POPULATION DYNAMICS OF *MAGELLANIA FRAGILIS*, A BRACHIOPOD DOMINATING A MIXED-BOTTOM MACROBENTHIC ASSEMBLAGE ON THE ANTARCTIC SHELF

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A dense assemblage of the brachiopod *Magellania fragilis* was sampled by trawl and underwater photography during the expedition ANT IX/3 (1991) of RV 'Polarstern' on the shelf of the Lazarev Sea, Antarctica. Mean abundance and biomass estimates for *M. fragilis* were 26·15 individuals m^{-2} and 1·13 g AFDM m^{-2}, respectively. Growth bands visible on the shell were interpreted as annual growth marks caused by the strong seasonality of food input to the benthos and were treated as size-at-age data. The von Bertalanffy growth function L_t (mm) = 51·67 $(1 - e^{-0.020 (t + 1.326)})^{0.828}$ described these data best. The annual somatic P/B ratio was very low, 0·046 y^{-1}, and annual production amounted to 0·052 g AFDM m^{-2} y^{-1} at this particular site. These results indicate that *M. fragilis* is a comparatively slow-growing species with very low annual productivity.

INTRODUCTION

The Brachiopoda were the dominant group of benthic filter feeding marine invertebrates from the early Cambrian, when they arose over 550 million years ago, until the end of the Permian period. However, they suffered greatly in the Permo-Triassic mass extinction event, and have not regained their previous position of dominance in the subsequent 250 million years. Despite this, around 120 living genera are known (James et al., 1992), and they are present in all of the world's oceans at depths from the intertidal to over 6000 m. Living brachiopods are relatively little understood and researched. This is mainly because they are abundant only at sites in the deep sea, fjordic inlets, cryptic habitats such as caves, and in Antarctica, although they are present in some numbers in nearshore habitats in New Zealand and on the west coast of North America (James et al., 1992).

Foster (1974) described 37 species representing 21 genera from Antarctic and sub-Antarctic localities. He also found that brachiopods were fairly common, with high frequencies of occurrence in all Antarctic waters, but that their abundance tended to be low, and densities only occasionally approached 50 ind m^{-2}. Locally some species can attain higher numbers than this, and *Liothyrella uva* (Jackson, 1912) occurs at densities in excess of 3000 ind m^{-2} in caves and rocky overhangs at Signy Island in the South Orkney Islands (L.S.P., personal observation).

Life history patterns of brachiopods were classified as being of two types by Thayer

(1981). These were either large, slow-growing species with relatively large numbers of offspring for brachiopods, or micromorphic species with few offspring. The former tend to be representative of high latitude communities, while the latter occur predominantly on coral reefs. His ideas, however, were based on few data, and the small number of studies so far on growth and population dynamics of brachiopods have tended to suggest that life spans are well within the ranges found for other taxa (Rickwood, 1977; Doherty, 1979; Stricker & Reed, 1985; Collins, 1991). Of those four studies Rickwood (1977) and Stricker & Reed (1985) assessed rates of growth in laboratory populations. The only work to investigate changes in size of tagged individuals (Doherty, 1979) found no growth in all tagged animals (N=14) over a 248-d period. So far comprehensive population data on abundance, biomass, growth and productivity are not available for brachiopods from any locality.

Magellania fragilis (Smith, 1907) has a circum-Antarctic distribution and is usually found attached to small pebbles, bryozoans, corals and gastropod shells. It is a moderately large species, with a maximum reported length of 49·5 mm and occurs at depths between 119 and 1254 m (Foster, 1974). The present study is an assessment of parameters measured from a population encountered and sampled by the RV 'Polarstern' in the Lazarev Sea. The combination of high quality underwater photography and trawl sampling has allowed good estimates of abundance, biomass, growth and productivity to be calculated.

