

Some Ecological and Physiological Strategies for Energy Conservation of the Antarctic Clam, *Laternula elliptica*

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ABSTRACT. This paper reviews on the recent investigation on the feeding and metabolic strategies of the Antarctic filter-feeding bivalve, *Laternula elliptica* in relation to extremely seasonal food availability (primary production) in the Antarctic waters. An experimental study revealed that *L. elliptica* has an exploitation strategy, viz. a high food consumption rate in summer during which food is in sufficient supply. Reduced summer metabolism of *L. elliptica* as compared with temperate bivalves, despite the apparent high feeding rates, appears to be another important strategy for enhancing the scope of growth, since this clam inhabits Antarctic nearshore waters where food may be in short supply for up to 9 months of the year.

Key Words: Antarctica, bivalve, *Laternula elliptica*, metabolism

Introduction

The Antarctic soft-shelled clam, *Laternula elliptica* is endemic to the Antarctic waters, and widely distributed in shallow and sheltered areas around the Antarctic Continent. *Laternula elliptica* occurs at about 20 to 30 m depths as dense patches on the order of tens of individuals per m² dominating the infaunal biomass in soft bottoms (Stout and Shabica 1970; Hardy 1972; Zamorano *et al.* 1986; Ahn 1993, 1994).

High biomass of Antarctic benthic invertebrates has generally been explained as a consequence of slow growth, delayed maturation, and increased longevity (White 1984), and these features have been considered as a direct response to low temperature. Intuitively this is an appealing explanation. In fact, most polar marine animals grow slowly, reproduce slowly and have very low rates of metabolism. However, when we examine these features more closely, it turns out that there is no convincing evi-

dence for a direct limitation by low temperature. In some cases where seasonal pattern of the growth has been examined, growth has been found to be slow only when averaged over the year. Figure 1A shows the seasonal pattern of growth in a small-sized Antarctic bivalve *Lissarca miliaris* in inshore waters at Signy Island. The sharp increases in growth rate are associated with phytoplankton bloom, and during the same period temperature increase was less than 2°C (Fig. 1B). The changes in growth rate of this species cannot adequately be explained in terms of a direct response to the slight increases in temperature unless this species is highly sensitive to temperature. The temperature coefficient, Q_{10} is used to estimate the increase in a rate of a biological process produced by raising temperature 10°C. The Q_{10} values are commonly 2 to 3 for biological processes such as respiration, growth, and outside the range of 1 to 5 is unusual for unstressed organisms. In this case, doubling the growth rate by a temperature increase from -2 to 0°C would imply a Q_{10} of 32. This is clearly non-biological.

As one of the largest bivalve species in the Antarctic, *Laternula elliptica* appears to grow rapidly

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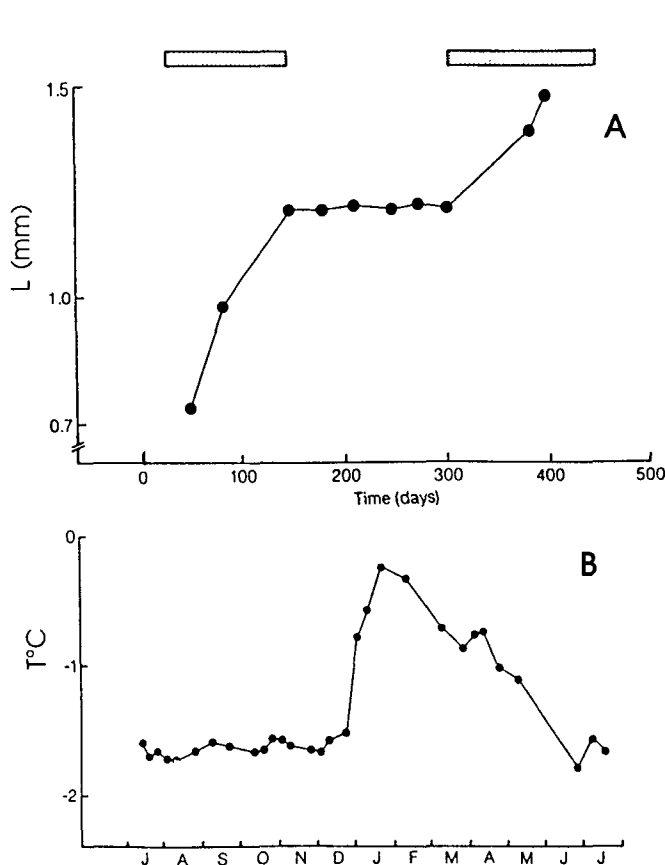


