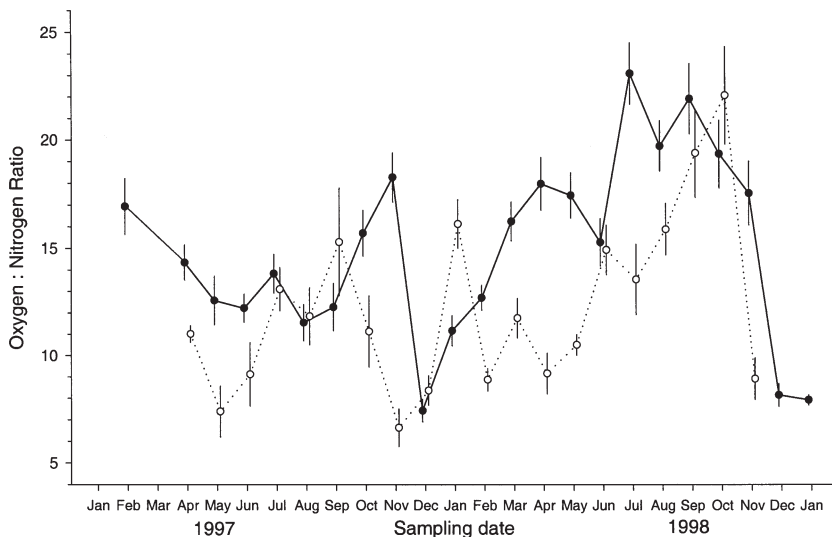


Fig. 6. *Sterechinus neumayeri*. O:N ratios for North (●) and South Cove (○) sea urchins. O:N ratio was calculated as $\text{ng-at oxygen consumed ind.}^{-1} \text{h}^{-1}$ divided by $\text{nmol ammonium excreted h}^{-1}$. To convert from $\mu\text{mol O}_2$ to ng-atoms multiply by 2000. Regressions of O:N ratio against urchin size (test diameter) were not significant for any of the monthly samples. Data always fall in the range 5 to 26, indicating a protein-based metabolism, although pronounced decreases in the ratio are apparent at both sites during the early austral summer

the lowest ratios (7 to 8) were recorded early in the austral summer (December) at the end of both 1997 and 1998. These lows were followed by small rises during the remaining summer and winter periods. This pattern was clearer at both sites during the 1998 winter than in 1997.

DISCUSSION

Environmental seasonality

The strong seasonal variability in water-column autotrophic standing stock recorded here is consistent with patterns found at other Antarctic locations (Clarke 1988, Rivkin 1991, Clarke & Leakey 1996). The intense bloom lasted a few weeks during the austral summer, and was contrasted by a greatly reduced phytoplankton standing stock throughout the winter months. Plankton produced in the pelagic zone is the basis of many benthic food webs (Graf 1992), and advection or flux of material from the pelagic to the benthic environment can take place over a short timescale (Bodungen et al. 1985, Bathmann et al. 1991, Karl et al. 1991). The strong seasonal variation in food availability to the benthos is contrasted by minimal fluctuations in temperature at polar latitudes. At Rothera, the seawater temperature varied between -1.8 and $+1.2^\circ\text{C}$ during this study. Brockington & Clarke (2001) recorded the metabolic cycle of starved *Sterechinus neumayeri* exposed to natural variations in temperature in the absence of food, and found that temperature alone accounted for only 17% of the summer metabolic rise whereas 83% was caused by increased physiological activity (i.e. feeding, growth and spawning) associated with the intense phytoplankton bloom.

MO₂ and echinoid biomass in relation to polar seasonality

The MO₂ rate of *Sterechinus neumayeri* had prominent summer peaks in MO₂ and prolonged winter minima, which reflects closely phytoplankton abundance in both form and timing. *S. neumayeri* is a generalistic feeder (McClintock 1994). Such a strategy has been suggested to increase fitness by allowing feeding over a much longer period (Dell 1972). Echinoids from the North Cove study site were observed to feed only on sediment, whereas those from South Cove had a more varied diet including sediment, macroalgae, bryozoan

fragments, crustaceans and also seal faeces (Brockington et al. 2001). Feeding (measured as rate of faecal egestion) took place only during the period of the pelagic bloom, and indicated that *S. neumayeri* was reliant on downward flux and advection of settled phytoplankton for a substantial part of its energy intake. The strong annual variability in MO_2 was shown by echinoids from both populations, despite the broader diet of the South Cove population. This indicates that a greater breadth of diet did not support higher metabolic rate beyond the duration of the summer phytoplankton bloom.

