# Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*

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## SUMMARY

Summer and winter growth rates were assessed separately for a population of the Antarctic brachiopod *Liothyrella uva* between early January 1992 and December 1993. Annual shell growth rates (1.6–2.3 mm yr$^{-1}$ for a 5 mm individual; 0.96–1.44 mm yr$^{-1}$ for a 20 mm specimen) were two to six times slower than those reported for temperate species. Growth in specimens less than 20 mm in length was faster in 1992 than in 1993, although differences between years over the whole size range were not significant. Surprisingly, growth was much faster in winter periods than during the summers. A 5 mm long individual grew five times faster in winter than in summer, and for a 20 mm long specimen the difference was 13 times. This runs contrary to current ideas on the effects of seasonality on the biology of polar marine invertebrates, but may be an effect of maximizing the efficiency of resource utilization. Comparisons with previous work showed shell growth to be decoupled from periods of tissue mass increase, and also from the main period of phytoplankton productivity. Oxygen consumption of 75 of the specimens used in the growth study was measured to test the hypothesis that basal metabolic rates should be inversely correlated with growth rates. Unexpectedly, an analysis of residuals produced no significant relationship, positive or negative, between growth rate and basal metabolism ($F = 1.37$, $p = 0.25$, $n = 75$).

## 1. INTRODUCTION

Growth rates of Antarctic benthic invertebrates are, with few exception very slow (Arntz *et al.* 1994). The few exceptions, two sponges at McMurdo Sound (Dayton *et al.* 1974), three ascidians at King George Island (Rauschert 1991) and a bryozoan species at Signy Island (Barnes 1995*a*), together with the fact that many Antarctic pelagic invertebrates grow quickly during the summer months, have been used to argue that growth is not limited by temperature (Clarke 1991). The alternative hypothesis is that resource limitations are the cause of reduced growth rates. It has also been argued that a major cause of resource limitation is the intense seasonality of phytoplankton biomass, which means that over 90% of the food supply is confined to a 2–3 month period in an average year (Clarke 1983, 1988; Clarke & North 1991; Clarke & Peck 1991).

Recent studies on several Antarctic suspension feeding taxa at Signy Island have, however, found that feeding extends through large parts of the year, from a minimum period of six months to feeding continuously (Barnes & Clarke 1995). Their data indicate that these organisms feed on small phytoplankton in the 2–20 μm size range, which accounts for less than 10% of the annual phytoplankton

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biomass, but is present for most of the year (Clarke & Leakey 1996). Furthermore, growth in some Antarctic bryozoans has been shown to proceed continuously throughout the year (Barnes 1995a). The ideas of energetic limitations to animal physiology in polar benthos causing reduced physiological rates are not necessarily affected by these findings, as those species with extended periods of feeding and growing during the year are exploiting a resource supply that is comparatively limited at all times. Thus, species exploiting the highly abundant supplies which are only present for short periods (less than four months) are temporally restricted in resource availability, while others are dependent on a low level of resource available throughout the year. There may even be a third group of suspension feeders that switch the size range exploited at different times of the year, but such species have yet to be identified.

The underlying assumption behind most of the above argument is that growth is tied closely to periods of feeding. Data on growth for the Antarctic infaunal bivalve *Yoldia eightsi* showed that juveniles increase in shell length at the same rate throughout the year (Peck & Colman 1997). Tissue mass, however, increased during the summer and early autumn and decreased during the rest of the winter. *Y. eightsi* is a deposit feeder, and the periods of tissue mass increase coincided with periods of enhanced food supply. From these data it is not possible to differentiate between the possibility that shell growth and tissue growth are decoupled in *Y. eightsi*, or whether the tissue mass increase is due to material being stored by the bivalves for use in growth during other parts of the year. In the former, tissue growth would occur during periods of feeding, whereas in the latter both shell and tissue growth would proceed together, but would be decoupled from feeding.

Continuous steady growth is likely to be a more efficient use of resources than short periods of high activity, and would be a more adapted strategy in areas of low resource supply. High efficiency of resource use has been identified as a characteristic of brachiopods (James *et al.* 1992; Peck 1993, 1996; Peck *et al.* 1997). In a study of tissue mass cycles in the Antarctic brachiopod *Liothyrella uva* (Broderip 1833), Peck & Holmes (1989) found that all tissues increased in mass during the summer. Periods of increase in shell length during the year in *L. uva* are, therefore, of interest.