Fig. 1. (A) Seasonal pattern of the growth of an Antarctic bivalve *Lissarca miliaris* in inshore waters at Signy Island. The bars represent the approximate duration of the phytoplankton bloom (from Richardson 1979); (B) Seasonal variation in sea water temperature at the same site (from unpublished data of British Antarctic Survey).

reaching a shell length of approximately 10 cm in about 10 years (Fig. 2). This growth rate is much higher than other Antarctic bivalve species, although it is reportedly lower than those of the related temperate species with similar ecological niche such as the soft clam, *Mya arenaria* (Ralph and Maxwell 1977a). Recently, using the record of stable isotope ratios in shell carbonate, Brey & Mackensen (1997) demonstrated that shell growth occurs largely in summer, that is during the warmer and productive period. This implies that the growth rate would be much higher if averaged only for summer period. The above-mentioned examples strongly imply that Antarctic marine benthic organisms have a potential to grow rapidly whenever food is provided sufficiently regardless of low temperature. What has to be stressed is that the relative importance of food on the growth of marine organisms may be much

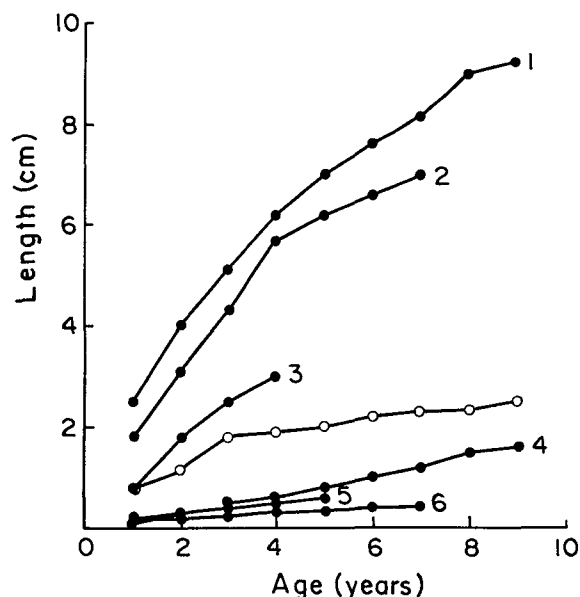


Fig. 2. Comparisons of growth rates of temperate and polar bivalve species (after Everson 1977). The open circle represents the temperate bivalve species *Venus striatula* (Milport, UK), and the closed circles with a number represent polar species. 1, *Laternula elliptica*; 2, *Adamussium colbecki*; 3, *Gaimardia trapesina*; 4, *Yoldia eightsi*; 5, *Kidderia bicolor*; 6, *Lissarca miliaris*.

greater in the Antarctic waters than in temperate waters, because seasonal variation of sea water is much smaller in the Antarctic waters, although seasonal variations in the growth and reproduction of Antarctic marine organisms have occasionally been related to those slight summer increases in temperature.

