

Growth geometry and measurement of growth rates in marine bryozoans: a review

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ABSTRACT

The relationship between age and size in colonial marine organisms is problematic. While growth of individual units may be measured fairly easily, the growth of colonies can be variable, complex, and difficult to measure. We need this information in order to manage and protect ecosystems, acquire bioactive compounds, and understand the history of environmental change. Bryozoan colonial growth forms, determined by the pattern of sequential addition of zooids or modules, enhance feeding, colony integration, strength, and/or gamete/larval dispersal. Colony age varies from three months to 86 years. Growth and development, including both addition of zooids and extrazooidal calcification, can be linear, two-dimensional across an area, or three-dimensional. In waters with seasonal variation in physico-chemical parameters, bryozoans may exhibit a growth-check, like an annual “tree-ring”, showing interannual variation. Growth in other bryozoans are measured using chemical markers (stable isotopes), direct observation, or by inference. Growth rates appear to be dependent on the method of measurement. Calcification rate (in g CaCO₃/y) offers a way to compare growth among different growth forms. If the weight of carbonate per zooid is fairly consistent, it can be directly related to the number of zooids/time. Careful consideration of methods for

measuring and reporting growth rate in bryozoans will ensure they are robust and comparable.

INTRODUCTION

Bryozoans are lophophorate aquatic invertebrates which typically form colonies by iterative addition of modular clones (zooids). Freshwater species are uncalcified; the majority of marine species are calcified, so that there is an extensive fossil record of marine bryozoan colonies. When calcified colonies grow large, they can provide benthic structures which enhance biodiversity by provision of sheltered habitat. Agencies who wish to manage or protect these productive habitats need to understand the longevity and stability of these structures. But how are size and age related in colonial organisms? We do not automatically know the age of a large bryozoan colony. While growth rate of zooids may be relatively easily measured, the growth rates of colonies can be highly variable, difficult to measure, and complex. Yet without this information, it is difficult to manage or protect ecosystems based on bryozoan colonies, or to grow them for bioactive compounds, or to understand the carbonate record held in them. After several decades of struggling with growth rates in bryozoans, the authors here review and discuss the following issues in bryozoans: zoarial



growth form, maximum size, age, growth (increase in size), and measurements of growth rate (increase in size over time).

SHAPE OF A BRYOZOAN

The individual zooids that make up bryozoan colonies are fairly simple boxes or tubes, with more or less ornamentation. Normal feeding zooids (autozooids) are sometimes aided by zooids who specialise in support, cleaning, or reproduction (heterozooids). Together with extrazoidal carbonate, they make up the colony. Bryozoan colony growth form is thus determined by the pattern of addition of zooids, the same way that the shape of a knitted garment is determined by the addition of stitches.

Most bryozoan colonies start out as a spot (sexually-produced ancestrula). Then the first zooid buds from the ancestrula, but it is the one after the first budding that makes the pattern (Fig. 1). In simple iterative growth, new modules are added sequentially, often in some regular arrangement (Hageman 2003). Zooids can be added in a line, or at the tips of branches, or along an edge, on the substrate or lifting erect off it. This kind of growth results in a small number of simple growth forms, from runners and trees to sheets and mounds (Nelson *et al.* 1988; Smith 1995). Combinations of these simple primary modules can form more complex colonies with secondary structural design units (composed of the primary modules) (Hageman *et al.* 1998; Hageman 2003).

Theoretically, a modular colony could take almost any form, but, in reality, bryozoan colonies tend to occur in a few basic forms, some of which have evolved repeatedly in different clades (McKinney and Jackson 1989). They achieve: access to food particles in the water, integration of the colony (connections between zooids), strength and resistance to water flow/predation, reduction of interaction with other species, competitive advantage, and capacity to distribute larvae into the water (McKinney and Jackson 1989). Bryozoan colonial growth form nomenclature tries to capture this variation, with varying degrees of success.

Early on, bryozoan colonial growth forms were often given names that referred to an exemplar taxon, usually a genus (e.g., Stach 1936; Lagaiij and Gautier 1965). So, a bryozoan that grew an erect flexible leafy colony like that of the genus *Flustra* was referred to as flustriform. This archetypal system was summarised by Schopf (1969). As noted by Hageman *et al.* (1998), each category was made up of a combination of characteristics, with no systemic recognition of shared or common characters. It was cumbersome, difficult for non-specialists, and although there were a great number of categories (with different systems for cheilostomes and cyclostomes), they failed in aggregate to describe all the variety in bryozoan colonial forms.