There have been two studies so far on shell growth in Antarctic brachiopods and these were both based on analyses of growth bands. They found that both *Magellania fragilis*, from the Weddell Sea, and *Liothyrella uva* from Signy Island grow slowly and live to more than 50 yr (Brey *et al.* 1995; Peck & Brey 1996). Peck & Brey (1996) also found that major (alpha) growth bands in the valves of *L. uva* shells were not laid down annually, but with a periodicity of 1.84 yr. The authors conjectured that entrainment must be either to an environmental cycle with a biennial periodicity which occasionally breaks down, or to an endogenous cycle with an approximate biennial

periodicity. Strong interannual variations in reproduction have been found in *L. uva* (Meidlinger *et al.* 1997) and, as no environmental cycle with a periodicity of around 2 yr has yet been found in Antarctica, endogenous cycles such as those associated with reproduction seem to be the most likely causes of the sub-biennial growth bands.

Metabolism and growth are two of the major processes of energy utilization by animals, and the study of trade-offs between them has been an active and productive area of ecology in recent years (Sibley & Calow 1986; Wieser 1994). Good evidence has been produced to show that they are linked in temperate bivalve molluscs, especially *Mytilus edulis*, and that individuals with low basal or standard metabolic requirements have enhanced growth rates (Hawkins & Day 1996). Genetic studies have also been carried out in conjunction with the work on metabolism and growth, which has shown that more heterozygous individuals have the lower metabolic and faster growth rates (Hawkins 1995; Hawkins & Day 1996; Koehn 1987; Koehn & Shumway 1982). It might be expected that species living in energy limited environments, such as brachiopods living in Antarctic seas, would reduce their extraneous metabolic costs to a minimum, and that inter-individual trade-offs between basal metabolism and growth would be more apparent than in conditions of higher, or more predictable resource supply.

The current study investigated differences between summer and winter growth rates between January 1992 and December 1993 in field populations of the brachiopod *Liothyrella uva* at Signy Island, Antarctica. Basal metabolic rates of individuals of known growth performance were also assessed as oxygen consumption of individuals after 35 days of starvation.

## 2. MATERIALS AND METHODS

### (a) Growth measurements

*Liothyrella uva* usually lives in clumps of up to 58 animals (L. Peck, personal observation) attached by their pedicles to a central individual. Sixty clumps comprising between two and 12 brachiopods were collected from ledges and overhangs between 5 and 20 m depth at two sites near the British Antarctic Survey station on Signy Island, South Orkney Islands (60° 43′ S, 45° 36′ W). A total of 324 specimens was used in the study. The length of all individuals in each clump was measured to the nearest 0.1 mm using Vernier calipers.