In the Antarctic marine environment primary production is extremely seasonal. In some nearshore waters the amplitude of the seasonal variation in standing stock is extremely high when compared with temperate waters, and the summer-time standing stock is more than two order of magnitude greater than winter value (Clarke *et al.* 1988; Clarke and Leakey 1996). It is, therefore, likely that food for benthic filter-feeding herbivores like *Laternula elliptica*, which feed primarily on phytoplankton, may be in short supply for up to 9 months of the year, and these benthic filter-feeders would be expected to have a strategy to maximize energy gain when food resources are in sufficient supply, by which these organisms may sustain energy flow into growth and reproduction.

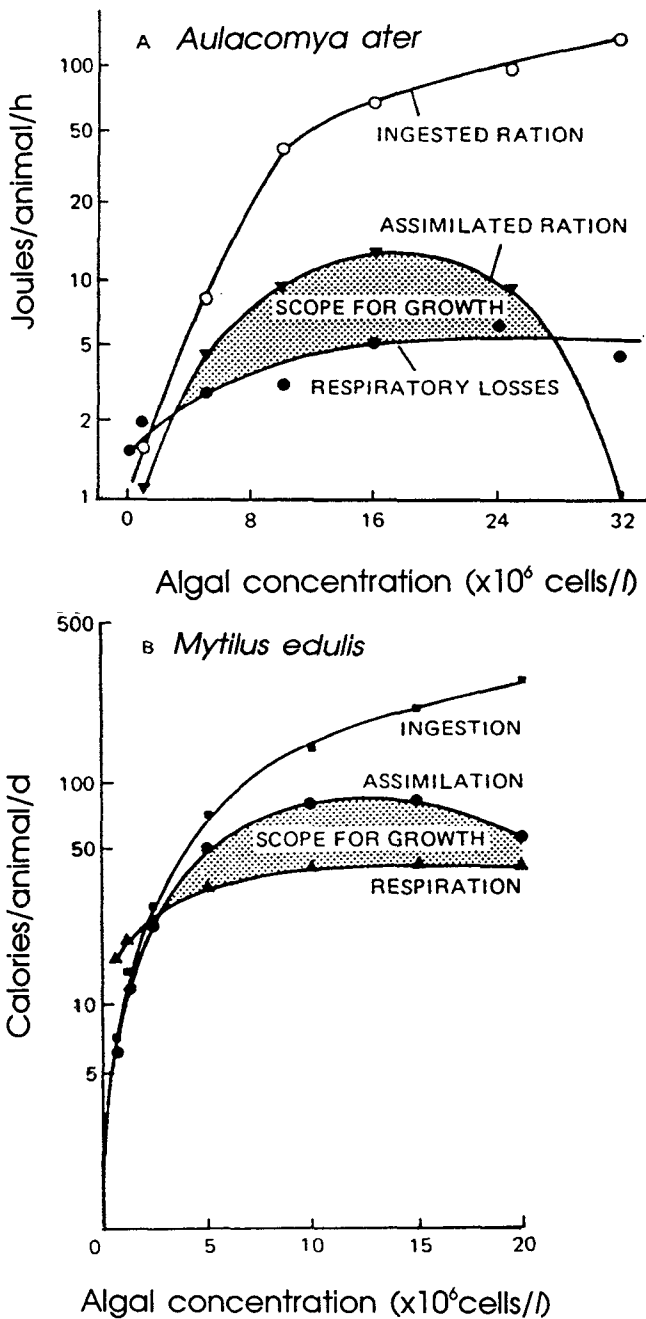


Fig. 3. The scope for growth of two filter-feeding mussel species in temperate waters is plotted against food concentration. Data of *Aulacomya ater* are from Griffiths & King (1979) and data of *Mytilus edulis* from Thompson & Bayne (1974). These figures show how a maximal value of the scope for growth, that is amount of energy available for growth could be achieved by adjusting food consumption and metabolic energy expenditure.