A complete cessation of feeding was recorded for *Sterechinus neumayeri* for a 7 mo period in winter 1997, and for 4 mo in winter 1998 (Brockington et al. 2001). During such periods, metabolism must be fuelled by body reserves. The data presented here indicate that biomass was lost by a standard 24.4 mm urchin in the non-feeding winter period at a rate of 2.8 to 18.8 $mg\ mo^{-1}$. The strong contrast in standard individual AFDM between sites was related to differences in reproductive condition of the 2 populations: Brockington (unpubl. data) found that individuals from the North Cove site exhibited a higher gonad index ($\sim \times 3$) than those from South Cove despite their narrower diet. Release of gametes takes place at the start of the austral summer, although gonad maturation occurs throughout the year (Pearse & Giese 1967, Brockington pers. obs.), indicating that overwintering reduction in biomass resulted from metabolic demands alone. The energy content of macrobenthic aquatic invertebrate tissue has been summarised by Brey et al. (1988), who suggest that a conversion factor of 23 $kJ\ g^{-1}$ AFDM may be used to convert mass data to energy. Using this conversion, the amount of energy liberated by the reduction of standard individual biomass in the winter non-feeding period was between 64.4 and 432 $J\ mo^{-1}$ (Table 1).

The power generation during the non-feeding period of the austral winter may also be calculated from MO_2 via the use of an oxycalorific coefficient. Brafield & Llewellyn (1982) provide data for oxycalorific coefficients for different metabolic substrates. An appropriate conversion is 0.434 $J\ \mu mol\ O_2$ based on substrate utilisation, as indicated by the mean winter O:N ratio. These data are compiled for periods when feeding is entirely absent. The agreement of these 2 energy use estimates (mass loss and

MO_2) suggest that it is unlikely that the echinoids derived any significant nutritional benefit from other sources (e.g. dissolved organic compounds) during the austral winter. The rate of loss of AFDM by *Sterechinus neumayeri* during the non-feeding periods is low. Lares & Pomory (1998) demonstrated that *Lytechinus variegatus* lost 30% of its initial total organic content during 10 wk starvation, and that the maximum time that *L. variegatus* can survive without food is ~ 90 d. In contrast, *S. neumayeri* from the North Cove site lost 4.6 and 14.8% of its initial AFDM during the 1997 and 1998 winters.

Antarctic fishes (Clarke & Johnston 1999) and bivalve molluscs (Peck & Conway 2000) have lower metabolic rates than similar species from temperate or tropical environments. The metabolic rates found here for *Sterechinus neumayeri* are at similar levels to those recorded by Belman & Giese (1974) working on the same species, although their use of wet mass precludes accurate comparison with the data presented by this study. Although the scatter in the data is wide, the respiratory rate of echinoids increases with increasing temperature (Fig. 7), and *S. neumayeri* has one of the lowest rates reported for any sea urchin. This finding agrees with that of Féral & Magniez (1988), who also