The central animals in each clump were tagged using fish tags, and clumps were attached to lengths of 5 mm nylon rope. They were attached at 300 mm intervals using 2 mm plastic cable ties attached to the central brachiopod and threaded between the fibres of the nylon rope. The nylon ropes were returned to rocky overhangs at three sites in Borge Bay (figure 1). They were stretched between stainless steel climbing pegs hammered into cracks at either end of the overhangs. The three sites chosen represented
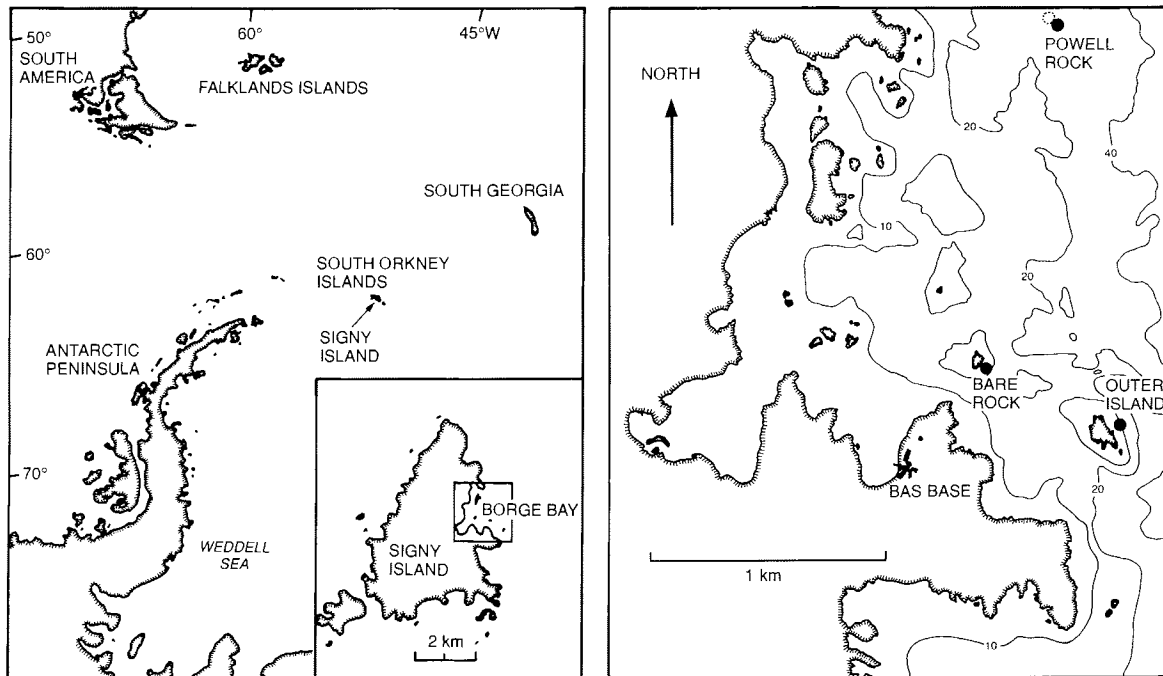
Figure 1. Experimental sites where growth rate trials were deployed in Borge Bay, Signy Island. Site one was at Bare Rock (6 m depth), site two at Outer Island (11 m depth), and site three at Powell Rock (6 m depth). Figure redrawn from Stanwell-Smith & Barnes (1997).

two different habitat types. Sites one and two were deep overhangs containing large populations of brachiopods, and were at 6 m and 11 m depth, respectively. They were less than 400 m apart and were the main sites from which specimens were collected for the study. The third site was an overhang at 6 m depth with a strong macroalgal stand of *Desmarestia* at the entrance, but it had no brachiopods inhabiting it. It had strong tidal water movements, but was protected from ice-scour.

Experiments were initiated in early January 1992. At site one the brachiopods were retrieved and remeasured at the end of the following two summers and winters until December 1993 when the study was terminated. During the initial collection and subsequent collections for remeasurement care was taken to minimize stress to the brachiopods. They were held underwater at all times during transport from the experimental site to the station aquarium, and were always returned to the overhangs within 48 h of collection. At sites two and three the whole string of brachiopods were left in place for the full two years of the experiment. Thus site two acted as a control for the repeated biannual disturbance at site one.

Growth rates were calculated from growth increments using the general von Bertalanffy growth curve:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})^D,$$

and fitted using a SIMPLEX nonlinear program (Press *et al.* 1986).

(*b*) *Respiration rate assessments*

At the end of the growth experiment 75 specimens were held in laboratory aquaria in 1.2 μm filtered

(Whatman GF/C) seawater for 35 days, after their final lengths had been measured. This was to ensure that their metabolic rates were close to basal levels. Periods of this duration have previously been shown to be necessary for oxygen consumption ($VO_2$) in *L. uva* to reach basal levels (Peck 1989). The respiration rates of the brachiopods were then measured using closed bottle methods and a couloximeter to assess oxygen content of respirometers, as previously described (Peck & Uglow 1990; Peck & Whitehouse 1992; Peck 1996).

Ash-free dry mass (AFDM) was determined for each specimen after $VO_2$ assessments were completed. It was assessed as the difference between dry mass (24 h at 60 °C) and the mass remaining after ignition at 475 °C for 24 h. Total AFDM (including shell organic matter) was used because of the presence of large numbers of mantle extensions, called caeca, in the shell valves, which may account for over 50% of the organic content of a punctate brachiopod (Curry & Ansell 1986; Peck *et al.* 1987).