In the 1980s and 1990s, carbonate sedimentologists who wanted to categorise bryozoans without excessive investment in species identification developed a hierarchical classification system, where a few characteristics were combined to make a simple code to describe overall colonial shape (Nelson *et al.* 1988, revised and expanded by Bone and James 1993; Smith 1995). Colonies were described as erect, encrusting, or free-living; then subdivided into various shapes (e.g., branching, articulated, rooted). These categories were rather broad-brush and took no account of “rampant convergent evolution” (Taylor and James 2013, p. 1186), or of the different ecological roles played by different shapes. An alternative, using a classification based on the ecological function of growth forms (e.g., McKinney and Jackson 1989) was inadequately supported by genuine ecological understanding of bryozoan ecology on different scales (Hageman *et al.* 1998).

Hageman *et al.* (1998) reviewed all this and developed an “Analytical Bryozoan Growth Habit Classification”, in which they characterised bryozoan colonial forms using eco-morphological categories: orientation, attachment to substrate, construction, arrangement of zooecial series, arrangement of frontal surfaces, secondary skeletal thickening, structural units and their dimensions, frequency and dimensions of bifurcation, and connections between structural units, along with substrate type. These twelve fundamental

characters provided a complex but comprehensive and systematic method of describing the great diversity of bryozoan colony forms. Hageman revisited this classification in his 2003 review of colonial growth in diverse bryozoan taxa.

It is relevant to note that cyclostomes zooids are tubes, where cheilostome zooids (usually) make more-or-less rectangular boxes. These modules combine differently, but often make remarkably similar growth forms (Fig. 2).

Since Stach (1936), researchers have been enthusiastic about using colonial growth form as an indicator of (paleo)environment (reviewed by Smith 1995; Hageman *et al.* 1997). Despite the appealing notion that different growth forms must be adapted to different environments, and the development of a standardized and statistically robust method (Hageman *et al.* 1997), rigorous investigations

have often failed to show robust correlations with depth, water speed, or temperature (e.g., Liuzzi *et al.* 2018). Certain broad general trends can be observed, for example: that fragile small colonies are probably not representative of strong hydraulic energy. That is not to say that bryozoans do not have potential as environmental indicators; there are, for example, assemblages that are strongly related to habitat (e.g., Wood and Probert 2013), as well as useful environmental geochemical signals in their skeletal carbonate (e.g., Key *et al.* 2018).

SIZE OF A BRYOZOAN

Individual zooids in marine bryozoans are tiny, usually 0.1 to 1 mm across. In a given species, zooid size range is characteristic and sometimes diagnostic. However, at least some species of bryozoans grow

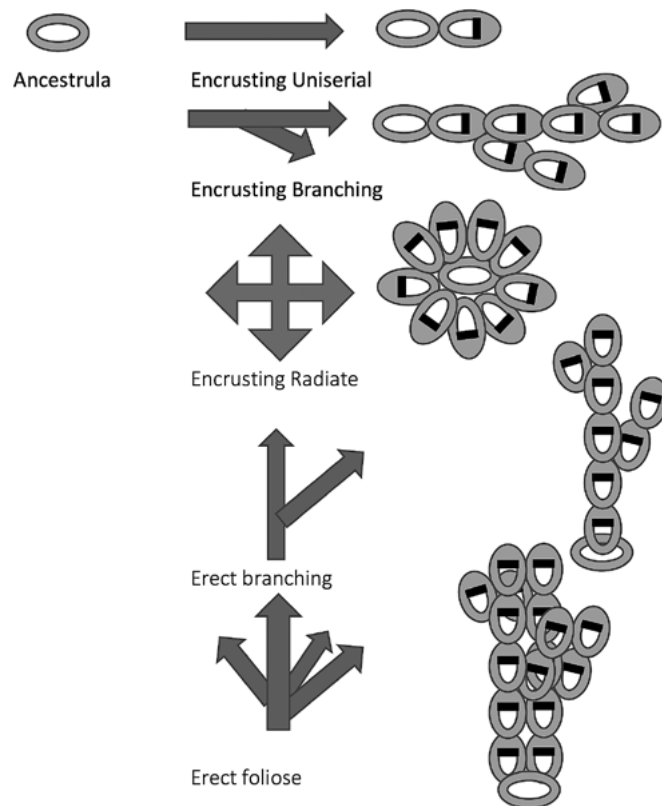


Figure 1. Iterative growth in bryozoans: many ways to combine individual zooids. Multi-laminar and other complex forms are made by iterating these multi-zooid modules.



larger zooids in cooler waters/seasons (see review in Amui-Vedel *et al.* 2007), which has been used as an environmental indicator (e.g., McClelland *et al.* 2014). Zooid size and arrangement are generally held to be optimal for feeding currents (see, e.g., Ryland and Warner 1986).