MATERIALS AND METHODS

Sampling

During the Antarctic expedition ANT IX/3 of RV 'Polarstern', a dense assemblage of brachiopods was encountered at one station on the shelf of the Lazarev Sea (8 March 1991, 69°57′S 11°49′E, 210–220 m water depth). At this station, one Agassiz trawl sample of 15 min duration was taken. The net had a 1x3 m mouth opening, 20x20 mm mesh size in the front section and 10x10 mm in the central section and cod end. About 50% of the brachiopods caught (~5000 specimens) were hand-picked from the sample and stored in 70% ethanol. Additionally, 79 underwater still photographs covering an area of 0·98 m² each were taken by a camera system released by a ground weight following the protocol of Gutt (1988) and Gutt et al. (1991). Abundance was estimated from those brachiopods clearly identifiable on these photographs, the minimum length for accurate identification was ~5 mm.

Size-mass relations

In the laboratory, length, width and height of a subsample of *Magellania fragilis* (895 specimens) was determined to the lower 0·1 mm using vernier callipers. Dry mass (DM) and ash-free dry mass (AFDM) of 40 specimens covering the whole size range present were determined by drying at 80°C for 24 h and subsequent ignition in a muffle furnace at 500°C for 24 h. Size–mass relations of the form:

$$M = a\,S^b \tag{1}$$

were established by an iterative non-linear fitting algorithm (SIMPLEX, see Press et al., 1986).

Growth

We interpreted the growth band pattern visible on the surface of the shells as annual growth marks. These bands were counted on the dorsal valve of 81 specimens covering the whole size range, and the general growth model of Schnute (1981)

$$S_t = \left[Y_1^B + \left(Y_2^B - Y_1^B \right) \cdot \frac{1 - e^{-A(t-\tau_1)}}{1 - e^{-A(\tau_2-\tau_1)}} \right] 1/B \tag{2}$$

was fitted to these data by the SIMPLEX algorithm. The model includes four parameters, the two constants A (time^{-1}) and B (dimensionless) and the size Y_1 and Y_2. The two age values τ_1, τ_2 are chosen by the user, e.g. lowest and highest age in sample. The starting values of Y_1 and Y_2 are set accordingly. Special cases of this general model resemble various historical growth models such as the von Bertalanffy, Richards, or Gompertz models.

Productivity

Somatic production was computed using the mass-specific growth rate method according to Crisp (1984) from (i) the size-frequency distribution, (ii) the size-growth function and (iii) the size–mass relation. Production per total sample, P_S, was computed by

$$P_s = \sum N_i M_i G_i \tag{3}$$

where N_i is the number of animals in size class i, M_i is the mean individual body mass in size class i, and G_i is the corresponding annual mass-specific growth-rate (see Brey, 1991; Brey et al., 1990, for detailed explanation). The annual somatic production/biomass ratio, P/B, was calculated from production, P_S, and somatic biomass per total sample, B_S, where

$$B_S = \sum N_i M_i. \tag{4}$$

Annual production per square metre was computed by multiplying the P/B ratio with an estimate of average biomass, B, derived from mean body mass per total sample, M_{mean}, and mean abundance computed from the underwater still photographs, N_{foto} :

$$P = P/B \, M_{mean} \, N_{foto} \, [\text{g m}^{-2} \, \text{y}^{-1}]. \tag{5}$$

RESULTS

Sampling site and epibenthic community

The sediment at the sampling site consisted of sand mixed with gravel and small stones up to 15 cm diameter. The epibenthic community consisted mainly of brachiopods,
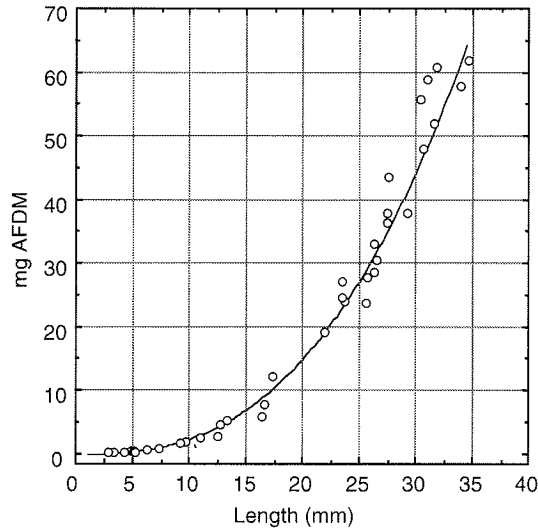
Figure 1. Relation between body mass (mg AFDM) and length (mm) in *Magellania fragilis*.
$AFDM=0.005L^{2.672}$; Residual sum of squares = 434.4.