3. RESULTS

(*a*) *Mortality*

Mean mortality rates (figure 2) at site one for each period returned to the sea were 15.7% (s.e. = 0.973). Summer and winter periods were not significantly different (ANOVA, $F = 0.19$, $p = 0.71$, 3 d.f.). At site two the mortality rate for the whole two-year period was 17.7%, which was not significantly different from the mean value for site one ($t = 2.11$, $0.2 < p < 0.1$). Subtracting the mean mortality rate for site one from the two-year value for site two should remove mor-
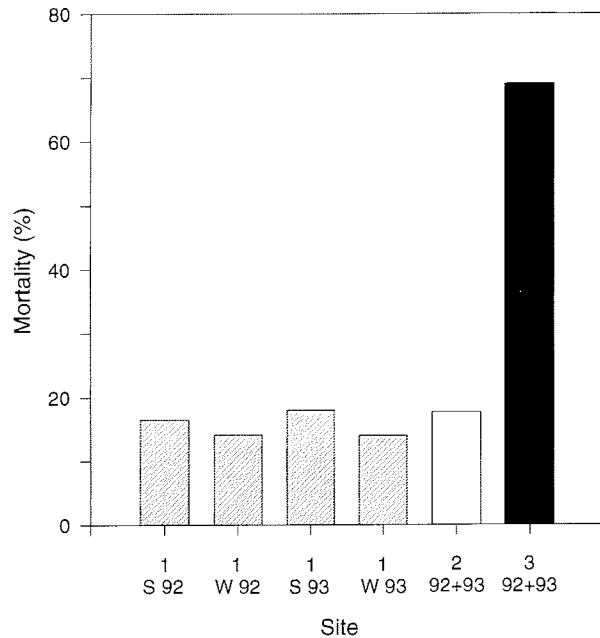
Figure 2. *Liothyrella uva*: mortality rates at the three different sites. Hatched bars indicate six monthly mortalities at site one; open bar indicates mortality over two years at site two; black bar shows mortality over two years at site three. S indicates summer periods, W indicates winter periods; numbers indicate years.
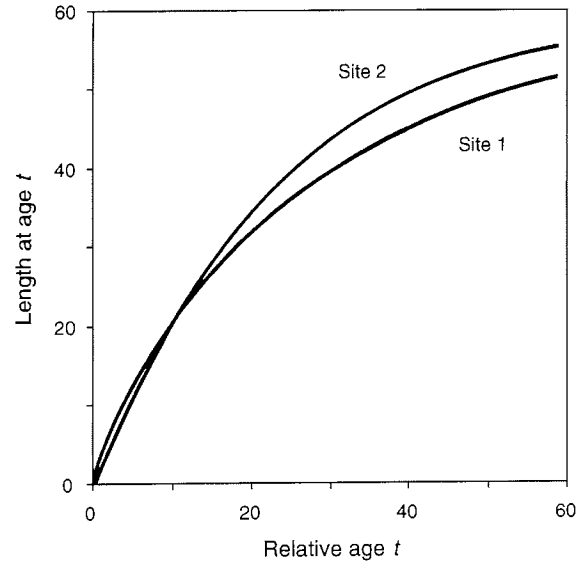


Figure 3. *Liothyrella uva*: growth at two sites. At site one specimens were remeasured at six monthly intervals; at site two they were measured at the start and end of the two year experiment. General von Bertalanffy functions were fitted to both datasets (site one: $K = 0.0297$, $D = 0.7914$; site two: $K = 0.0451$, $D = 1.0749$; $L_\infty$ was set to 60 mm to cover the whole size range). Age is 'relative', because theoretical age-at-length zero $(t_0)$ cannot be computed from size increment data.

tality due to handling effects. That mean mortality at site one was not significantly different from overall mortality at site two indicates that natural mortality was below the threshold for detection. The mortality rate at site two would have needed to be 18.8% to have been significantly higher than the mean for site one. This would correspond to an extra 3.1% over the extra 18 months duration at site two, or 2% per year. Natural mortality over the two-year period of the experiment was, therefore, significantly less than 2% per year. At site three the mortality rate, 68.9% over the two-year period, was significantly higher than at the other two sites $(t = 54.7, p < 0.001)$. Also at site three, 64% of the clumps set out had been broken or were absent at the end of the experiment.

