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Growth and carbonate production by *Adeonellopsis* (Bryozoa: Cheilostomata) in Doubtful Sound, New Zealand

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Abstract

The erect arborescent bryozoan *Adeonellopsis* sp. is an important component of the attached fauna on rock faces in Doubtful Sound, New Zealand. A program of marking and harvesting, radiocarbon dating, and morphometric study was undertaken to determine age, growth rate, and carbonate production rate of these colonies. Data from 40 branches on each of five colonies show a growth rate of 6.9 mm/yr in branch length. Colony growth rate varied, with 71% of growth (5 mm per branch) occurring from mid-summer and to mid-winter, and 29% (2 mm per branch) from mid-winter to late summer. Since proximal secondary thickening is common in adeoniform species, and occurs in *Adeonellopsis*, additional carbonate may be precipitated annually by this means. The largest colonies found in Doubtful Sound, some up to 30 cm in diameter, may be as much as 20 yr old, and precipitate calcium carbonate at a rate of 24 g $CaCO_3$/yr. At Bauza Island, where our study was carried out, population densities of one large colony/m produced carbonate at a rate of 24 g $CaCO_3/m^2/yr$; maximum theoretical density could produce carbonate at 1042 g $CaCO_3/m^2/yr$. Carbonate produced at these rates would accumulate in sediments at 4–174 cm/kyr, reasonable rates for temperate carbonates. *Adeonellopsis* provides substrate for epizoa and hiding places for motile organisms. They form a potentially important fiord microhabitat, and their longevity allows both more ephemeral organisms and young longer-lived colonies to grow under their protection.

Keywords: Bryozoa; calcification; growth rate; New Zealand

1. Introduction

The erect, robust-branching bryozoan *Adeonellopsis* is a large conspicuous subtidal species found throughout New Zealand (Nelson et al., 1988). Initially all New Zealand members of the Adeonidae (Gymnolaemata: Cheilostomata: Ascophorina) were classified as *Adeonellopsis yarraensis* (e.g. Gordon, 1984, 1986), but it is now clear that at least five morphologically similar *Adeonellopsis* species occur in New Zealand and Australian waters (Lidgard and Buckley, 1994).

The *Adeonellopsis* species which occurs in Doubtful Sound, Fiordland in southwestern New Zealand is probably morphospecies B of Lidgard and Buckley (1994). Colonial growth begins with a small encrusting spot which sprouts a

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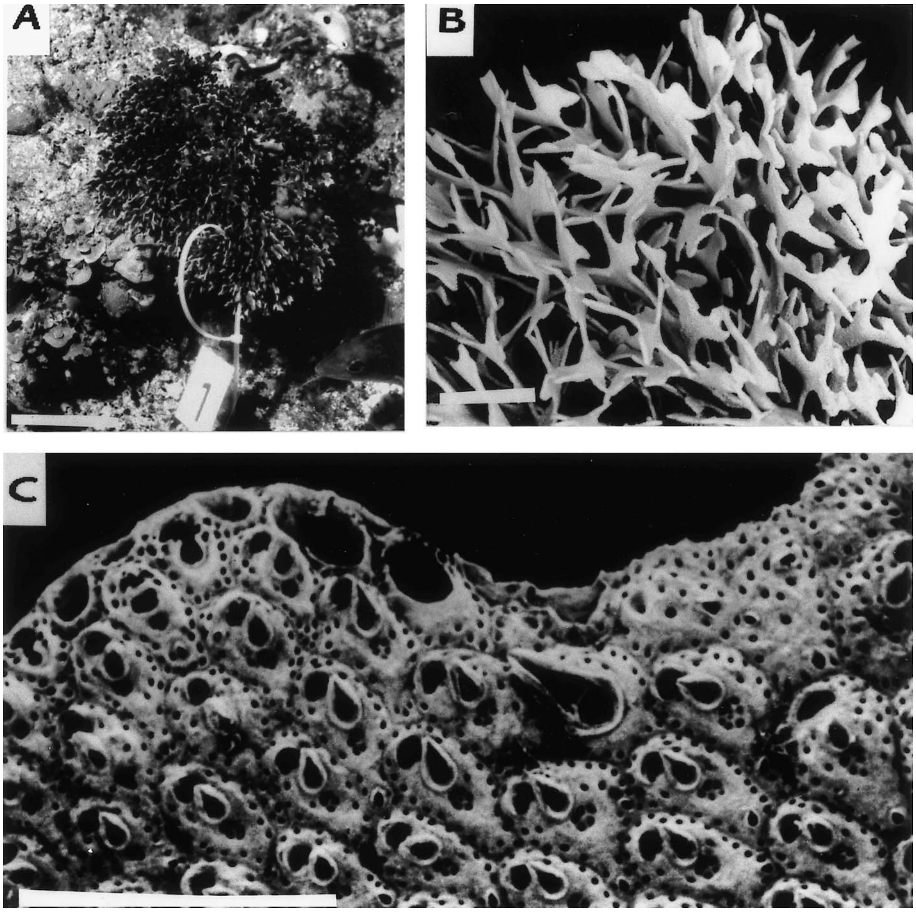