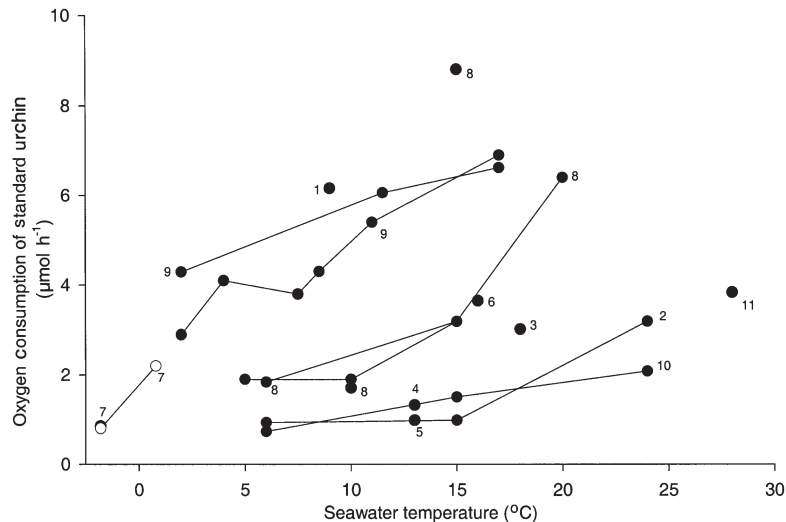


Fig. 7. Plot of respiratory rate of various echinoids against environmental temperature. Data compiled from Féral & Magniez (1988) and from summary in Lawrence & Lane (1982). 1: *Abatus cordatus*; 2: *Allocentrotus fragilis*; 3: *Arbacia lixula*; 4: *Evechinus chloroticus*; 5: *Goniocidaris umbraculum*; 6: *Lytechinus anamesus*; 7: *Sterechinus neumayeri*; 8: *Stronglyocentrotus purpuratus*; 9: *Stronglyocentrotus droebachiensis*; 10: *Stronglyocentrotus franciscanus*; 11: *Tripneustes ventricosus*. Data converted to $\mu mol\ O_2\ h^{-1}$ where necessary, and corrected to a standard individual of 30 mm test diameter, 5.5 g wet mass, 2.3 g dry mass or 0.7 g ash-free dry mass. Single data points indicate individual determinations for a species at ambient temperature, points linked by lines indicate studies for a single species over a range of temperatures. (o) Data for *S. neumayeri* from this study. The overall trend is for increasing oxygen consumption with increasing environmental temperature

showed a decrease in metabolic rate for echinoids with decreasing environmental mean seawater temperature. Such findings contrast with predictions that the mitochondrial proliferation observed in polar species (Johnston et al. 1994, 1998, Guderley 1998) should lead to elevated resting metabolic rates due to increased costs of mitochondrial maintenance at low temperatures (Pörtner et al. 1998). The reduced whole organism metabolic rate in comparison with that of warmer-water species helps to explain the considerably reduced rate of consumption of body reserves under polar conditions.

Aerobic factorial scope is the maximum increase in metabolic rate over resting displayed by a species. Basal metabolic rates are reduced under polar conditions, and consequently a fixed factorial scope will result in a greatly reduced absolute power generation for cold-water species compared to similar warm-water forms. The specific dynamic action of feeding (SDA) response may be indicative of maximum metabolic (aerobic) capacity for sessile or sluggish marine ectotherms (Peck 1998). The rise in metabolic rate following consumption of a meal is associated with the costs of processing the meal and consequent growth, and in echinoids may comprise an anaerobic component due to a poor internal circulatory system (Bookbinder & Shick 1986). SDA factorial responses are independent of habitat temperature, although under polar conditions the duration of the response is extended, allowing the total extent of the SDA response to remain constant at different ambient temperatures. Peak factorial scopes determined from investigation of the SDA response are in the range of 1.6 to 2.5 times pre-feeding levels for sedentary polar species (Peck 1998). These estimates correlate well with the $\times 2.4$ to $\times 3.8$ seasonal rise in metabolism for *Sterechinus neumayeri* determined in this study.

Despite their inherent stenothermy, many members of the Antarctic benthos show normal responses to temperature (measured as Q_{10}) over the range they normally encounter (White 1975, Ralph & Maxwell 1977, Ikeda & Hing Fay 1981, Peck 1989, Pörtner et al. 1999). These Q_{10} values are in the range of 2 to 3, and may be applied to the winter resting metabolic rates derived by this study to estimate the increase in basal rate which may be expected due to the warmer seawater temperatures of the austral summer. Assuming a Q_{10} of 2.5, the change in temperature from -1.8 to $+1.2^{\circ}\text{C}$ recorded at Rothera during this study would result in a summer increase over winter metabolic rates of $\times 1.3$; compared with observed increases in field rates of $\times 2.4$ and $\times 3.8$ in 1997 and 1998 at North Cove. Accurate calculation of the summer basal metabolic rate is confounded by concomitant changes in mass of the standard-sized individual in the transition

to the summer period. Without correcting for mass, the rise of $\times 1.3$ due to temperature accounts for 13% of the summer respiratory rise in 1997/98 (compared to the 1997 winter) and 21% in 1998/99 (compared to the 1998 winter) at North Cove. The data therefore support the conclusion of Clarke (1993), and indicate that the slight seasonal elevations in temperature encountered at polar latitudes have only a minor influence upon the seasonal oxygen demand.

