

Growth and age of the Antarctic bryozoan *Cellaria incula* on the Weddell Sea shelf

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Abstract: We analysed growth of the arborescent Antarctic cheilostome bryozoan *Cellaria incula* by stable carbon and oxygen isotope analysis. The growth of one complete branch of *C. incula* takes one year, i.e. owing to the bifurcate colony structure two new branches grow from each branch of the previous generation. The maximum age of a *C. incula* colony is likely to be more than 14 years. Annual production-to-biomass ratio is 0.67, the highest value hitherto measured for any benthic invertebrate south of 62°S. Comparatively fast growth and high productivity identify *C. incula* as a pioneer species which is able to quickly occupy spatial niches produced by iceberg scouring on the Antarctic shelf.

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Introduction

The cheilostome bryozoan genus *Cellaria* is common on the Weddell Sea shelf and slope (at 53% of all trawl stations, Zabala *et al.* 1997; and at 54% of all underwater photo stations, Gutt & Starmans 1998). Four species of *Cellaria* have been recorded in the Weddell Sea to date, among which *Cellaria incula*, Hayward & Ryland 1993 seems to occur in rare but dense patches (Zabala *et al.* 1997).

Cellaria incula shows arborescent growth, i.e. each colony branch (i.e. internode) bifurcates into two new branches. The nodes between subsequent branches consist of organic ligaments only, thus allowing a certain structural flexibility for the colony. Branches are of the non-maculate radial type (McKinney 1986) and consist of 7 to >30 alternating whorls of four zooids each, depending on branch length (Fig. 1, see also Hayward 1995).

In shelf areas disturbed by iceberg grounding, *Cellaria* is a typical pioneer taxon (Gutt *et al.* 1996). The effects of iceberg scouring on the Antarctic shelf fauna are well documented (Gutt *et al.* 1996, Gutt & Starmans 1998), but the dynamics of the recolonization process are poorly understood. One of the major problems is the lack of information on growth, age and reproduction of the pioneer taxa which initially colonise the denuded areas.

Methods

Sampling

We used 54 multibox corer samples collected during the RV *Polarstern* expeditions ANT VI/3, ANT VII/4 and ANT IX/3 between 1987 and 1991 in the Weddell Sea (Gerdes 1990, Gerdes *et al.* 1992, Brey & Gerdes 1998) to determine bryozoan biomass. An average factor of 0.07 (Brey *et al.* 1998, Ricardi

& Bourget 1998, this study) was applied to convert wet mass to ash free dry mass (AFDM). So far the bryozoan fauna of these samples has not been analysed taxonomically.

The share of *Cellaria* spp. in total bryozoan cover of the sediment surface was estimated from underwater still photographs taken at 46 stations (2818 m² in total) above 1000 m water depth during the expeditions ANT III, ANT VI/3, ANT VII/4 and ANT IX/3 between 1985 and 1991 (Gutt & Starmans 1998). We combined these data with bryozoan biomass to derive an estimate of *Cellaria* spp. biomass.

For morphometric analysis and stable isotope measurements we used colonies of *Cellaria incula* collected by Agassiz trawl during the expedition ANT V/3 (1986/87) at two stations in the Weddell Sea, station 508 (72°49.2'S, 19°29.9'W, 535 m) and station 561 (72°52.5'S, 19°39.2'W, 433 m).

Morphometric relationships

Relationships between branch length, number of zooid series and branch mass were based on 10 samples. Dry mass (DM) was determined after drying for 24 h at 60°C, ash content after 24 h at 500°C. Ash free dry mass (AFDM) is the difference between DM and ash.

Growth analysis

Cheilostome bryozoans of the genus *Cellaria* precipitate a calcareous skeleton consisting mainly of calcite (Bader *in press*, Wefer & Berger 1991). The ratio of the stable oxygen isotopes ¹⁸O and ¹⁶O ($\delta^{18}\text{O}$) in the skeletal carbonate depends on seawater isotope composition, temperature (high T → low $\delta^{18}\text{O}$; low T → high $\delta^{18}\text{O}$) and salinity (low S → low $\delta^{18}\text{O}$; high S → high $\delta^{18}\text{O}$) during shell deposition. The ratio of the stable carbon isotopes ¹³C and ¹²C in shell carbonate of benthic