## (b)  Growth rates

Overall growth rates at sites one and two were not significantly different (figure 3). Maximum ages calculated from these two sets of data are 71 yr (54.1 mm length) at site one and 46 yr (47.2 mm length) at site two, respectively. Growth rates calculated as shell increment per day at site one were approximately six and 12 times faster in winter than summer for 10 mm and 20 mm length individuals, respectively (figure 4). The maximum winter growth rate for a 5 mm individual was 9.3 μm d$^{-1}$, whereas in summer it was 2.7 μm d$^{-1}$.

There were differences in growth between the two years. In 1992 growth was faster in both summer and winter periods than in 1993 (table 1), however, an ANOVA comparison indicated that although the effect of season (the difference between summer and
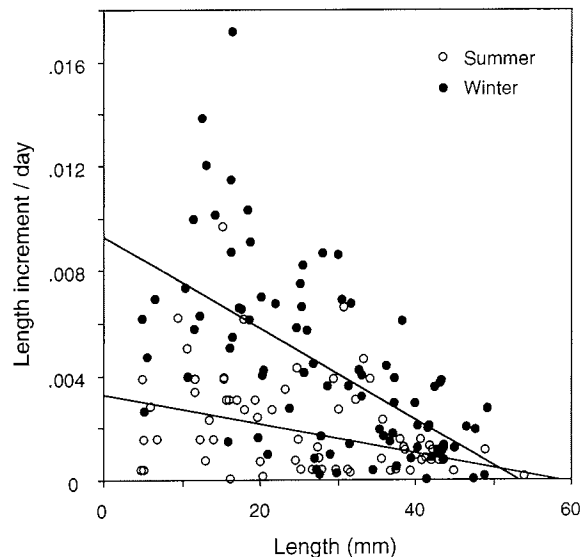


Figure 4. *Liothyrella uva*: Growth rates (mm d$^{-1}$) plotted against brachiopod shell length (mm) for summer and winter periods in 1992. Growth was significantly faster in winter than summer (ANOVA: $F = 43.99$; $p < 0.0001$; 1,161 d.f.).

winter) had a significant effect on growth increment produced $(F = 43.99, p < 0.0001)$, the overall difference between years was not significant $(F = 1.80, p = 0.18)$. In both winters animals throughout the whole size range of the population grew. However, in the first summer only brachiopods less than 43.8 mm in length produced growth increments, and in the second summer only specimens less than 24.9 mm in length increased in size.

Table 1. *Liothyrella uva: daily growth increments* (mm d$^{-1}$) *for specimens of* 5, 10, 20 *and* 40 mm *length, for summer and winter periods in 1992 and 1993. Figures in parentheses denote standard error,* * *denotes brachiopods of* 40 mm *in length and above, which did not increase in length during the austral summer of 1993*

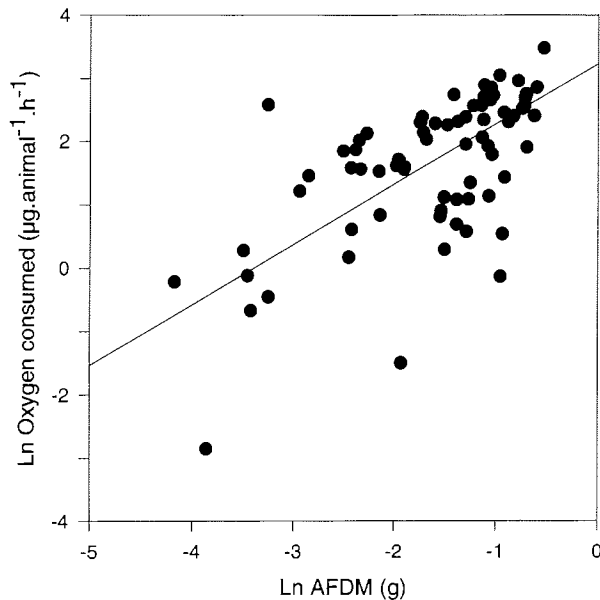| | 1992 | | 1993 | |
| --- | --- | --- | --- | --- |
| shell length | summer | winter | summer | winter |
| 5 | 2.67 (0.53) | 9.25 (1.05) | 1.89 (0.83) | 6.88 (0.68) |
| 10 | 2.33 (0.44) | 8.13 (0.89) | 1.42 (0.70) | 6.17 (0.58) |
| 20 | 1.63 (0.31) | 5.88 (0.60) | 0.46 (0.47) | 4.75 (0.39) |
| 40 | 0.25 (0.35) | 1.39 (0.62) | * | 1.91 (0.39) |