but also of sponges, bryozoans, polychaetes, amphipods, serolid isopods, echinoids, holothuroids and ophiuroids. *Magellania fragilis* was found to be the dominant brachiopod species, only two of the 900 brachiopod specimens examined belonged to a different species, *Magellania joubini* (Blochmann). Besides *M. fragilis*, which contributed about 60% to the total number of macrobenthic specimens, no other species occurred in high numbers. It was remarkable that there was a complete absence of hexactinellid sponges.

Morphometry

Length (L), width (W) and height (H) of *M. fragilis* were related linearly (functional regression, see Ricker, 1973): $W=0.479+0.827L$, $r^2=0.947$, N=895; $H=-1.487+0.555L$, $r^2=0.955$, N=895; $H=-1.784+0.670W$, $r^2=0.899$, N=895. Mass and length were related exponentially: $DM=0.040L^{2.860}$, $r^2=0.992$; $AFDM=0.005L^{2.672}$, $r^2=0.988$ (see Figure 1). The ratio of AFDM to DM increased slightly with length, $AFDM/DM=0.055+0.001L$, $r^2=0.590$, N=40, and amounted to 6.5% on average.

Abundance and biomass

The number of specimens of *M. fragilis* counted on each of the 79 photographs taken ranged from 5 to 52 individuals, and the mean overall abundance was 25.76 ind m^{-2} (95% C.L. =±2.47; Figure 2). Animals <5 mm in length could not be seen on the photographs, but were sampled by the trawl (Figure 3). Assuming the size-frequency distribution of the trawl sample to be representative of the population as a whole, the abundance figure was corrected for that part of the population below 5 mm length (1.5%, see Figure 3). The corrected estimate was 26.15 ind m^{-2}. Mean individual body mass (M_{mean}=35.86 mg AFDM ind^{-1}) was calculated from the length-frequency distribu-
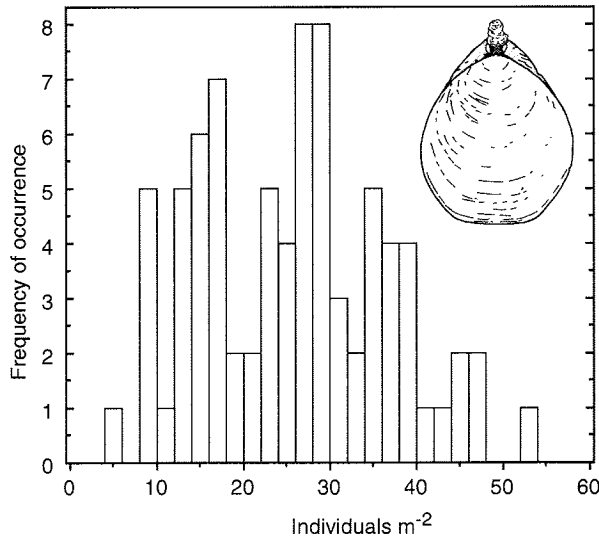
Figure 2. Frequency distribution of the number of specimens (N m^{-2}) of *Magellania fragilis* based on the 79 still photographs.

tion (Figure 3) and the length–mass relation (Figure 1). This was corrected to 43·03 mg AFDM ind^{-1} by using a factor of 1·2 to allow for weight loss due to ethanol preservation (see Brey, 1986; Howmiller, 1972 and references therein). On this basis mean population biomass was estimated at 1·13 g AFDM m^{-2} (26·15 43·03 / 1000).