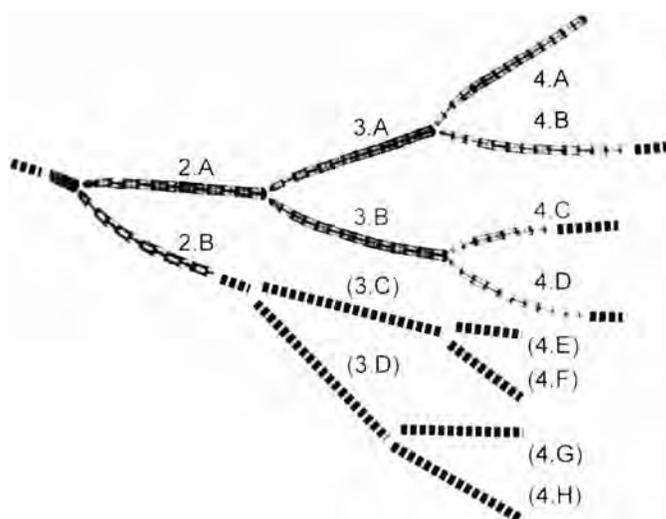


Fig. 1. X-ray photograph of one *Cellaria incula* colony fragment indicating the arborescent growth pattern of this species. Branch generations are indicated by numbers (1, 2, 3, 4). Stippled lines indicate missing branches. Total length of the fragment is about 15 mm. Note that branch no. 1 is not necessarily the first branch of the complete colony.

invertebrates depends mainly on changes in $\delta^{13}\text{C}$ of seawater bicarbonate mediated by primary production. Phytoplankton enriches ^{12}C during growth and hence degradation of sedimented matter results in isotopically lighter carbonate in near bottom water (Emrich *et al.* 1970, Krantz *et al.* 1987). Therefore $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ can be used to analyse seasonality of growth in living or fossil calcareous species (see Forester *et al.* 1973, Krantz *et al.* 1987, Wefer & Berger 1991).

For isotope analysis (IARMS), branches of *C. incula* were cleaned of organic matter by incubation in NaOCl solution (Forester *et al.* 1973), rinsed with water and dried. We cut a branch into subsequent slices of about 0.5–0.7 mm length using a scalpel. Each sample was weighed and reduced to 100–150 μg mass by cutting off small parts at both ends.

Stable oxygen and carbon isotopes of these samples were measured with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. The precision of measurements is better than $\pm 0.06\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.08\text{‰}$ for $\delta^{18}\text{O}$, respectively, based on routine measurements of a laboratory working standard. Data are related to the Pee Dee belemnite (PDB) standard through repeated analyses of National Bureau of Standard (NBS) isotopic reference material 19 (Hut 1987).

Results

Morphometric relationships

The dry mass of *C. incula* consists of 5.8% organic matter (AFDM) and 94.2% ash. Average length of one branch is 8.17 mm ($s d = 1.81, n = 296$) corresponding to 15.4 series of