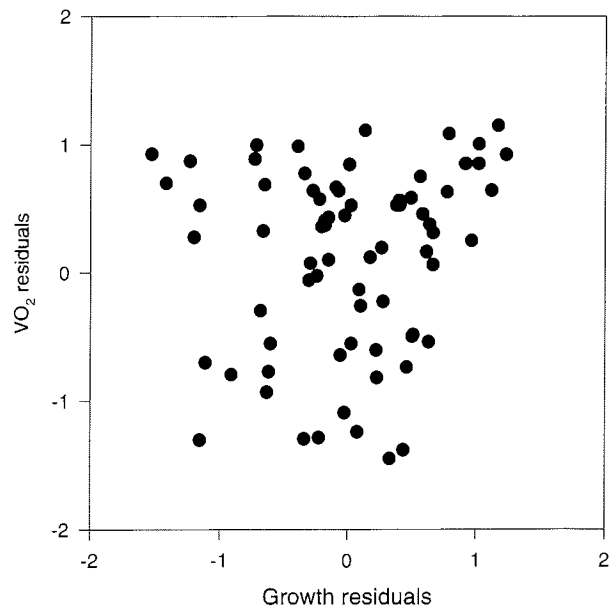Figure 5. *Liothyrella uva*: oxygen consumption (μg $O_2$ animal$^{-1}$ h$^{-1}$) and brachiopod AFDM ($g$). Note logarithmic axes.



Figure 6. *Liothyrella uva*: residuals from the regression of $VO_2$ versus AFDM ($VO_{2res}$) plotted against residuals of daily growth rate versus shell length ($G_{res}$). There was no significant relationship between the variables: $VO_{2res} = 0.117 + 0.153G_{res}$ ($n = 72$; $r^2 = 0.005$; $F = 1.37$; $p = 0.25$).

### (c) Oxygen consumption

Basal metabolism, as oxygen consumed (μg animal$^{-1}$ h$^{-1}$) was related to brachiopod AFDM ($g$) by the equation,

$$\ln VO_2 = 3.03 + 0.90 \ln \text{AFDM}$$

($n = 74$, $r^2 = 0.35$, $F = 40.1$, $p < 0.001$, figure 5).

Plotting residuals of a regression of daily growth increments versus brachiopod length with residuals of the $VO_2$ versus AFDM regression should indicate any relationship between individual growth rate and basal metabolism. However, no significant relationship between basal metabolism and growth rate was found when this was done (figure 6).

## 4. DISCUSSION

### (a) Growth rates

The annual shell growth rates for *Liothyrella uva* of 1.6–2.3 mm yr$^{-1}$ for a 5 mm length individual and 0.96–1.44 mm yr$^{-1}$ for a 20 mm length brachiopod are slow. They are between 15% and 50% of those

reported for temperate brachiopods (Doherty 1979; Collins 1991). There was considerable seasonal variability in the growth rate of *L. uva* and the fastest rates obtained (about 9 μm d$^{-1}$ for a 5 mm specimen) are comparable with moderate or slow annual rates for temperate species. Comparing the fastest rates obtained for *L. uva* with overall annual rates for temperate brachiopods is, however, not a reasonable one. Seasonal variation in shell growth of temperate brachiopods has not been studied. However, it is highly likely that there is seasonal variation in the growth of temperate species, and even if not as intense as that seen here would indicate that maximum growth rates in *L. uva* are considerably less than maximum rates in temperate brachiopods