Size of bryozoan colonies within a species, unlike that of its zooids, varies greatly. A colony becomes mature (sexually reproductive) once it has enough zooids to support embryo production (Nekliudova *et al.* 2019), usually 30-130 zooids, but embryos have been reported in species ranging from 3 to 2700 zooids (Jackson and Wertheimer 1985). A bryozoan “spot” colony can be viable at only a few mm², but equally, at the other end of the spectrum, one encrusting bryozoan (*Einhornia crustulenta*) can cover 8290 mm² (Kuklinski *et al.*

2013). Large erect bryozoans today are generally 10-30 cm tall but Cocito *et al.* (2006) reported modern *Pentapora* colonies in the Adriatic that reached 1 m in height; there are fossil bryozoans that appear to reach a similar size (Cuffey and Fine 2006).

Colony size has been measured in many ways: linear extent (height, width, thickness, diameter), area, volume, and number of zooids. The most natural measurement depends on the colony form. In fact, each main colony form has an obvious method of measuring it (Table 1). Thus, size in one-dimensional colonies is measured in length, whereas sheet-like colonies are sometimes measured in area (or in extension of diameter for flat nearly-circular colonies). Lumpier multilaminar three-dimensional colonies could be measured in volume, but in fact generally are not measured at all, due

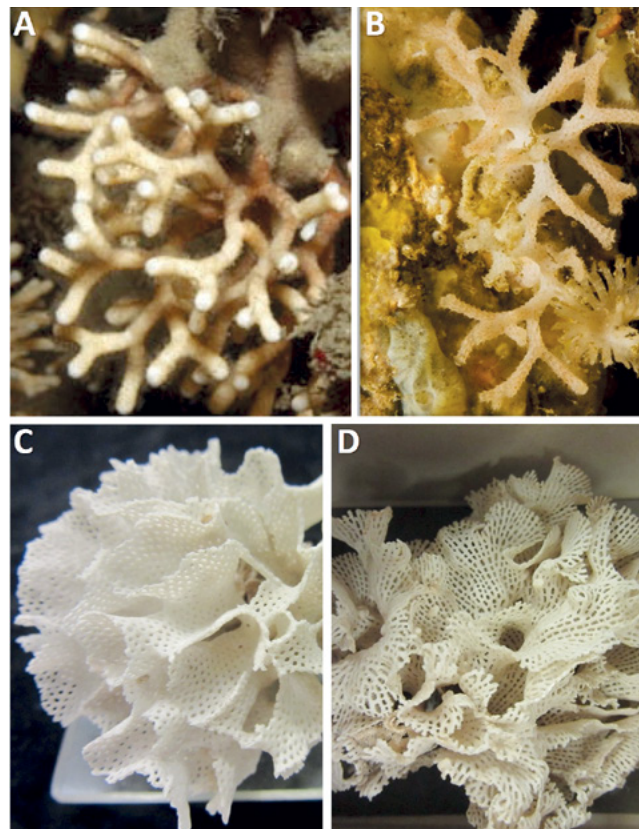


Figure 2. Convergent growth forms from different clades of bryozoans.

(A) *Diaperoecia* sp. (stenolaemate cyclostome); (B) *Galeopsis porcellanicus* (gymnolaemate cheilostome); (C) *Hippellozoon novaeselandiae* (gymnolaemate cheilostome); (D) *Hornera foliacea* (stenolaemate cyclostome).

to the challenges presented by their shape (but see Sokolover *et al.* 2018).

Sometimes researchers add to their measurements the spatial density of zooids (i.e., number of zooids/mm²). In general, this measurement appears to limit counts to autozooids, and it is worthwhile considering whether or not heterozooids deserve counting in this context. There is also a lack of comparability between cheilostome box-like zooids and stenolaemate tube-like zooids.