Energy Conservation in Bivalve Mollusks

It has generally been known that there are at least two strategies of energy conservation in bivalve mollusks. One is *Exploitation strategy*, that is, when food resources are abundant, a maximal energy gain

may be derived by a high food consumption rate, although a high feeding rate is associated with a relatively low absorption efficiency and a higher metabolic cost. An alternative strategy, *Reduction of metabolic costs* may be important under conditions of limited food availability, because with very low metabolic rates, organisms could survive for a long period of time without food, or alternatively more energy could be allocated for growth (Bayne and Newell 1983). These two strategies are closely related to food (algal) concentrations in ambient sea water, and therefore, it is possible that an organism actually shift from one to the other strategy as food concentration changes, or sometimes use both strategies.

Figure 3 shows some examples how these two strategies have been utilized by temperate bivalves. As shown in these figures, as algal concentration increases, filtering rate increases being accompanied by increase in ingested ration. High feeding rates are, however, associated with a relatively low absorption efficiency and a higher metabolic cost, and the scope for growth could decrease even although the total ingested ration increases. Too much food could also have a negative effect on filtering rate by clogging filtering organs like gills. At extremely high food concentrations, both filtering rate and the amount of assimilated ration decrease, while metabolic rates only slightly increase. Thus metabolic rate increases with increasing food concentration but not a linear fashion. Metabolic rates also increase with increasing food concentrations in many filter-feeding bivalves, because of increased oxygen demands for food processing following feeding and the specific dynamic action such as protein synthesis (Jobling and Davis 1980; Jobling 1983).

Energy Conservation of the Antarctic Clam *Laternula elliptica*

Little studies have been done on feeding and metabolic strategies of the Antarctic benthic invertebrates in relation to the extremely seasonal food supply. Recently some investigations were conducted on

Laternula elliptica to figure out its life-history strategies for energy conservation dealing with extremely seasonal food availability. What has been described below is part of these investigation on this species.

Feeding ecology and physiology

Ahn (1993) showed that *Laternula elliptica* had high rates of fecal production ($0.26\text{--}2.17\text{ mg dry wt g wet wt}^{-1}\text{ d}^{-1}$) similar to those of a typical filter-feeding bivalve, *Mytilus edulis* in temperate water at equivalent food (seston) concentrations. High fecal production rate reflects high feeding activity, implying that *L. elliptica* has an exploitation strategy of a high consumption rate during summer time to maximize energy gain. Another study on this species (Ahn 1997) revealed that *L. elliptica* are being well fed during most of the summer period. In Fig. 4, organic carbon content and Chl. *a*/phaeopigment ratio of fecal materials of *L. elliptica* are plotted against the Chl. *a* concentration in sea water. Organic carbon content and Chl. *a*/phaeopigment ratio of fecal materials were used as indices reflecting assimilation efficiency. At high algal concentrations ingested algal cells were often partially digested and even egested as intact cells, and changes in fecal composition reflect differences in assimilation efficiency in bivalves (Morton 1983). These composition increased with increasing Chl. *a* concentration in sea water within most of the range tested ($0.7\text{--}3.7\ \mu\text{g Chl. } a\ l^{-1}$). It was also reported that more undigested cells were microscopically observed in fecal materials at higher Chl. *a* concentrations which indicated that *L. elliptica* was being fed in excess during most of the experimental period.

An apparent high food consumption rate, and enhanced food availability for most summer periods predict that metabolic rate of this species may be somewhat elevated in summer, although many cold-water marine organisms are known to have very low metabolic rates when compared to the related temperate species. Metabolic rates are known to increase with increasing food concentrations in many marine invertebrates, because of increased oxygen demands for food processing and the specific dynamic action following feeding such as protein