The intensity of seasonality in the physiology and ecology of Antarctic benthic invertebrates is currently under debate. The prevailing hypotheses are based on the strong seasonality of the physical environment and phytoplankton bloom and predict

strong seasonality in organismal variables such as growth, especially in suspension-feeding species dependent on microalgae (Clarke 1983, 1988; Clarke & North 1991; Clarke & Peck 1991). The predictions from such hypotheses are that growth will be seasonal and in phase with periods of phytoplankton productivity. Recently (Barnes 1995a) found that Antarctic bryozoans exhibit a wide range of growth strategies from seasonal through to totally aseasonal (continuous throughout the year). The feeding strategies of these bryozoans have also been shown to be continuous or to extend through large parts of the year. This implies that they are feeding on material in the nanoplankton (2–20 μm) size range. Phytoplankton in this size range are present in the water column for much longer periods than the major phytoplankton bloom, which mainly comprises microphytoplankton (greater than 20 mm diameter).

Growth rates of juveniles of the infaunal bivalve mollusc *Yoldia eightsi* are even and continuous throughout the year (Peck & Colman, in preparation), and are also decoupled from cycles in tissue mass (AFDM), which are seasonal and related to periods of resource supply. The faster winter shell growth rates found here for *L. uva* are surprising in that they are completely out of phase with periods of high food abundance (the summer phytoplankton bloom), but are also not compatible with continuous steady feeding and growth throughout the year. Peck & Holmes (1989) found that *L. uva* has an annual AFDM cycle in phase with the summer bloom. As for *Y. eightsi*, therefore, tissue mass cycles and shell growth are decoupled, but for *L. uva* shell growth is not even through the year, but faster when its probable food supply is low.

Brachiopods have recently become recognized as exhibiting low energy lifestyles (James *et al.* 1992; Peck 1992; Peck *et al.* 1997). It is this feature which may be the key to interpreting the patterns observed here. The major life history traits quoted in discussions of their low energy lifestyles are low metabolism, growth and activity levels. However, another evident characteristic is their low tissue content compared to the volumes they occupy (Rudwick 1970; Curry & Ansell 1986; Peck 1993). This character can be viewed as an adaptation which reduces maintenance metabolic costs, enabling brachiopods to survive in areas where resource supplies are low, or temporally restricted, and is thought to enhance the efficiency of resource utilization. The low observed tissue density also reflects a reduction in cellular machinery and the separating of growth functions from feeding would be expected if the efficiency of resource use were extreme, as the biomass of an individual needed to perform functions would be minimized, reducing extraneous metabolic costs. A high efficiency strategy of this type, producing a reduction in overall cellular machinery for specific tasks, would be expected to restrict the scope for activity or metabolic power generation of these organisms. Such a restriction in metabolic power generation has been observed in *L. uva* (Peck 1996).

Summer growth rates found here were faster in 1991/92 than 1992/93, but rates were not significantly different between years. Bands on shells are caused by a cessation of growth, and should ideally be viewed as growth check marks. In *L. uva* they are most likely produced in alternate summers and their production dictated by reproductive events. It is possible, therefore, that a growth check was laid down in most specimens in the summer of 1992/93, and not in 1991/92. There was a strong phytoplankton bloom in both of these years, although maximum summer temperatures in 1991/92 were approximately 0.5 °C cooler than in 1992/93 and the lower temperature was associated with a longer preceding period of sea ice duration (Clarke & Leakey 1996). However, these differences are small and unlikely to have produced the reduction in growth between the 1991/92 summer and the 1992/93 summer.

A recent assessment of reproduction in *L. uva* found great inter-annual variability in reproductive activity, with the possibility of long-term cycles in reproductive events (Meidlinger *et al.* 1997). There was a strong release of larvae in October 1991 as shown by the study of larval development in *L. uva* by Peck & Robinson (1994) from that summer. This suggests that shell growth may be faster in the summers following spawning and reduced to form growth checks in alternate years. It thus appears that there may be a trade off between somatic growth and reproductive investment on a two-year cycle and that this may be the cause of the sub-biennial periodicity in growth band formation reported for *L. uva* by Peck & Brey (1996). Cessations of growth resulting in the formation of growth bands should be clearly visible in the shell microstructure, an this would be a mechanism for assessing the period when bands are laid down. However, such detailed investigations of shell structure in *L. uva* have not as yet been conducted.