Fig. 1. *Adeonellopsis* sp. from Doubtful Sound, New Zealand: (A) living colony in situ on the wall of Bauza Island in 12 m water depth (scale = 5 cm); (B) bleached and dried colony (scale = 1 cm); (C) scanning electron micrograph showing zooid characteristics (scale = 1 mm).

bilaminar sheet. Branches grow and fork, forming a fairly dense bush-like colony some 20–30 cm high (Fig. 1A). The branches are flattened, about 3–6 mm wide, and bluntly rounded at the tips (Fig. 1B). Individual zooids show the ornateness typical of ascophorine cheilostomes; they are diamond-shaped, about 0.5×0.25 mm in size, with various pores, avicularia and concavities on the frontal wall (Fig. 1C).

Adeonellopsis species mainly precipitate aragonite with 0–11 (mean 3.1) wt% calcite (Smith et al., 1998). The calcite contains on average about 6 wt% $MgCO_3$, which is relatively high for New Zealand bryozoans (Smith et al., 1998). Much of this carbonate deposition occurs as (possibly secondary) calcification toward the colony bases (Cheetham, 1986). Extrazooidal thickening toward the colony bases results in the eventual occlusion of the entire zooidal frontal surfaces (Lidgard and Buckley, 1994; Lidgard, 1996). This increasing secondary calcification results in stronger colonies able to resist breakage; young adeoniform colonies have been shown to withstand current as rapid as 3 m/s (Cheetham et al., 1981; Cheetham, 1986).

In Doubtful Sound, the purplish–black colonies of *Adeonellopsis* can be found growing in reasonably exposed areas on the steeply sloping rock walls near the entrance of the fiord. These rock walls are home for a diverse range of encrusting organisms; *Adeonellopsis* is one of the more prominent (see Fig. 1A). Its arborescent bilaminate growth form provides numerous interstices for attached epifauna.

Doubtful Sound is a temperate fiord on the west coast of South Island, New Zealand. It extends 33 km from Deep Cove to its mouth at the Tasman Sea and has a number of significant side branches (Fig. 2). As with other fiords in the region, Doubtful Sound is steep sided and deep, reaching a maximum depth of 434 m, but with a shallow sill of 40–60 m protecting the entrance. The region receives very high rainfall, as much as 8000 mm/yr, as a result of the prevailing moisture-laden westerly winds blowing off the Tasman Sea. The rainwater accumulates humic substances as it percolates through the catchment's forest and creates a darkly stained low salinity layer on the surface of the fiord. This layer, up to 10 m thick depending on rainfall, filters out much of the light striking the surface of the fiord. Coupled with low current and minimal wave action, the low light conditions mimic deepwater conditions and enable usually deepwater and cryptozoic species to live at SCUBA-accessible depths. *Adeonellopsis* is not common within Doubtful Sound, but in some localized areas, such as around Bauza Island (Fig. 2), colonies may be found at depths from 10 to 25 m at densities ranging from 0.01 to 1 colonies/m^2.