Growth

Steromicroscopic investigation revealed the growth band structure in the shells of *M. fragilis* to be caused by two features: (i) changes in the distance between punctae on the
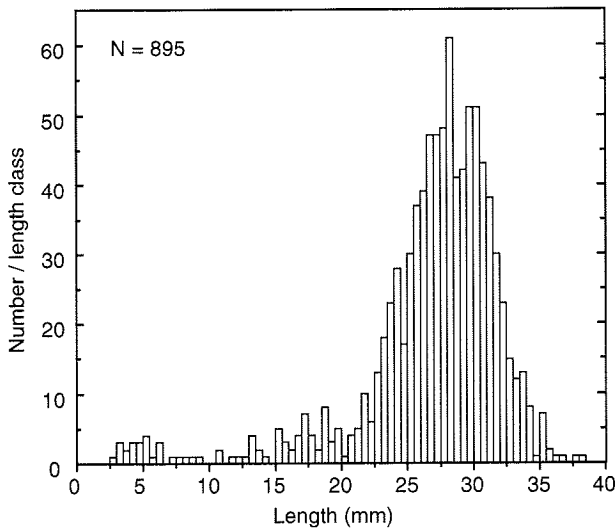

Figure 3. Length-frequency distribution of *Magellania fragilis* from trawl sample.

length axis, accompanied by (ii) the frequent formation of ridges in the areas of increased punctae density. The distinctness of these growth marks, however, varied considerably. Specimens with poor definition of growth marks, and specimens with irregular shape of the valves were excluded from the analysis. Growth bands were counted in 81 specimens. Schnute's (1981) general model was fitted to these 81 length-at-age data pairs and the resultant growth function was

$$Y_1 = 2.545, \, Y_2 = 35.244, \, A = 0.020; \, B = 1.207 \tag{6}$$

(with $\tau_1 = 0$ and $\tau_2 = 48$); N=81; $R^2 = 0.896$.

This result corresponds to a generalized von Bertalanffy function with the parameter values

$$L_t \text{ (mm)} = 51.67 \, (1 - e^{-0.020 \, (t + 1.326)})^{0.828}. \tag{7}$$

Productivity

The annual P/B ratio was computed to be 0.046 y^{-1} by the mass-specific growth-rate method. From this, annual somatic production for the investigation site was estimated as

$$P = 0.046 \times 1.13 \text{ g AFDM} = 0.052 \text{ g AFDM m}^{-2} \text{ y}^{-1}. \tag{8}$$

DISCUSSION

Investigations of the type described here have not been conducted on polar brachiopods before, and are rare for brachiopods from anywhere in the world. Previously studies based on size-frequency distributions of populations have been reported for temperate intertidal species (Percival, 1944; Paine, 1963; Thayer, 1977), as well as for shallow subtidal (Doherty, 1979; Curry, 1982; Collins, 1991) and deep water brachiopods (Laurin & Gaspard, 1987). Stewart (1981) studied three species of articulate brachiopod from New Zealand and found maximum densities between 5 and 18087 ind m⁻². However, few of the above investigations assessed average population densities and none went on to calculate ecological parameters such as P/B ratios. In the following sections we will discuss our results on *Magellania fragilis* with emphasis on the ecological significance of this species and brachiopods in general.

Abundance and biomass estimates

The brachiopods visible on the photographs were counted several times, yet some specimens >5 mm length may have been missed. The low frequency of smaller size classes of *M. fragilis* in the trawl sample (Figure 3) may be caused by size-selective sampling. However, the shape of the size-frequency distribution does not show the rather steep increase in numbers in the 10–20 mm length range to be expected from the 10x10 mm mesh size (compare with figure 4 in Brey, 1991). Size selectivity may have been reduced by a certain amount of mesh clogging by sponges and other fine material, and by the fact that the brachiopods are attached to pebbles of various size. Size-

selective hand picking of brachiopods from the sample may be another source of bias, but it was carried out by carefully sorting small lumps of the trawled material. Abundance (26·15 ind m^{-2}) and biomass (1·13 g AFDM m^{-2}) may still be under-estimated slightly, but are likely to be close to the true values for this particular benthic site.