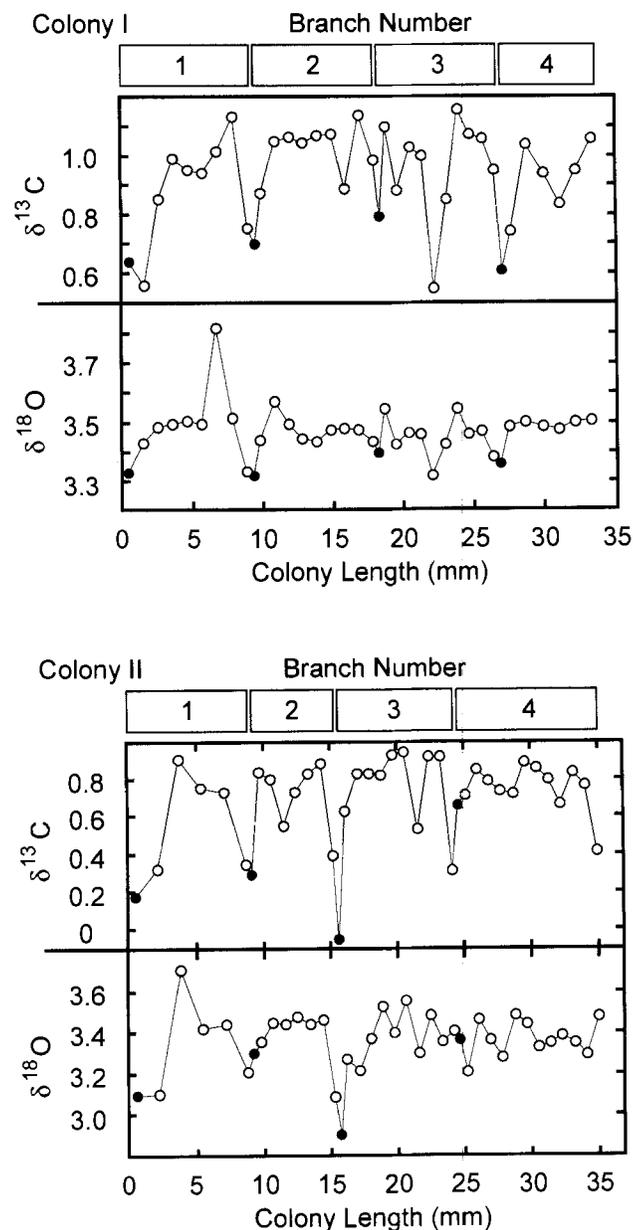


Fig. 2. Stable isotope ratios along four subsequent branches of each of two different *Cellaria incula* colonies. Dots indicate first sample of each branch.

zooids, 62 zooids, 161 μg AFDM and 2612 μg ash.

Growth

The X-ray photograph in Fig. 1 shows the arrangement of branches in a *C. incula* colony fragment. The largest fragment found consisted of 14 subsequent branch generations. Neither surface examination nor X-ray photography revealed any kind of growth band structures in the branches of *C. incula*.

To check whether *C. incula* stable isotope profiles show any regular patterns, isotopes were measured along four subsequent branches of two colony fragments. The analysis

revealed a distinct isotope ratio pattern (Fig. 2). Both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ tend to be lowest at the beginning and at the end of a branch, albeit $\delta^{13}\text{C}$ shows this pattern more clearly than $\delta^{18}\text{O}$ does. Only one sample from the middle of a branch shows isotope ratios as low as the terminal samples (Fig. 2, colony I, branch 3).

The question whether different lengths of "parallel" branches (branches originating from one bifurcation) result from differences in growth rate or from differences in age was analysed by comparing carbon isotope profiles of two sets of

parallel branches. We plotted the isotope profiles of parallel branches according to absolute sampling position (mm length) and according to relative sampling position (% total length, Fig. 3). In both plots the distance between the two curves was measured at equally spaced points along the isotope profile of the shorter branch (colony I: 37 measurements, colony II: 49 measurements). The average distance between the two curves was significantly (ANOVA, $P=0.05$, $n=86$) smaller (0.138 units of $\delta^{13}\text{C}$) when using relative sampling position compared to absolute sampling position (0.178 units of $\delta^{13}\text{C}$), indicating that parallel branches of different length grew in the same time interval, and hence with different rates. The branch set (I and II in Fig. 3) showed no significant effects.

To analyse statistically whether isotope ratios are consistently lower at the branch ends, 133 isotope measurements referring to 12 branches of *C. incula* were normalised with respect to branch average, pooled and sorted into 11 intervals of relative branch length (0–5%, 5–15%,