## (b) Mortality

The mortality rates reported here, at less than $2\%$ yr$^{-1}$ (and possibly much lower than this) are low. Brey *et al.* (1995) found a left-skewed size–frequency distribution for a population of another Antarctic brachiopod *Magellania fragilis*. They suggested three possibilities for such a distribution: highly episodic recruitment, low mortality compared to growth rate or size dependent mortality with large size providing a refuge from mortality factors. *L. uva* has similar size–frequency distributions at sites around Signy Island (L. Peck, unpublished data). The low mortality rates found here suggest that the left-skewed size distributions are caused by low mortality compared to growth rate (which is also low), and not due to episodic recruitment.

Mortality rates have been shown to be very high for juvenile and small brachiopods in temperate localities, and large size forms a refuge from mortality factors (Doherty 1979; Collins 1991). Rates of mortality are almost universally high for larvae and new recruits of marine benthic invertebrates in general.

The study here was confined to specimens greater than 4 mm in length, and it is probable that the major size classes with high mortality rates were not sampled. Brood sizes range from 100–4000 embryos in *L. uva* at Signy Island, and reproduction possibly occurs on a biennial cycle (Meidlinger *et al.* 1997). As specimens live to greater than 50 yr of age and reproduce for about 40 yr, each female on average will be expected to produce 20 broods, and hence 2000–80 000 embryos. Overall mortality rates must, therefore, be in excess of 99%. In this context mortality in the early stages of life must be very high, but survival to the sizes used in this investigation (greater than 4 mm in length) provides a refuge from the major mortality factors.

The Antarctic nearshore environment is one characterized by intense physical disturbance (Peck & Bullough 1993; Arntz *et al.* 1994; Barnes 1995*b, c*). In shallow sites (less than 30 m depth) brachiopods are mainly restricted to cryptic habitats, primarily crevices, rocky overhangs and caves, where they are protected from the effects of ice-scour. All three sites studied here were protected from ice-scour. However, there was very high mortality at site three, which was probably due to physical damage from the strong wave surge at that site, as many of the clumps had been broken or removed during the experiment. This suggests that the distributions of some species of articulate brachiopods may be limited by physical disturbance other than ice-scour. At deeper sites *L. uva* occurs progressively in more open locations at Signy Island (D. Barnes, personal communication). Ice-scour and physical disturbance are, therefore likely to be major mortality factors in this environment. Predation, on the other hand, is slight. No observations of predators feeding on *L. uva* were made during the three years of the study, and no specimens lost to predators. However, several specimens held in aquarium tanks have been drilled and eaten by an unidentified muricid snail.

### (c) *Respiration*

The lack of a relationship between growth performance and basal oxygen consumption in *L. uva* is surprising. Growth and metabolism, along with activity and reproduction, are the major routes of energy utilization by animals. It would be expected in species where activity levels are low, such as brachiopods, that trade-offs between growth and basal metabolism would be apparent, and that individuals with reduced maintenance costs would have a greater scope for growth (Bayne & Newell 1983). It might be expected that this would be even more apparent in species inhabiting resource limited environments, such as polar oceans. However, it is possible that in low energy lifestyle species living in reduced resource supply environments that basal metabolic rates are reduced to such low levels that any scope for inter-individual variation is strongly limited. This is supported by the fact that oxygen consumption in cold water brachiopods is between 0.1 times and 0.5 times that of similar sized bivalve molluscs (James *et al.*

1992). Clearly the effects of a highly seasonal polar environment on inter-individual variation in physiological performance requires further investigation.

## 5. CONCLUSIONS

Growth rates in the Antarctic brachiopod *Liothyrella uva* are slow and highly seasonal. Shell growth was 5–13 times faster in winter than in summer. Shell growth was decoupled from periods of tissue mass increase and also from the major periods of phytoplankton productivity. Mortality rates were less than 2% yr$^{-1}$, and probably less than 1% yr$^{-1}$. The ability of brachiopods to separate physiological functions to different parts of the year is clearly advantageous in low energy supply environments.

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