Review

Some Ecological and Physiological Features of the Antarctic Clam, *Laternula elliptica* (King and Broderip) in a Nearshore Habitat on King George Island

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Abstract : The Antarctic clam *Laternula elliptica*, is one of the most representative benthic invertebrates in the Antarctic nearshore waters. Endemic to the Antarctic, *L. elliptica* is widely distributed around the Antarctica occurring as dense patches in shallow sheltered areas and exhibits high biomass. Despite its apparent ecological importance, *L. elliptica* has rarely been studied until recently probably due to difficulties in sampling in the ice-impacted waters. Recent studies have revealed various aspects of its ecology and physiology. In this review, some physiological and ecological characteristics of this species are discussed in relation to some prevailing features of its habitat environment, in particular physical instability of habitat substrates and extreme seasonality of food availability.

Key words : Antarctic clam, distribution, food, growth, ice impacts, *Laternula elliptica*.

1. Nearshore habitat environment

The Antarctic benthic environment is characterized by a deep and narrow continental shelf, and the majority of the benthic environment belongs to the deep water which is physically homogeneous and stable. In other words, there are little variations in temperature and salinity. One exception is the highly seasonal, but predictable food input from overlying water. *L. elliptica* occurs in the shallow nearshore waters that constitute a very small part of the Antarctic benthic environment. The nearshore environment, however, is strikingly different from the deep water environment and also from any other parts of the world, and benthic organisms living in this area are subject to variable environmental changes. Ice-abrasion is a prevailing physical factor affecting spatial distribution and other biological processes of benthic organisms. Ground or drifting icebergs frequently crush the bottom

effectively eliminating sessile organisms, even infaunal organisms (Shabica 1972; Gruzov 1977; Richardson and Hedgpeth 1977), and anchor ice is plucking up the bottom animals (Dayton *et al*. 1969, 1970; Dayton 1989). Temperature and salinity also change as ice forms and melts, although the range of variation is not as wide as in temperate waters.

As in the pelagic environment, water column primary production in the Antarctic nearshore marine environment is extremely seasonal and limited to a short period of summer (Clarke *et al*. 1988; Clarke and Leakey 1996). In the nearshore waters, however, there are various sources of organic matter other than phytoplankton, such as ice algae and benthic diatoms. In particular, benthic microalgae have been considered as an important food source for water column and benthic herbivores when other food sources are scarce (Gruzov 1977; Palmisano *et al*. 1985; Dayton *et al*. 1986; Rivkin and Putt 1987; Gilbert 1991). Resuspension of benthic diatoms by wind mixing has been postulated as an important process increasing

microalgal food stocks for Antarctic shallow water herbivores (Krebs 1983; Berkman *et al.* 1986; Gilbert 1991; Klöser *et al.* 1994), and demonstraed in some nearshore waters on King George Island (Brandini and Rebello 1994; Ahn *et al.* 1997). Ahn (1997) suggested that *L. elliptica* may rely on benthic diatoms while phytoplankton production is low, and the high biomass may occur due to a tight coupling of benthic primary production and a rapid and efficient utilization of organic matter by *L. elliptica*. Mercuri *et al.* (1998) reported that this bivalve densities in the Potter Cove were highly correlated with benthic diatom coverage, strongly supporting that benthic microalgae comprise an important food item of benthic herbivores like *L. elliptica*. Thus, the Antarctic shallow water suspension-feeders like *L. elliptica* may be not food-limited as much as we would thought, and input of other food sources (particularly benthic diatom) may play a role in sustaining the high biomass (Ahn *et al.* 1997; Gili *et al.* 2001). Relative importance of these alternative food sources to water column production and their seasonal variations, however, are largely unknown.

Physical perturbation by ice and extreme seasonality of food availability have already been considered to have a profound effect on various aspects of physiological and ecological functioning of the Antarctic nearshore marine benthic invertebrates (Pearse *et al.* 1991). From an ecological viewpoint, the mechanisms by which this bivalve species has adapted to such a particular environmental setting are of great interest.