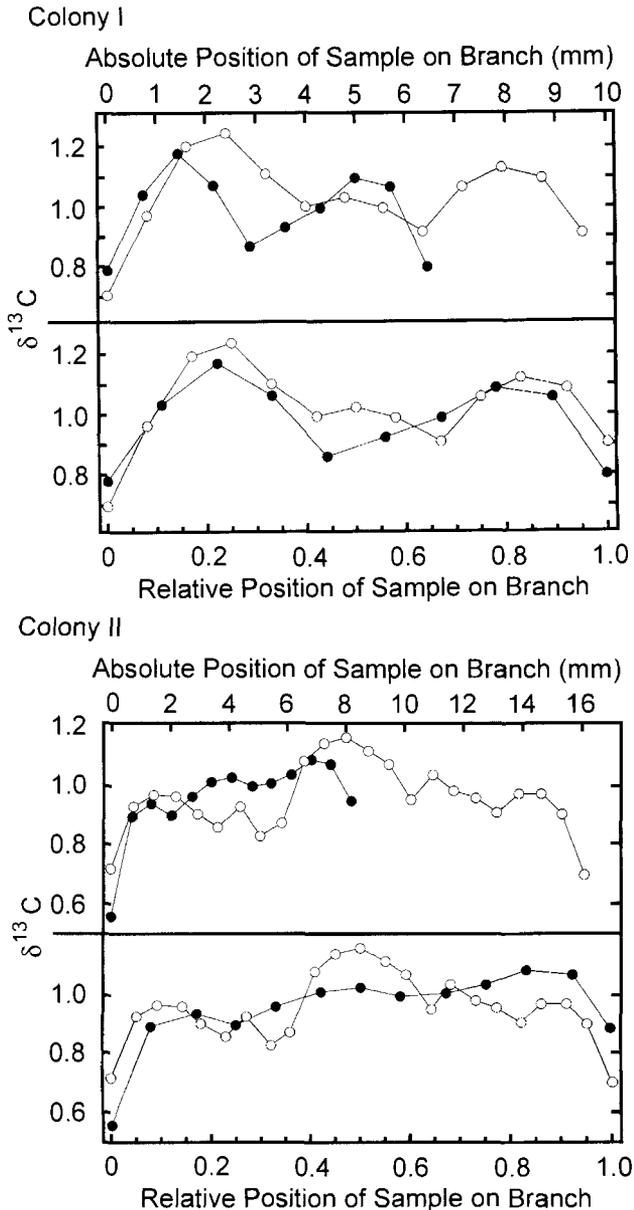


Fig. 3. Stable isotope ratios along parallel branches (A and B according to Fig. 1) of different length (dots = shorter branch, circles = longer branch). Data are plotted corresponding to absolute branch length (mm, upper graph) and to relative branch length (% , lower graph).

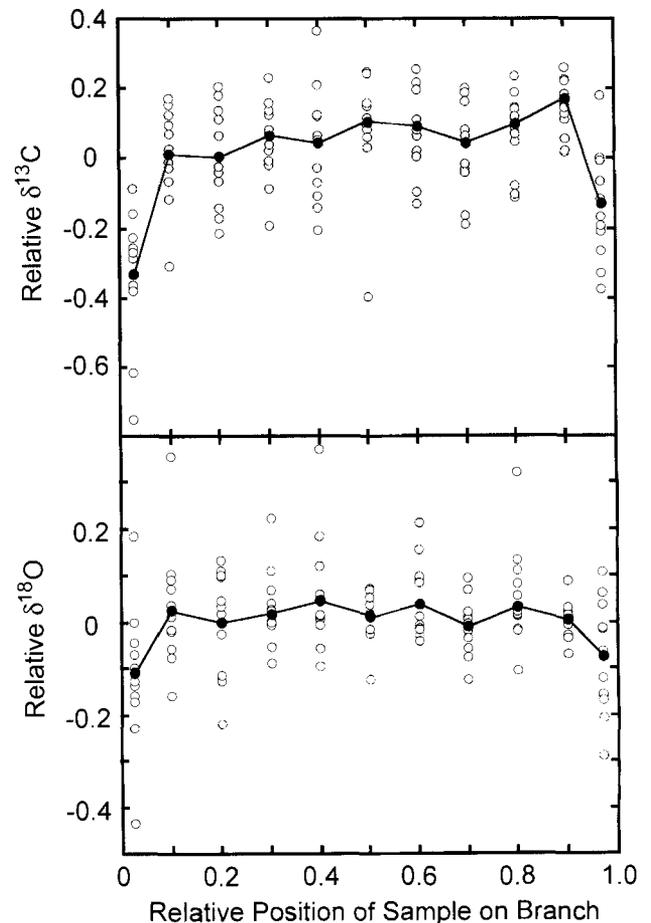


Fig. 4. Stable isotope ratio versus sample position in *Cellaria incula* (133 measurements, 11 branches, 3 different colony fragments). Relative isotope ratios: measured value minus average value of branch. Relative position: Branch length divided in 11 intervals (0–5, 5–15, ..., 85–95, 95–100%). Dots represent average relative isotope ratio per branch interval.

85–95%, 95–100%, see Fig. 4). An ANOVA of the Box-Cox transformed data with subsequent Games-Howell post-hoc test of means (Sokal & Rohlf 1995) revealed no significant differences in $\delta^{18}\text{O}$ among branch intervals. However, $\delta^{13}\text{C}$ was significantly lower in the 0–5% interval ($\alpha = 0.05$) as compared to all intervals except the terminal 95–100% interval, and significantly ($\alpha = 0.05$) lower in the 95–100% interval compared to the 25–35%, 55–65%, 75–85% and 85–95% intervals.