As is the case with most bryozoans, age, growth, and carbonate production rates of *Adeonellopsis* are unknown. While non-colonial organisms often have an upper limit to their age, which may be determined fairly easily using population dynamic theory, colonies, which add more and more genetically identical individuals to a single structure, may theoretically live forever (Palumbi and Jackson, 1983). This 'clonal building block' strategy means that individuals live and die but the colony itself can grow and thrive. Size of a colony is thus not a good indicator of age. A better estimate of age and growth rate is important in understanding fiord benthic ecology, development and succession; life history and evolution of the Bryozoa; and productivity both in the benthic food web and of skeletal carbonate, which later may become sediment and eventually limestone.

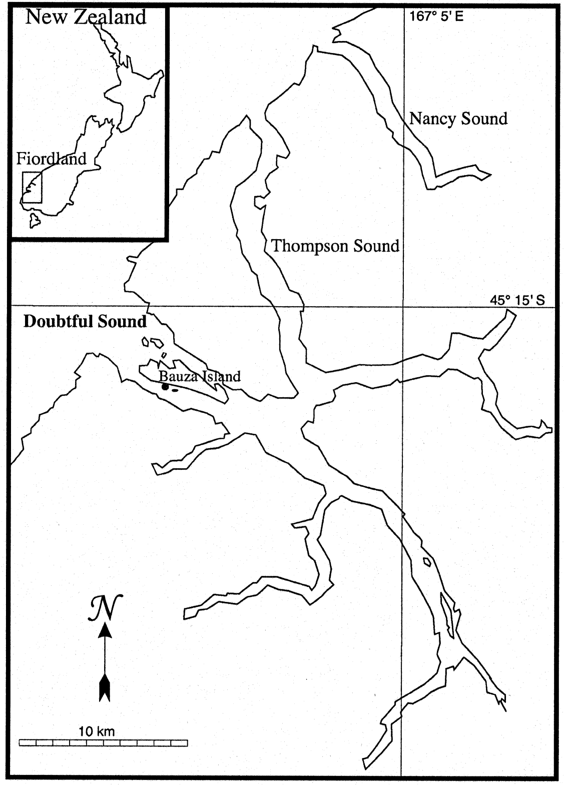

Fig. 2. Location map of Doubtful Sound in western South Island, New Zealand: New Zealand; Doubtful Sound, with study site near Bauza Island marked.

The most direct ways to ascertain colony growth rates are by laboratory culture and in situ observation. Both are problematic. Bryozoans are generally difficult to culture, and large, long-lived species have never been maintained in the laboratory for more than a few weeks. Large complex erect zoarial growth forms are difficult to assess using photogrammetry or in situ measurement, and breakage during handling is common. We have, therefore, taken three indirect but independent tactics for quantifying growth rate and carbonate productivity: marking and recapture, radiocarbon dating, and morphological analysis. Taken together, they enable us to characterize growth and carbonate production of *Adeonellopsis* in Doubtful Sound.