Growth

The von Bertalanffy growth function, L_t (mm) = 51·67 (1 - e$^{-0·020\,(t\,+1·326)}$)$^{0·828}$, is, to our knowledge, the first growth curve established for a brachiopod. However, there may still be doubt that this is a valid description of the growth of *M. fragilis*. We cannot prove that the growth bands have been formed annually, although there is much evidence that growth in those species depending directly on food input from the pelagic zone is extremely seasonal in the Antarctic (e.g. Clarke, 1988; Brey & Clarke, 1993; Brey et al., in press). Peck (1987) reported a 15–20% difference in metabolic activity between summer and winter, i.e. food and no food periods, in the brachiopod *Liothyrella uva* from Signy Island, southern Orkney Islands. These are all factors which would suggest the bands are annual. Errors are possible, however, as not every growth band on the shells was easily identifiable, and the amount of scatter in our data (Figure 4) indicates the possibility of misreadings. In addition to this the separation of adjacent bands became increasingly difficult with increasing shell size, which may have caused some underestimation of the number of bands in larger specimens.

Despite these uncertainties, we assume the above growth function to be representative for *M. fragilis*. The type of potential errors in this study would suggest that the removal of inaccuracies would result in an estimate of even slower growth, higher maximum age and lower productivity, if any changes were necessary. The present growth curve already indicates *M. fragilis* to be a rather slow-growing species, even compared to other Antarctic macrobenthic invertebrates (see Brey & Clarke, 1993).
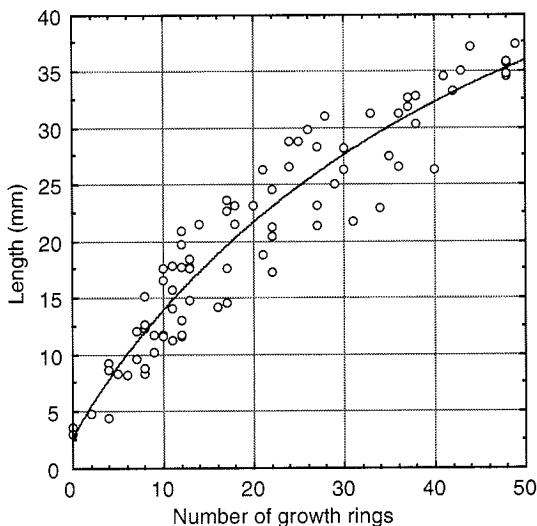

Figure 4. Length-at-age data from growth band readings and superimposed general von Bertalanffy growth function. L_t = 51·67 (1 – e$^{-0·020\,(t\,+1·326)}$)$^{0·828}$; N=81, r^2=0·896.
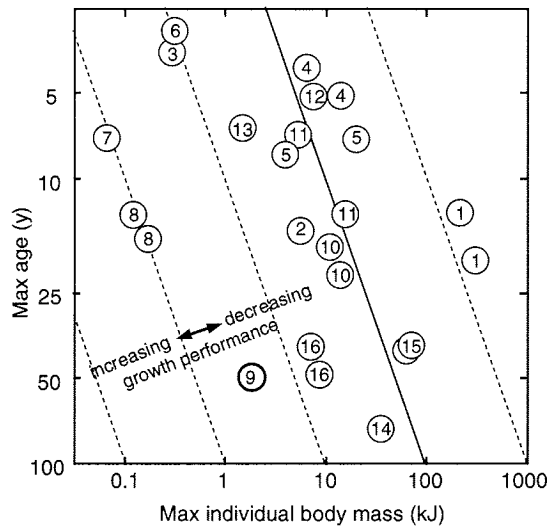
Figure 5. Growth performance in Antarctic macrobenthic species. Auximetric grid of $\log(1/A_{max})$ versus $\log(M_{max})$. Diagonal lines represent lines of equal growth performance, $\psi = \log(M_{max}/A_{max})$. Solid diagonal line represents $\psi = 0$. (1) *Adamusium colbecki*, (2) *Aega antarctica*, (3) *Ampicteis gunneri*, (4) *Bovallia gigantea*, (5) *Chorismus antarcticus*, (6) *Laevilacunaria antarctica*, (7) *Lissarca miliaris*, (8) *Lissarca notorcardensis*, (9) *Magellania fragilis*, (10) *Nacella concinna*, (11) *Ophionotus hexactis*, (12) *Philine gibba*, (13) *Serolis polita*, (14) *Sterechinus antarcticus*, (15) *Sterechinus neumayeri*, (16) *Yoldia eightsi*. Several species are represented by data from more than one population. For data sources see Brey & Clarke (1993) and Brey et al. (in press). For *M. fragilis*, the average conversion factor for benthic invertebrates (23·09 kJ g AFDM⁻¹) of Brey et al. (1988) was used.