Length of branch n and length of the subsequent branch $n+1$ of *C. incula* are only weakly correlated (geometric mean regression acc. to Ricker (1973): $L_{n+1} = 0.415 + 0.966 \cdot L_n$; $r = 0.234$, $P = 0.053$, $n = 69$). Branch $n+1$ is on average of the same length as branch n , but variability in this relationship is high.

Productivity

Based on the above results - one new generation of branches per year (i.e. $N_{br+1} = 2 \cdot N_{br}$) and average branch mass of 161 μg AFDM and 2612 μg ash, a model of colonial growth can be established. The increase in colony mass with time is exponential. Production, i.e. new growth, doubles each year, and hence annual production-to-biomass ratio (P/B ratio) approximates 0.67 yr^{-1} after about six generations (Fig. 5).

Biomass and production

Few bryozoans are found below 1000 m water depth (Fig. 6). From average bryozoan biomass (multibox corer: 679 mg AFDM m^{-2} , range: 0–14 099 mg) and the share of *Cellaria* spp. in sea bottom cover by bryozoans (underwater still photographs: *Cellaria* = 4.4% of all bryozoa, range: 0–61%) average biomass of *Cellaria* spp. is estimated to be

30 mg AFDM m^{-2} . Provided that the P/B ratio of 0.67 yr^{-1} computed for *Cellaria incula* is approximately similar to other Antarctic *Cellaria* species, annual production of *Cellaria* spp. amounts to about 20 $\text{mg AFDM m}^{-2} \text{ yr}^{-1}$ which is equivalent to about 10 $\text{mg C m}^{-2} \text{ yr}^{-1}$.

Discussion

Growth

The carbon isotope profiles analysed (Figs 2 & 4) clearly indicate that branch growth of *C. incula* starts during one period of low $\delta^{13}\text{C}$ (high primary production) and is completed during the next period of low $\delta^{13}\text{C}$. In the Weddell Sea, peak primary production and sedimentation are restricted to a short period in summer (Bodungen *et al.* 1986, Bathmann *et al.* 1991). Hence we can conclude that in *C. incula* one generation of branches represents one year of growth, although some branches may grow for two years (see Fig. 2, colony I, branch 3).

The $\delta^{18}\text{O}$ profiles show a similar pattern, but less distinct than $\delta^{13}\text{C}$ (Fig. 4). This may be caused by the small annual temperature range (-1.8°C to -1.0°C , Arntz *et al.* 1992) as well as the short-term variability in hydrodynamic conditions on the Weddell Sea shelf. Here, the interaction of different water masses and currents affects water temperature and salinity (Fahrbach *et al.* 1992, Helmer & Bersch 1985).

As indicated by the $\delta^{13}\text{C}$ profiles (Fig. 4), the larger part of each branch of *C. incula* is formed during periods of low overall primary production (high $\delta^{13}\text{C}$), i.e. this bryozoan seems to grow when food is rare. The distinct seasonal peak in phytoplankton biomass and production is formed by

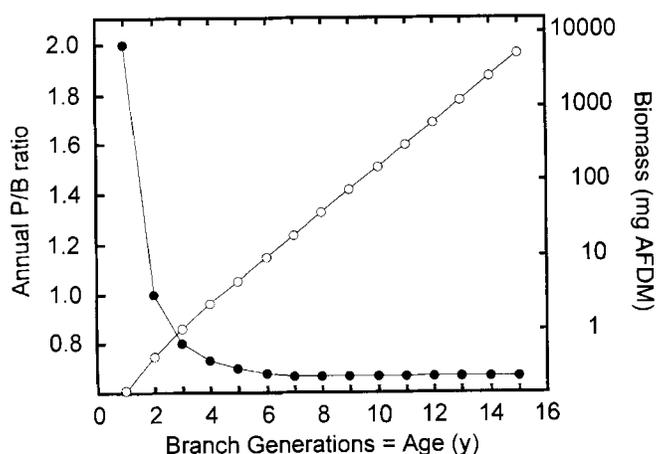


Fig. 5. Growth model of a *Cellaria incula* colony. Parameters: 161 μg AFDM average branch mass (Total DM = AFDM \cdot 17.24), one generation of branches per year. Circles: Biomass at end of year, Dots: P/B ratio = New production/average biomass.