2. Spatial distribution

There are not many quantitative studies on spatial distribution of *L. elliptica*. However, this species is likely absent in intertidal and very shallow subtidal zones (<5 m), apparently due to ice impacts frequently occurring at this zone. Even at water depths greater than 5 m, crushed or unburied *L. elliptica* apparently by grounded icebergs have occasionally been observed by SCUBA divers in some habitats in the Marian Cove (pers. communication with the divers) as well as in other areas (Shabica 1972). On the King George Island, a high number of *L. elliptica* were observed in shallow and sheltered areas such as Marian Cove (Ahn 1993), Collins Harbour (Ahn 1994) and Potter Cove (Mercuri *et al.* 1998). In the areas near the King Sejong Station, *L. elliptica* occurs from 5 m down to 35 m in various sediment types (Ahn 1993, 1994). In Marian Cove tremendously high densities (up to

170 inds m^{-2}, unpublished) were found around 20-30 m depth, where bottom sediment consists mostly of mud mixed with sand and gravel. Although habitats deeper than SCUBA diving depths (>35 m) have rarely been investigated, within the depth range of 5-30 m, the density tends to increase with increasing water depth (reviewed by Ahn 1994). In the nearby Potter Cove (62°14'S, 58°48'W), on the other hand, dense patches of this bivalve species were observed from sandy mud to sandy sediment at much shallower habitats (5-15 m) (Mercuri *et al.* 1998). The highest density ever reported was 346 inds m^{-2} at 5 m depth in the Potter Cove where the bottom sediment consisted of 95 % sand and was covered by dense assemblage of benthic diatom.

Ice impact is likely a prevailing factor affecting the vertical distribution of *L. elliptica*, particularly determining the upper limit of its vertical distribution in a habitat. *L. elliptica* is known to burrow deep (frequently >50 cm) into sediment (Hardy 1972). Deep-burrowing seems to be a means for avoiding ice impacts occurring frequently in the shallow waters. A pair of stout and highly extendable siphons appears to be a morphological feature adapted to feed in the physically unstable substrate. With only the siphonal opening exposed at the surface, it feeds while the rest of the body is staying deep in the sediment to avoid ice impacts. Deep-burrowing can also be considered as a way to avoid predation. It was reported that once unburied at the surface by grounded icebergs etc., they were soon attacked by predators such as starfishes (Dayton *et al.* 1974; Zamorano *et al.* 1986). These epifaunal predators, however, are generally rare in severely ice-affected sublittoral zone, but increase in number in deeper water as substrate is physically stabilized (Dayton *et al.* 1970; Gruzov 1977; Richardson and Hedgpeth 1977), indicating that deep-burrowing is primarily a means to protect themselves against ice impacts.

Despite the disruptive effects of ices, however, there seems to be some advantages in living at the relatively unstable shallow sublittoral substrates; more food. Mercuri *et al.* (1998) showed that the bivalve densities in the Potter Cove were highly correlated with benthic diatom coverage, indicating food (benthic diatoms) availability affects the spatial distribution of this bivalve species as well. Ahn (1994) previously suggested that a trade-off between physical stability of bottom substrate and food availability determine both the depth range of vertical distribution and the magnitude of *L. elliptica* biomass. Thus, both habitat stability and food availability likely affect the vertical distribution and the biomass, but

the relative importance of these two factors is to be assessed.

3. Growth

Many Antarctic marine organisms are characterized by slow growth, which has long been considered as a direct response to living in a cold environment (White 1984). Slow growth and some other biological features of Antarctic marine invertebrates, however, are more likely responses to the strongly seasonal food availability rather than physiological inability to adapt to low temperature (Clarke 1983, 1988, 1990). 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, strongly implying that Antarctic marine benthic organisms have a potential to grow rapidly whenever food is provided sufficiently regardless of low temperature (Clarke 1983). In fact, many Antarctic marine organisms particularly herbivores show distinct seasonality in growth and reproduction in response to the extreme seasonal variation of primary production (Clarke 1988).

As one of the largest bivalve species in the Antarctic, *L. elliptica* grows to a shell length of approximately 10 cm in 20 years or so (Ralph and Maxwell 1977a; Urban and Mercuri 1998). Smaller clams, however, appear to have much higher growth rates, reaching to 6 cm in 4 to 5 years (Ralph and Maxwell 1977a; Urban and Mercuri 1998), and the growth is likely retarded after it is sexually mature at around 40 mm (Urban and Mercuri 1998; Choi *et al*. 1999). This growth rate is relatively lower than those of the related temperate species with similar ecological niche, such as the soft clam, *Mya arenaria* (Ralph and Maxwell 1977a). Growth of *L. elliptica*, however, seems to be highly seasonal. Recently Brey and Mackensen (1997), using the record of stable isotope ratios in shell carbonate, demonstrated that shell growth occurs largely in summer. Both δO^{18} and δO^{13} values were lower in the wider bands which were formed in spring and summer, that is warmer and productive period, indicating growth rings are being formed annually. This also implies that the growth rate would be much higher if averaged only for summer period, and that food is likely the most important factor influencing the growth of *L. elliptica*.