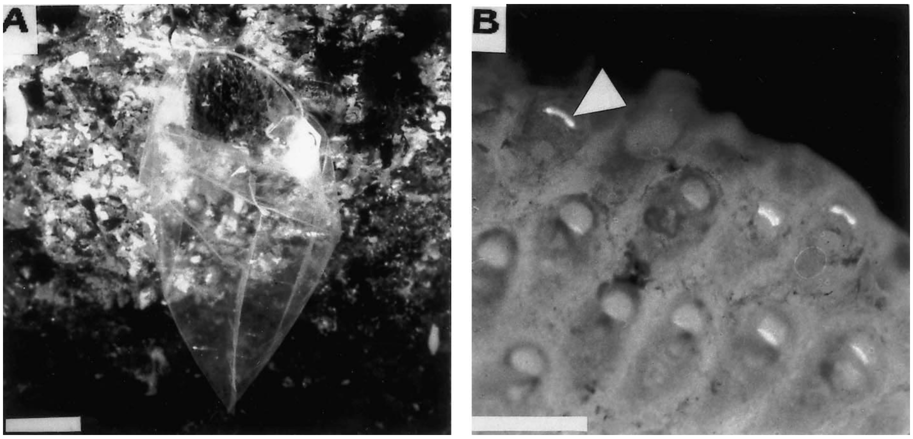

Fig. 3. Staining with calcein: (A) in the field, a plastic bag is anchored over a single colony of *Adeonellopsis* (scale = 4 cm); (B) fluorescent bands (arrowed) in zooid carbonate of an *Adeonellopsis* colony collected 24 h after staining (scale = 0.5 mm).

2. Methods

2.1. Marking and recapturing

Tetracycline hydrochloride and calcein (2,4-bis-[*N*,*N*′-di-(carbomethyl)-aminomethyl]fluorescein) have both been used successfully to 'tag' the calcified elements of a variety of live organisms, including fish (Tsukamoto, 1988; Wilson et al., 1987), brachiopods (Rowley and McKinnon, 1995) and echinoderms (Stump and Lucas, 1990; Dobson and Stancyk, 1994). Tetracycline and calcein incorporated at the site of calcification fluoresce when viewed under ultraviolet (UV) light (Suzuki and Mathews, 1966; Kobayashi and Taki, 1969; Seeto, 1992). Calcein was selected as the preferred marker for this study as it is reported less toxic than tetracycline (Wilson et al., 1987; Rowley and McKinnon, 1995) and proved very successful in ophiuroids (Stewart, 1995, 1996). To our knowledge this is the first time calcein has been used on bryozoans.

Using the method of Stewart (1995), excess calcein (<2 g) was dissolved in 100 ml of sterile seawater to make a saturated solution and the pH was adjusted to 8.5 with NaOH. At Bauza Island, Doubtful Sound, five suitable *Adeonellopsis* colonies were located at depths from 12 to 15 m using SCUBA on 27 January 1998. Each colony was enclosed in a polythene bag of roughly 10 l capacity fastened around the base of the colony using cable ties. The saturated solution was loaded into 25-ml plastic syringes and 10 ml was injected into each polythene bag. The bagged colonies were then left for 24 h before the bags were removed (Fig. 3A). The site was revisited 6 months later on 28 July 1998 and three of the five marked colonies were removed, killed in 70% alcohol, and stored. Seven months later, on 24 February 1999, the study site was revisited and the remaining two colonies were located and retrieved.

In the laboratory, specimens were placed in individual plastic containers and soaked in full strength household bleach solution (sodium hypochlorite) for 6 h to remove the soft tissues. The skeletal colony remains were washed in gently running tap water for 1 h to remove all traces of the sodium hypochlorite solution, then placed in a drying oven at 60°C until completely dry. The dried colonies were gently broken into smaller units and examined under UV light using an Olympus Vanox microscope equipped with a reflected light fluorescence attachment AH3-RFC (Fig. 3B). Distance from the last calcein-marked zooid to the tip of each branch was measured using an eyepiece micrometer (± 0.1 mm).

2.2. Radiometric dating

A large colony (about 25 cm high) was collected from Bauza Island, Doubtful Sound on

28 January 1998, killed in ethanol, bleached, rinsed, dried and weighed. The oldest part of the colony, near the base, was sectioned off and picked clean of epizoa and detritus under a binocular microscope. The sample was weighed, washed in an ultrasonic bath, acid-washed using 2 M dilute HCl for 100 s, rinsed and dried. Radiocarbon age was determined at the University of Waikato Radiocarbon Dating Laboratory.