Maximum age was 49 y in our sample (Figure 4) and body mass at this age was just above 92 mg AFDM.

Non-linear growth functions are not directly comparable, but Pauly (1979) and Moreau et al. (1986) proposed an index of growth performance based on the parameters K and L_∞ of the von Bertalanffy function to compare growth in different species. Using this index, Arntz et al. (1994) have already demonstrated that growth performance in Antarctic species is, on average, lower than in species from non-polar regions. Here we used a new index of growth performance $\psi = \log(M_{max}/A_{max})$ based on maximum body mass and maximum age observed in the population. This index is directly proportional to those developed by Pauly (1979), but does not require knowledge of the growth function parameters (Brey, unpublished data). Figure 5 shows all growth performance data of Antarctic species hitherto available (Brey & Clarke, 1993; Brey et al., in press) in an auximetric grid, i.e. a logarithmic plot of $1/A_{max}$ versus M_{max}. Besides the small bivalve *Lissarca*, the brachiopod *M. fragilis* exhibits the lowest growth performance of all species compared.

Productivity and mortality

The low growth performance and the left-skewed size-frequency distribution of *M. fragilis* points towards low productivity. Indeed, the annual somatic P/B ratio of 0·046 y⁻¹ is one of the lowest ever recorded for Antarctic benthic invertebrates; only the
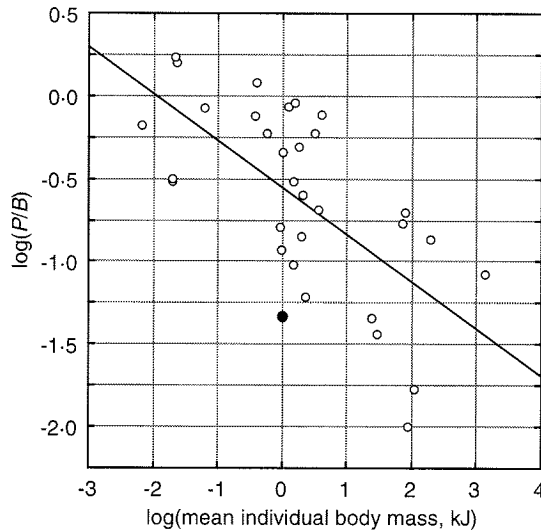
Figure 6. The annual somatic P/B ratio of *Magellania fragilis* (dot) compared with populations of other Antarctic macrobenthic species. For data sources see Brey & Clarke (1993) and Brey et al. (in press).

shallow water echinoderms *Sterechinus neumayeri* and *Odontaster validus* have been found with lower values, and these species are known to invest 75–90% of their annual production into gonads and not into body mass (Brey et al., in press; Dayton et al., 1974). The low P/B ratio of *M. fragilis* becomes even more evident if the relationship between body mass and productivity is taken into account (Figure 6).

The commonest type of population size-structure in brachiopods, and in benthic invertebrates in general, is a right-skewed one, with distributions dominated by juvenile or small individuals. This suggests a relatively constant mortality rate throughout the lifetime, i.e. the dominant mortality factors are size independent (James et al., 1992). Left-skewed size-frequency distributions as found in *M. fragilis* have also been observed in the only deep-water brachiopod studied so far (Laurin & Gaspard, 1987) and other benthic invertebrate populations (e.g. Sainsbury, 1982; Tudorancea & Florescu, 1969). They suggest either (i) very episodic recruitment events, or (ii) a relatively low mortality rate compared to growth rate, leading to high numbers of older animals in the larger size classes, or (iii) that mortality may be size dependent, and that size may form a refuge from the main mortality factors.

Ecological significance

The very low productivity of *M. fragilis* indicates that this species plays only a minor role in the energy flow through Antarctic benthic communities, despite its high frequency of occurrence and widespread distribution. It is only in those limited areas of extraordinarily high abundance and biomass, such as our investigation site, that it would contribute significantly to benthic consumption, respiration and production. However, these patches seem to be rare (Foster, 1974), and it is still unclear which physical and biological factors control their formation. During the last 10 y, many sites of

similar depth and bottom type have been encountered by RV 'Polarstern' in the Weddell Sea and adjacent areas, but they all lacked dense assemblages of *M. fragilis*. It also remains unclear if the absence of the otherwise common hexactinellid sponges at the sampling site may indicate negative interactions between these sponges and the brachiopods.