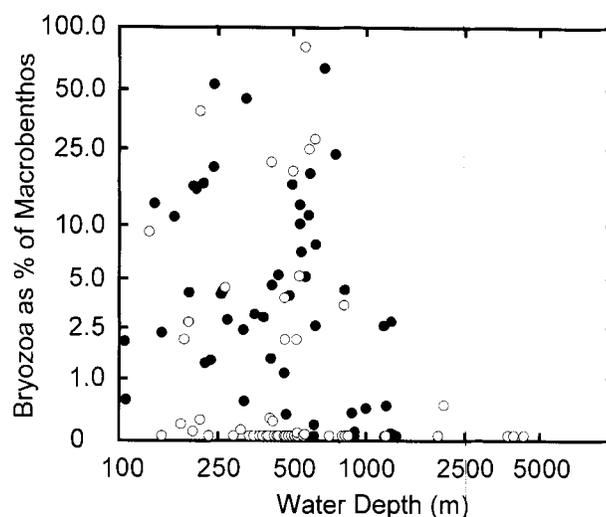


Fig. 6. Share of bryozoans in the Weddell Sea and Lazarev Sea benthos. Circles = AFDM of bryozoans in % of total macrobenthic AFDM (data from 54 multibox corer sampling stations). Dots = % coverage of sediment surface by bryozoans (data from 55 underwater photo sampling stations).

microplankton (>20 μm , Bodungen *et al.* 1986, Smetacek *et al.* 1990). Sedimentation and subsequent release of isotopically lighter CO_2 during degradation of this material induces the $\delta^{13}\text{C}$ signal in the bryozoan skeleton carbonate.

Most bryozoans, however, are assumed to feed on particles < 20 μm , i.e. nanoplankton (Winston 1977, Winston & Heimberg 1986) and not on the larger microplankton cells. Nanoplankton biomass and production is about 10% of total phytoplankton (Rivkin 1991), and its availability is much less seasonal than microplankton availability, as indicated by year-round data from Signy Island (Barnes & Clarke 1994, 1995) and McMurdo Sound (Rivkin 1991). Information on nanoplankton seasonality in the south-western Weddell Sea is limited, but autotrophic as well as heterotrophic nanoplankton seems to be present throughout the year (Detmer & Bathmann 1997, Hewes *et al.* 1990, Smetacek *et al.* 1990), even in areas covered with sea ice (Garrison *et al.* 1993). This may enable *C. incula* to feed and grow for several months of the year, as observed in a number of bryozoan species at Signy Island (Barnes 1995, Barnes & Clarke 1994, 1995), provided the plankton is transported down to shelf depths by vertical mixing.

The largest colony fragment found in our samples consisted of 14 subsequent branches; thus, maximum attainable age of *C. incula* is likely to be >14 yr. *Cellaria incula* grows much more slowly (about 8 mm branch length yr^{-1}) and reaches a much greater age than the only boreal *Cellaria* species investigated to date, *Cellaria sinuosa* from the English Channel. This species attains a maximum age of about two years and grows at a rate of 40 mm branch length yr^{-1} (Bader in press). *Cellaria incula* does not get exceptionally old, however, when compared to other Antarctic bryozoans, i.e. *Cellariella watseri* (9 yr) and *Alloeflustra tenuis* (26 yr) from Signy Island (Barnes 1995) or *Meliceria obliqua* (50 yr) from the Weddell Sea (Brey *et al.* 1998).

Production and productivity

Annual P/B ratio of *C. incula*, 0.67, is distinctly higher than in other high-Antarctic tentaculates, the brachiopod *Magellania fragilis* (0.05 yr^{-1} , Brey *et al.* 1995a) and the bryozoan *Meliceria obliqua* (0.10 $^{-1}$, Brey *et al.* 1998). Actually, this P/B ratio is the highest one measured so far for any benthic invertebrate south of 62°S (Fig. 7). The production model established above (Fig. 5), however, is rather simplistic, because it assumes

- i) that all distal branches grow synchronously,
- ii) branch length does not change with age (although our data do not indicate the opposite, see Fig. 5), and
- iii) there is no loss caused by hydrodynamic damage or by predators.