2.3. Morphometric study

During bleaching for the calcein marking experiment it was noted that a number of the branches of each colony exhibited well-defined regrowth after apparent breakage. It was assumed that the breakages occurred while the colonies were being initially bagged and marked with calcein and that regrowth had taken place in the ensuing 6 months. The length, breadth and number of zooids per unit length were noted for each regrowth. Small fragments of branches, both regenerating and not, were dried in an oven at 60°C and weighed, and mass of carbonate deposited per zooid was calculated. It was difficult to remove regenerating branches intact and some carbonate was always lost. The number of branches per unit of colony surface area was calculated by photographing colonies, laying a 1-cm^2 grid over the print and counting growing tips in each grid square.

Three branches from each of three colonies of *Adeonellopsis* were used to quantify carbonate volume. Each branch was cut transversely at three distances from the growing tip for a total of 27 thin sections. The thin sections ranged from 4.15 to 110.55 mm from the growing tip (mean = 49.91 mm). With a PC-based digital image analysis system, the skeletal area for each thin section was measured. First, the branch's total transverse area was measured; then the pore space area was measured. The total skeletal area was calculated by subtracting the pore space area from the total transverse area. The percent skeletal area was calculated as total skeletal area divided by total transverse area. The morphometric measurement error was 3.01% based on repeatability experiments.

3. Results

3.1. Marking and harvesting

Calcein marking was only partially successful. One hundred branches from each colony were examined. The number showing fluorescent calcein marks ranged from 40% to 51% with some showing only faint marks. Forty branches showing clear marks were measured from each colony (Table 1). The mean increase in length of branches during the first 6 months of the experiment (mid-summer to mid-winter) was 5.2 mm ($n = 120$, S.D. = 1.2) (Table 1). The mean increase in branch length for the entire 13 months was 7.2 mm ($n = 80$, S.D. = 1.8) indicating mid-winter-to-late-summer growth was slower with just 2.0 mm being added in the 7 months from July 1998 to February 1999. Assuming the same average amount of growth in colonies 4 and 5 (Table 1) as measured in colonies 1–3, a *t*-test revealed that the growth in summer and autumn (mean of 5.2 mm) was significantly ($P < 0.001$) greater than the 6-month winter and spring growth (mean = 1.8 mm).

3.2. Radiometric dating

The 15-g basal section of a large *Adeonellopsis* colony (Waikato number Wk-6443) gave a radiometric age of 'modern', signifying that it was deposited after 1950. The maximum age of the colony at the time of collection was therefore 48 yr. Total colony height was 25 cm, so the colony increased in height a minimum of 5.2 mm/yr. The colony weighed 180 g (dry but not entirely clear of internal encrusters) indicating a minimum carbonate production rate of 3.75 g/yr.

3.3. Morphometric study

Mean increase in length of regenerates from break to growing tip was 4.5 mm ($n = 15$, S.D. = 1.4). However, some regenerating portions of colonies had begun to develop side branches in the 6-month period from initial breakage. If these branches were included, overall increase in length rose to 7.2 mm ($n = 15$, S.D. = 3.7) for 6 months. The number of zooids per regenerated branch