Previous studies reported that high benthic biomass in some Antarctic shallow waters was related to high (primary) productivity and habitat stability (reviewed by Dayton 1990). Dayton (1990) suggested that food input is an important factor determining the densities and biomass of the benthic populations. In some shallow Arctic seas, low benthic biomass was reported to be directly related to limited food supply (Grebmeier and Barry 1991). Grebmeier and Barry (1991) suggested that in polar seas low temperature in itself is not a limiting factor for the growth of benthic fauna, and food supply is the dominant factor limiting benthic faunal biomass.

Despite deep-burrowing, the bivalve populations seem to be periodically eliminated from the bottom substrates by grounded icebergs. Shell fragments were frequently observed at depths as deep as 30 m by divers. From an evolutionary viewpoint, in this physically unstable environment, natural selection generally favors organisms with r-strategies, one of the strategies is a rapid growth. Moderate to high turnover (growth) rate during austral summer when food is abundant, therefore, might be necessary to sustain the high biomass in the ice-impacted shallow waters.

4. Strategies for rapid growth during summer

Given the rapid growth during summer, it would be expected that *L. elliptica* have some strategies to maximize food resources which are in sufficient supply only in the limited period of the year, by which these organisms may sustain energy flow into growth and reproduction. Reduced metabolism is likely one of the strategies. An experimental study showed that metabolic rates of *L. elliptica* measured in summer after feeding were several times lower than those of temperate species, and comparable to those of other Antarctic bivalves (Ahn and Shim 1998). Low metabolic rates are widespread among Antarctic marine invertebrates (Ralph & Maxwell 1977b,c; Luxmoore 1984; Peck *et al*. 1987; Peck 1989; Chapelle *et al*. 1994). The result from *L. elliptica* just adds to the previous findings. Low metabolic rate is, however, likely the result of selection for reduced maintenance energy expenditure under the limited food availability rather than a response limited by low temperature. In other words, with reduced metabolism, a relatively greater percentage of energy taken is able to be funneled into (invested to) growth and reproduction, and less is used for maintenance, leading to a high ecological growth efficiency (Clarke 1987). Another experimental study (Ahn 1993) showed that fecal production rates measured in summer were highly comparable to those of a typical filter-feeding bivalve *Mytilus edulis* in temperate waters, indicating that *L. elliptica* is able to feed actively regardless of low temperature whenever food is abundant.

The previous experimental studies thus suggest that *L. elliptica* have at least two strategies to maximize the food resources which are supplied in a limited period of the year: one is an exploitation strategy characterized by a high food consumption rate, and the other is reduced routine metabolism. In other words, active feeding with reduced metabolic rate during summer likely leads to a high growth efficiency and may contribute to sustaining its high biomass 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.

5. Summaries

1) Both vertical distribution and magnitude of biomass are likely determined by level of physical disturbance incurred by ice impacts and also by availability of the secondary food resources (in particular benthic diatom). High biomass occurs at depths where bottom substrate is relatively undisturbed, and densely covered with benthic microalgal mats.

2) Deep-burrowing appears to be an effective means to avoid ice impacts. Despite deep-burrowing, however, the bivalve populations are likely periodically eliminated from the bottom substrates by grounded icebergs. Moderate to high turnover (growth) rate, therefore, might be necessary to sustain the high biomass in the ice-impacted shallow water.

3) Growth of *L. elliptica* occurs largely in summer and the growth rate would be much higher if averaged only for summer period. Food availability is likely a key factor influencing the growth of *L. elliptica*.

4) Active feeding with reduced metabolic rate during summer likely leads to a high growth efficiency and may contribute to sustaining its high biomass in Antarctic nearshore waters.

5) Overwintering strategies of this species for a prolonged period of food-limitation which some believe is as long as 9 months are largely unknown. A seasonal study is needed to elucidate storage and utilization of energy substrate for winter food shortage.

Acknowledgements

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