Hence it is unrealistic to believe that *C. incula* may grow indefinitely with the rate observed here. It is more likely that

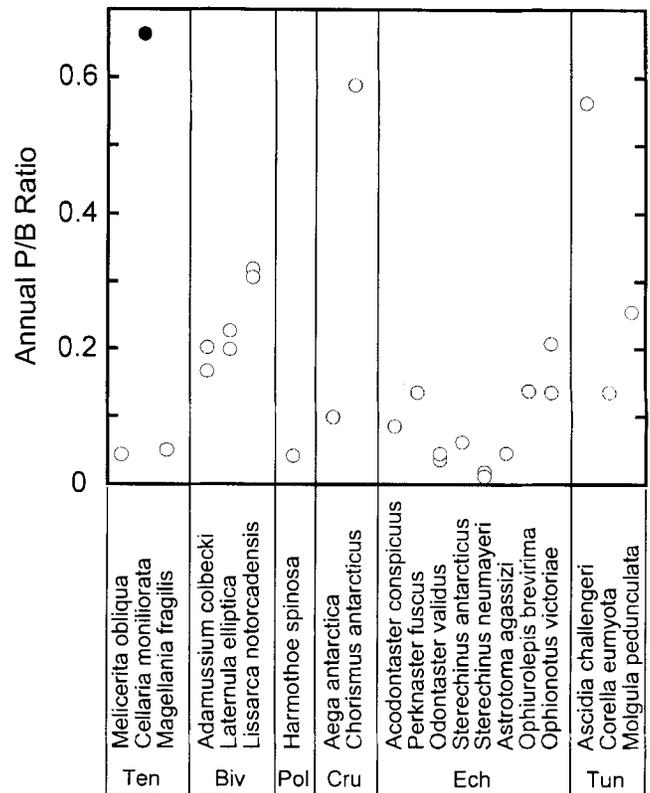


Fig. 7. Annual somatic P/B ratio of Antarctic benthic invertebrates from locations south of 62°S. Ten = Tentaculata, Biv = Bivalvia, Pol = Polychaeta, Cru = Crustacea, Ech = Echinodermata, Tun = Tunicata. Data from Brey & Clarke (1993), Brey *et al.* (1995a, 1995b), Dahm (1995), Gorny *et al.* (1993), Kühne (1997), Stiller (1995), Urban & Mercuri (1998).

population P/B ratio will decrease when a dense stock of *C. incula* reaches some kind of maturity. Intraspecific competition for space and food may play a significant role in this development. As to be expected from the differences in growth rate, the P/B ratio of the boreal *C. sinuosa* is distinctly higher and ranges between 0.74 and 1.19 yr^{-1} (calcification rate is 100 to 160 mg per year per colony, Bader in press; average colony mass is 135 mg, Bader personal communication 1998).

In terms of the whole Weddell Sea and upper slope (100–1000 m), the genus *Cellaria* is an insignificant member of the macrobenthic community, contributing about 0.1% to total macrobenthic biomass and about 0.4% to macrobenthic production (see Brey & Gerdes 1998). Hence probable errors in the estimate of average *Cellaria* biomass (see above) are rather irrelevant. Our data indicate, however, that bryozoans in general are very patchily distributed (Fig. 6) and that the share of *Cellaria* spp. in the bryozoans is highly variable (0–61%). Therefore *Cellaria* can play a more significant role locally, as indicated by Gutt *et al.* (1996), who found this genus to dominate the bryozoan fauna in iceberg scours (Gutt & Starman 1998). Unfortunately, multibox corer sampling and photo surveys have been carried out simultaneously at six

stations only, and therefore we cannot quantify biomass and production of *Cellaria* for each station separately.

Colonization potential

Pioneer species are generally characterized by more or less permanent recruitment potential, the ability for wide dispersal of recruits, fast growth, high P/B ratio, and early maturity (e.g. Grassle & Grassle 1974, Gray 1981, Levin 1984). We cannot quantify the potential of *C. incula* for rapid initial colonization of areas defaunated by icebergs, because neither seasonality and amount of reproductive output nor dispersal characteristics of recruits are known. Embryo carrying colonies, however, have been observed frequently in the Weddell Sea during summer (Zabala *et al.* 1997). After initial settlement the comparatively high growth rate and P/B ratio enable *C. incula* to occupy the space available very rapidly. Rapid growth is correlated with early maturity and reproduction in general (e.g. Banse & Mosher 1980), and hence secondary settlements of embryos produced by the initial colonizers may accelerate the occupation process. Growth rate and P/B ratio of *C. incula* may not be impressively high when compared to typical pioneer species of boreal soft bottoms such as spionide polychaetes (e.g. Gudmundsson 1985, Levin 1984, Santos & Bloom 1983), but obviously they are sufficient to out-compete many other Antarctic benthic species in initial colonization processes.

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