Table 1
Length of colony branch from last calcein mark to tip

Sample	6 months colony 1 (mm)	6 months colony 2 (mm)	6 months colony 3 (mm)	13 months colony 4 (mm)	13 months colony 5 (mm)
1	6.6	5.5	5.0	6.2	5.6
2	4.9	7.1	7.2	9.2	9.3
3	4.1	2.5	6.7	8.8	9.3
4	5.1	3.9	5.3	5.5	6.6
5	4.5	4.6	4.4	5.8	8.9
6	7.8	7.5	4.0	4.1	4.4
7	5.4	5.6	5.1	6.6	8.5
8	5.2	3.7	3.9	6.9	9.6
9	3.9	3.6	4.5	6.1	6.4
10	6.1	7.6	4.0	5.9	5.3
11	3.3	7.0	4.2	5.5	5.6
12	7.0	7.6	4.6	8.1	7.2
13	7.6	6.0	3.0	6.5	10.1
14	5.0	5.9	5.3	5.0	9.5
15	4.9	4.1	4.5	7.4	10.0
16	4.0	4.4	5.8	8.1	7.7
17	5.3	5.2	4.8	5.7	8.1
18	5.0	3.1	5.7	6.3	8.6
19	5.4	3.8	5.6	7.8	9.4
20	5.0	3.3	5.5	9.2	4.9
21	4.5	4.2	6.2	9.4	7.7
22	4.9	4.6	4.2	10.5	10.1
23	3.3	2.9	4.1	6.3	5.8
24	4.4	6.5	4.5	6.7	3.4
25	4.9	4.4	5.9	8.0	6.5
26	5.8	6.1	6.2	8.3	8.3
27	6.2	3.7	5.5	7.8	10.2
28	4.8	6.9	5.9	5.0	9.4
29	5.2	6.3	5.8	5.5	7.3
30	5.6	5.6	4.6	7.3	7.1
31	6.4	6.3	5.9	10.1	6.2
32	4.2	4.5	5.9	6.2	4.4
33	3.8	4.7	3.2	5.5	7.7
34	5.4	3.9	4.4	4.2	8.4
35	6.0	6.2	4.4	3.3	8.7
36	6.6	6.0	7.5	6.4	9.1
37	5.5	5.8	5.4	3.7	10.0
38	5.7	6.4	4.3	5.0	10.0
39	6.1	5.9	3.6	6.5	7.4
40	4.9	4.6	6.7	7.7	7.7
Mean	5.2	5.2	5.1	6.7	7.7
S.D.	1.0	1.4	0.9	1.7	1.8

Colonies 1, 2, and 3 were in the water 6 months over summer and autumn from January to July 1998. Colonies 4 and 5 were in the water for 13 months, from January 1998 to February 1999.

averaged 107 ($n=15$, S.D. $=51$) and the mean mass of carbonate added to each regenerated tip was 0.012 g ($n=15$, S.D. $=0.008$).

For non-regenerating fragments the relationship between number of zooids and mass of carbonate showed a very good correlation ($n=17$, $R^2=0.985$). The mass of carbonate can therefore be predicted in this species using the formula:

$$\text{g CaCO}_3 = (\text{no. of zooids} - 56.49)/6795.6$$

Measurements of mass of carbonate for *Adeonellopsis* branches which had been unaffected by calcein or breakage revealed a mean mass of 0.134 mg $CaCO_3$ per zooid ($n = 14$, S.D. = 0.032), compared with a mean mass of 0.108 mg per zooid ($n = 15$, S.D. = 0.007) for regenerating branches. This difference may be due to carbonate lost during removal of regenerated branches.

The number of branches per unit of colony surface ranged from one to seven branches/cm^2 ($n = 30$, mean = 3.5, S.D. = 1.5). The percent of the total colony volume that was skeletal ranged from 62.7% to 94.0% ($n = 27$, mean = 80.8%, S.D. = 8.3). This value increased significantly with increasing distance from the growing tip ($n = 27$, $R^2 = 0.418$) due to the secondary calcification that occurs toward the colony base in this genus (Cheetham, 1986). The cross-sectional skeletal area per branch ranged from 0.60 to 13.70 mm^2 ($n = 27$, mean = 4.76 mm^2, S.D. = 3.04). Thus a hemispherical colony of 15 cm diameter, with 3.5 branches per cm^2 of colony surface area and growing at 6.9 mm/yr, would produce 40 cm^3 $CaCO_3$/yr.

4. Discussion

4.1. Growth rate and colony age

Calcein marking indicates that annual growth averages about 6.9 mm/yr per branch with most of this growth (71%) occurring in summer and autumn. Similarly, morphometric study shows regeneration of 4.5–7.2 mm/yr. Radiocarbon dating supports this with a minimum rate of 5.2 mm/yr per branch. These data suggest a colony may increase in diameter by up to 14 mm/yr. Colonies of 15–20 cm diameter are regularly encountered in parts of Doubtful Sound. Our data indicate that these colonies may be 10–15 yr old. Rarely, very large colonies with diameters in excess of 30 cm are encountered. Such colonies may be more than 20 yr old. Both of these estimates assume a linear growth rate through colony astogeny. If the rate of growth slows with age, the colonies may be older.