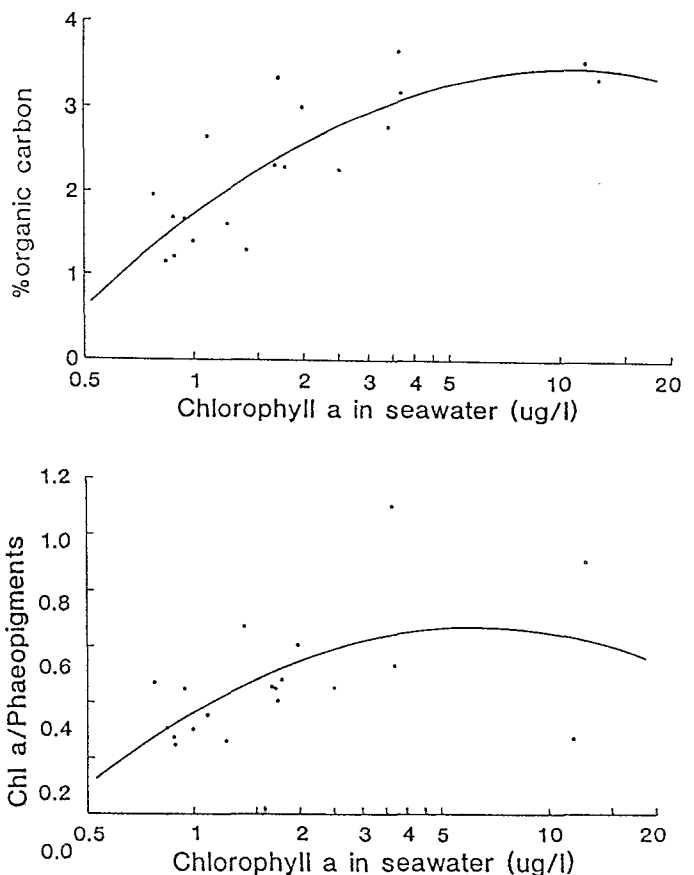


Fig. 4. Changes in the chemical composition in the fecal materials of *Laternula elliptica* at different algal concentrations in the flow-through culture tank (from Ahn 1997).

synthesis (Jobling and Davis 1980; Jobling 1983; Peck in press; see for review Bayne and Newell 1983). In addition Clarke (1991) postulated that oxygen consumption of polar organisms would increase in summer largely as a response to enhanced food availability and only slightly increase as a response to temperature increase.

Metabolism

As Clarke (1991) pointed out, some elevation of metabolism (due to active metabolism) would be expected for the Antarctic filter-feeding bivalve *Laternula elliptica* for a summer period with enhanced food availability. Since *L. elliptica* is sedentary, and not as locomotive as swimming fish, rise in oxygen demand is likely to be associated mainly with feeding, growth and reproduction. Recently Ahn & Shim (1998), however, showed that routine metabolic rates of *L. elliptica* measured for a summer period at moderate food concentrations ($0.44\text{--}3.4\ \mu\text{g}$