Our data indicate that *M. fragilis* exhibits a low-energy lifestyle typical of most brachiopods (Peck, 1992), primarily because of their very low metabolic rates (Shumway, 1982; Peck et al., 1986a,b, 1987, 1989b; Thayer, 1986), their low clearance rates while feeding (Rhodes, 1990; Rhodes & Thompson, 1992, 1993), the laminar flow and low speed of water movement through the mantle cavity during normal ventilatory activity (LaBarbera, 1981, 1984, 1990), and their common occurrence in habitats with low energy supply such as caves (Jackson & Winston, 1982; Jackson et al., 1971). This concept has been implicated as important for other aspects of brachiopod lifestyle including reproduction (Law & Thayer, 1990). Peck (1992) suggested that energy budgets were constrained because of the requirement for a large mantle cavity caused by the architecture of the lophophore. It was argued that the need for a large mantle cavity constrained mantle thickness, which contributed to the evolution of a low energy lifestyle by enhancing the importance of metabolic efficiency. One consequence of the low metabolic rates of articulate brachiopods is that they can survive long periods of starvation and are successful in areas with low or highly seasonal energy supply, typified by the present study site in the Lazarev Sea (James et al., 1992; Peck, 1992).

The low productivity and overall low abundance and biomass of *M. fragilis* also indicate that this species provides only little food for potential predators, which may be echinoderms (Fouke & LaBarbera, 1986), fish (Witman & Cooper, 1983) or gastropod molluscs (James et al., 1992). Even from the dense assemblage investigated here, predators could harvest only a maximum of 0.052 g AFDM m^{-2} y^{-1}, assuming the population remains in steady state.

Low predation pressure is assumed to be a general characteristic of articulate brachiopod populations and may be related to several features. Brachiopods have often been viewed as containing only small amounts of organic matter for their size, and were described as being 'relatively small organisms inhabiting large shells' by Curry & Ansell (1986). There is also some evidence to suggest that the energy contents of brachiopod dry tissues are significantly lower than those of bivalve molluscs (Peck, 1993). Articulate brachiopods have been shown to have large amounts of organic material located in the shell. Values of around 40% of total animal organic content were found by Curry et al. (1989), but this may range as high as 80% for small specimens in some species (Peck et al., 1989a). In punctate brachiopods much of this organic content is thought to be located in mantle extensions which traverse the shell, the caeca. The caeca contain cellular metabolizing tissue and play a role in the storage and mobilization of reserves; however, their function is not fully understood. The location of this tissue in the shell means that it is not readily available to predators. Combining this with the low organic content of brachiopod tissues (AFDM is only 6·5% of DM in *M. fragilis*), means that the returns for predators feeding on them are small. It is then surprising that when the costs to predators of gaining access to the tissues via drilling or crushing shells are compared to the returns obtained, brachiopods and bivalve mol-

luscs have similar values as prey items (Peck, 1993). However, other factors, such as the dispersed nature of brachiopod tissues, the very large mantle cavity and the low energy content per unit ash-free dry mass still militate strongly against brachiopods being consumed by predators. Another factor which has recently been proposed as being important in predation avoidance by brachiopods is the use of chemical defences (Thayer & Allmon, 1991; McClintock et al., 1993). However, more work is clearly needed before the reasons for the observed low levels of predation on articulate brachiopod populations can be fully understood.

In conclusion, *M. fragilis* seems to exhibit the typical life history strategy of articulate brachiopods, which is a combination of low energy lifestyle and low food value for predators. The combination of these two features enables them to succeed in typically low food environments such as the deep-sea or the Antarctic Ocean, which are also characterized by a high proportion of mobile, trophically generalistic and scavenging species (see e.g. Arntz et al., 1994; Gage & Tyler, 1991; Jumars & Gallagher, 1982).

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