Other studies of growth in large erect bryozoan species are few. A single colony of *Flustra foliacea* from South Wales was found to increase in height 12 mm/yr, approximately 37 500 zooids/yr, or 6 g $CaCO_3$/yr (Stebbing, 1971). Maximum colony age was 12 yr. One colony of *Pentapora foliacea* from the Irish Sea grew at an annual average rate of 2 cm/yr (Pätzold et al., 1987); the colony was about 3 yr old. A study of *Cellaria incula* from the Weddell Sea (Brey et al., 1999) showed a slower branch growth rate of 8 mm/yr, but colonies lived up to 14 yr. Bader (2000) showed that *Cellaria sinuosa* of the western English Channel grew about 40 mm/yr and her largest colonies were 1.5 yr old. *Adeonellopsis* is one of the longest-lived living erect bryozoans studied so far. In the fossil record, however, analysis of annual growth bands in *Pennipora anomalopora* from the Upper Cretaceous has found growth of 3 mm/yr, giving a maximum longevity of over 35 yr (Taylor and Voigt, 1999).

4.2. Carbonate production

At a density of 3.5 branches/cm^2 of colony surface area, a colony with a diameter of 15 cm, assuming a roughly hemispherical shape for the colony, is theoretically capable of adding about 23.7 g $CaCO_3$/yr. In the most densely settled area of Doubtful Sound this equates to 23.7 g $CaCO_3$/m^2/yr. The mass of carbonate added per zooid is very similar between regenerating and non-regenerating branches, differences being possibly attributable to loss of carbonate during removal of regenerated portions from the rest of the colony. A mean annual increase of 23.7 g $CaCO_3$ for a medium sized colony would equate to an addition of 150 000–200 000 zooids per annum. Given a diameter of 15 cm, in theory up to 44 large colonies of *Adeonellopsis* could fit into 1 m^2. We can postulate an upper limit to carbonate production by *Adeonellopsis*, then, of 1042 g $CaCO_3$/m^2/yr. In reality, of course, it is much lower.

Smith and Nelson (1994) found a rate of carbonate production for rapidly colonizing bryozoans in Hauraki Gulf, northern New Zealand to be similar to that for *Adeonellopsis*. They measured calcification rates of 25–740 mg $CaCO_3$/yr and calculated overall production to be 24–240 g $CaCO_3/m^2/yr$. Bader (2000) found production rates of 24–38 $g/m^2/yr$ for *Cellaria sinuosa*.

If we assume the density of skeletal carbonate to be 0.6 g $CaCO_3/cm^3$ (after Smith, 1970) then carbonate sediments would be produced at a rate of 4 cm/kyr in areas of high production by *Adeonellopsis*. This compares favorably with Smith and Nelson's (1994) calculated rate of 4–40 cm/kyr in Hauraki Gulf, northern New Zealand, and with accumulation rates of 1–10 cm/kyr reported in temperate carbonate sediments of the southern hemisphere (e.g. James et al., 1992).

4.3. *Temporal variation in growth and calcification*

Colony growth varied during the course of the experiment, with 71% of growth from mid-summer to mid-winter (~5 mm per branch) and less during the mid-winter-to-late-summer period (~2 mm per branch). It is possible that such change is correlated with reproductive activity with seasonal switching between somatic growth and gamete production. Or it could be due to exogenous influences. Phytoplankton blooms peak in Doubtful Sound in September and February (Lamare, 1997) providing an abundant food supply during the summer months. Water temperatures, too, are higher throughout summer, reaching 17°C in January from a winter low of 11°C in August (Stewart, 1996). Warmer water leads to increased metabolic rate and therefore higher production rates (e.g. see Ryland, 1970; Bader, 2000).