Nitrogen excretion

Although many echinoderms excrete some nitrogen as urea, echinoids are ammonotelic (Jangoux 1982, Stickle 1988). The major route for ammonium formation is through catabolism of both ingested and cellular protein. A seasonally changing pattern of ammonia excretion in relation to food availability was recorded for the ophiuroid *Ophiothrix fragilis* by Davoult et al. (1991), who found a $\times 2.7$ increase in the rate of ammonium excretion in summer compared to winter. Nitrogen excretion has been more intensively studied for bivalve molluscs, where again the major nitrogen product is ammonium. Significant seasonal changes in ammonium excretion were recorded for the temperate bivalve *Mytilus edulis* by Bayne & Scullard (1977). These were interpreted as responses to the seasonal gametogenic cycle and of the metabolic effects of changes in ration size and quality. For *Sterechinus neumayeri*, the very strong seasonal cycle of excretion provides a second method for evaluating the effects of intense seasonal food limitation under polar conditions. As for respiration, excretion of ammonium by *S. neumayeri* increases during the summer, although the timings of the changes in ammonium excretion do not exactly coincide with changes in MO_2 , giving rise to a seasonal variation in O:N ratio.

O:N ratio

Theoretical values for the ratio were calculated by Ikeda (1977) as 415 to oxidise pure lipid, falling to 6.8 for pure protein; intermediate values around 25 indicate 50% protein utilisation. Values less than 7 were found by Peck et al. (1987) and Peck (1996) for Antarctic brachiopods. Values down to 3 may be explained by differences in the C:N ratio of the particular protein (Mayzaud & Conover 1988). Some further additional variation will exist if nitrogen excretion and MO_2 for a given activity or process do not occur simultaneously.

The strikingly low values encountered in both years in the early part of the austral summer are indicative of

a metabolic substrate derived almost solely from protein. During the winter period the O:N ratio rose slightly, suggesting that although protein was still providing the major metabolic substrate, lipid or carbohydrate began to play an increasing role as winter progressed. A similar profile of gradually rising O:N ratio under prolonged starvation has also been recorded for other polar invertebrates, e.g. the limpet *Nacella concinna* (Clarke et al. 1994). Proximate composition estimated stoichiometrically from tissue elemental ratios (C:H:N) showed that both gut and gonad tissue were dominated by protein (54.7 and 40.9% respectively) (Brockington et al. 2001). Gut tissue also showed notably high concentrations of lipid (17%), and this tissue also underwent the greatest loss in mass during winter relative to its initial pre-winter value. Gonad was also found to contain 24% lipid and 15.8% carbohydrate at the start of winter, and it is likely that both gut and gonad tissue supplied energy to fuel metabolism during the non-feeding period.

Conclusion

The metabolic rate of *Sterechinus neumayeri* shows a strong seasonality and is correlated to the intense summer phytoplankton bloom development rather than to seawater temperature. The respiratory rate is one of the lowest recorded for regular echinoids. This reduced rate may be of importance in allowing efficient usage of body reserves during the extended non-feeding period of the austral winter. The sea urchin's seasonal factorial aerobic scope is comparable with aerobic scopes recorded for other Antarctic marine invertebrates. Because of the low basal aerobic rate, this indicates a constraint on the total power that may be generated in comparison to species from lower latitudes. The O:N ratio indicates that although protein is the main metabolic substrate, lipid and carbohydrate become more important as winter progresses. A sharp decrease in O:N ratios to around 7 indicates a change to a 100% protein-based metabolism at the onset of the summer season.

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