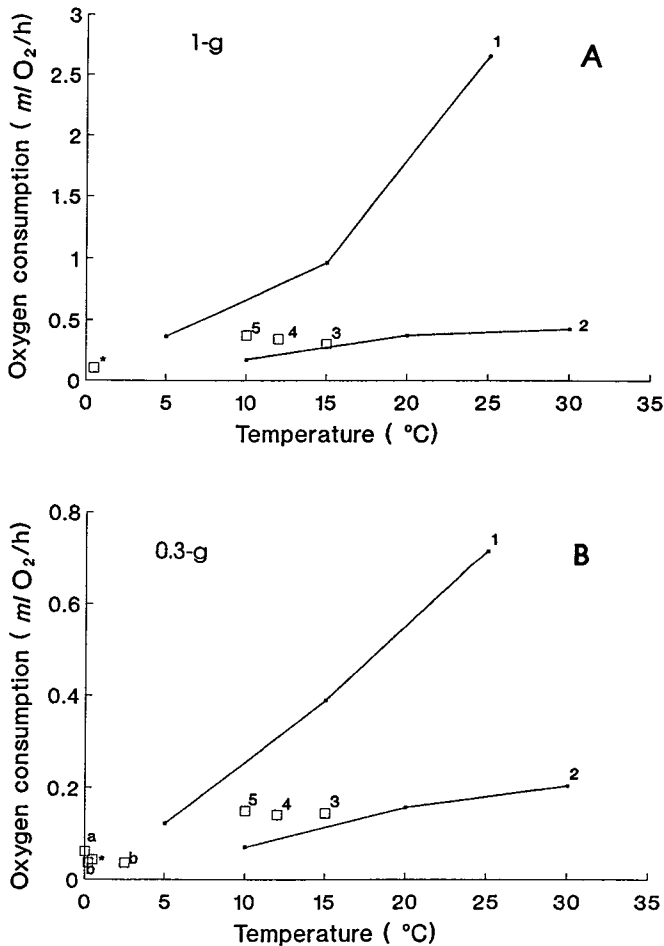


Fig. 5. The metabolic rates of *Laternula elliptica* in comparison with those of other temperate and Antarctic bivalve species. Since sizes of different bivalve species are so variable, the metabolic rates were compared for standard organisms of 1 g and 0.3 g TDW (except No. 1 in AFDW). The asterisk represents the oxygen consumption rate of *L. elliptica* measured in Ahn & Shim (1998). (A) For 1-g individuals, the rates were compared with those of oysters (1, 2) and mussels (3-5) in temperate waters. (B) For 0.3-g clams, a and b shows the metabolic rates of small-sized Antarctic bivalves. a is *Gaimardia trapesina trapesina* (Ralph and Maxwell 1977b), and b is deposit-feeding *Yoldia eightsi* (Davenport 1988). 1, *Ostrea edulis* (Rodhouse 1978); 2, *Crassostrea virginica* (Dame 1972); 3, *Mytilus edulis* (Bayne and Scullard 1977); 4, *Mytilus chilensis* (Navarro and Winter 1982); 5, *Mytilus edulis* (Vahl 1973).

Chl. *a* l⁻¹ with a mean of 1.47 µg Chl. *a* l⁻¹) was well below those of temperate species, and comparable to those of other Antarctic bivalves (Fig. 5).

Low metabolic rates have already been found in a wide variety of Antarctic invertebrates (Ralph and Maxwell 1977b, c; Luxmoore 1984; Peck *et al.* 1987; Peck 1989; Chapelle *et al.* 1994). The result for *Laternula elliptica* also adds to the previous findings.

Metabolic rates of *L. elliptica* might further increase with increasing food concentration. However, as shown in Fig. 3, metabolic rate of filter-feeding bivalves is not a linear function of food concentrations, and metabolic rates are likely to only slightly increase at higher algal concentrations. Further studies, however, are required to clarify this problem.

Summary

It has been stressed that reduced metabolism of polar marine organisms should be considered from a different aspect, not as a response limited by low temperature, but as an efficient mechanism of energy conservation. Organisms could be benefited from reduced metabolism under conditions of limited food availability. Given the high food consumption rate of *Laternula elliptica* during summer as indicated in a previous study (Ahn 1993), the reduced summer metabolism means higher growth efficiency in cold-water bivalves than in temperate bivalves even under conditions of high food availability. Apparent active feeding with reduced metabolic rate during summer thus might contribute to sustaining high biomass of *L. elliptica* in Antarctic nearshore waters where food may be in short supply for up to 9 months. Recently, Loo (1992) demonstrated that *Mytilus edulis* inhabiting boreal waters fed actively and were capable of absorbing food with reduced metabolic rates at around 0°C, and showed that mussels acclimated at very low temperatures exhibited biomass increase.

Future Studies

We clearly need further studies including molecular-level studies to better understand how the Antarctic marine benthic organisms have been well adapted in the particular environment, and how *Laternula elliptica* and possibly some other benthic invertebrates could achieve active feeding, rapid growth while keeping their metabolic rate as low as possible.

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