Three studies of growth in erect bryozoans (Stebbing, 1971; Pätzold et al., 1987; Bader, 2000) describe winter growth checks or substantial slowing in winter growth, with peak growth rates in late summer. *Adeonellopsis*, too, slows growth in winter, by a factor of about two. Interestingly, a study of growth in erect bryozoans in a polar environment (i.e. without pronounced seasonality) did not find a winter growth check (Brey et al., 1999).

In most adeoniform colonies, growth is not limited to branch tips. Older branches thicken by several mechanisms: frontal shield thickening, frontal budding, or by precipitation of extrazooidal skeletal material which covers existing zooids. This proximal thickening is common in adeoniform bryozoans, and provides relatively high strength especially near the colony base. Lower branches, then, approach a rounded cross-section, in contrast to the branch tips which are bilaminar and noticeably flattened (Cheetham et al., 1981).

Our measurements only take into account branch lengthening at the tips (6.9 mm/yr). Increasing calcification at the colony base and overall branch thickening mean that our estimate of carbonate production (24 g/yr for a colony of 15 cm diameter) is probably too low. Indeed, carbonate production should increase exponentially over the lifespan of the colony, due to both secondary calcification, and increases in the number of branches (Cheetham and Hayek, 1983).

Adeonellopsis appears to be well able to recover from minor damage, with regenerated tips growing at a very similar rate to non-regenerating branch tips. While adeoniform colonies can withstand high current speeds (Cheetham et al., 1981), the colony tips are very fragile and susceptible to impact breakage. We suggest that, in the Bauza Island environment, damage in situ in the absence of divers would be of a very minor nature. Predation on colonies was not observed, neither was there evidence of any. We estimate that should predation or diver-knock occur, repair and recovery could be effected within a very short time (about 6 months).

Adeonellopsis colonies add to environmental heterogeneity, projecting off a nearly vertical cliff. They provide substrata for epizoans such as brachiopods, other bryozoans, bivalves and tubeworms. They also offer hiding places for motile organisms, including ophiuroids and small fish. They lift the velocity profile off the fiord wall, providing a more sheltered environment around them. They thus create a significant fiord microhabitat which may last 15–20 yr, allowing more ephemeral organisms to flourish alongside them. Longer-lived colonies, such as the antipatharian black corals, may still find some shelter among *Adeonellopsis* colonies when young.

5. Summary and conclusions

Marking and harvesting, radiocarbon dating, and morphometric study combine to determine growth of 6.9 mm/yr in branch length of *Adeonellopsis* sp. in Doubtful Sound, New Zealand. The largest colonies found in Doubtful Sound, some 20 cm in diameter, may be as much as 20 yr old, and precipitate calcium carbonate at a rate of 24 g $CaCO_3$/yr. At Bauza Island, where our study was carried out, population densities of one large colony/m produce carbonate at a rate of 24 g $CaCO_3/m^2/yr$; maximum theoretical density could produce carbonate at 1042 g $CaCO_3/m^2/yr$. Carbonate produced at these rates would accumulate in sediments at 4–174 cm/kyr, reasonable rates for temperate carbonates.

Colony growth rate varies seasonally, with 71% of growth ($\sim$5 mm per branch) occurring from mid-summer to mid-winter, and much less ($\sim$2 mm per branch) from mid-winter to late summer. Our figures are probably underestimates, as proximal secondary thickening is common in adeoniform species, and does occur in *Adeonellopsis*, adding more carbonate each year. Such secondary thickening adds strength to the whole colony. While colony tips are easily damaged, they also regenerate rapidly.

Adeonellopsis colonies add to environmental heterogeneity, providing substrate for epizoa and hiding places for motile organisms. They lift the velocity profile along the fiord wall, providing a sheltered microhabitat. Their longevity allows more ephemeral organisms to flourish along with young specimens of more long-lived species.

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