Because of these different measurement schemes, comparisons of size among growth forms has been problematic and has required researchers to make unit conversions. For example, one could assume constant branch thickness in order to convert branch length to volume. Smith and Nelson (1994) managed this issue by measuring size in terms of weight of skeletal carbonate— which is independent of growth form.

AGE OF A BRYOZOAN

What are life and death to a bryozoan? New individual zooids begin budded at the edge of a colony (often at the “growing edge” or “growth tip” but sometimes frontally on top of old zooids). As the growing edge moves away, the zooids mature, sometimes reproduce sexually, and grow old. They can produce a brown body and then regenerate, they can produce extrazooidal thickening, they can die, and the chamber become empty, or they can bud frontally and essentially overgrow themselves (Ryland 1976). Life history is complex in bryozoans; age of a single bryozoan zooid is not well constrained. It could be important, though, for example, in studies where measuring zooids of the same generation is necessary, such as in age-growth-climate correlations (e.g., Key *et al.* 2018).

On a different scale, the colony’s lifespan is the time from metamorphosis of the larva into the ancestrula to the time the last zooid dies, and the colony ceases to function. Some colonies die from an event, like being eaten or crushed or buried. Theoretically, of course, a bryozoan colony is potentially immortal (McKinney and Jackson 1989). Even in a simple encrusting colony, however, age is

not necessarily related to size if fission and/or partial mortality have occurred (Jackson and Winston 1981). Most large erect species, on the other hand, appear to have a “normal maximum size,” possibly mediated by the mechanics of water flow and skeletal support.

Age in the context of a bryozoan colony is thus how long the colony has been functioning, specifically, time from metamorphosis of the larva into the ancestrula to time of death/collection. There are annuals and perennials among bryozoan colonies. An adult colony can die of old age after three months (e.g., as winter arrives) or last as much as 50 years (*Melicerita obliqua* in the Weddell Sea, Antarctica; Brey *et al.* 1998); *Celleporaria fusca* in the Gulf of Aqaba (Sobich, 1996) holds the longevity record of 86 years. A range of about 90 to over 30,000 days means that age of bryozoan colonies, of different species and in different environments, can vary over four orders of magnitude. Having said that, most large erect heavily-calcified marine specimens that have been studied are about 10-30 years old (Smith 2014).



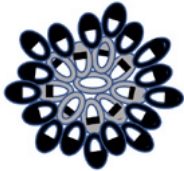


BRYOZOAN COLONY GROWTH

Growth is the increase in occupation of space. In bryozoans, there are different kinds of growth: 1. growth and development of the individual zooid (ontogeny), generally a short-lived and small-scale process; 2. growth and development of the colony by addition of zooids (which we call primary astogeny) which can be on the order of months or years or decades (Lidgard and Jackson 1989); and 3. growth of the colony by extrazooidal calcification (which we could call secondary astogeny) adding strengthening material that is not part of a zooid, also over the life of the colony.

In terms of measuring colony growth, there are only a few categories (Table 1). In general, growth can occur around the edges of a colony (radial growth) or be limited to one or two directions (linear growth), including, in frontal budding, up into the water column. The dimensionality of growth determines the dimensions that must be measured to encapsulate growth. Units of growth rate vary



Table 1. Three categories of geometry in bryozoan colonies, with relevant ways to measure size and growth.

Dimensions	New zooids added	Illustration (ancestrula empty, new growth in black)	Colonial growth form nomenclature	Comment	Growth increment measured over time
1 dimension (length)	In a line at the tip of the colony		Encrusting Uniserial Runners		Length Number of zooids (1 zooid in illustration)
	At the growing tip of each branch		Encrusting multiserial Branching runners Erect branching (all kinds) Erect flexible articulated	Each branch can be one zooid wide, or bilaminar, or a circle of zooids around a central core or even more complex Bifurcation angle and rotation around the branch axis allow branches to grow without running into each other	Additive length increase (= sum of all the new branch lengths) Number of zooids (3 zooids in illustration)
2 dimensions (area)	All along the edge, but flat on the substrate		Encrusting unilaminar Spots, circles Free-Living Caps	Sheets are usually circular unless they run into something or growth is not consistent around the edge (e.g. "belt" shaped colonies) Caps are curved versions	Increase in area, calculated for a circle of radius R Increase in area, calculated as length x width if roughly rectangular Number of zooids (17 zooids in illustration)
	Along the growing edge, away from substrate		Erect foliose Erect fenestrate Rooted sabres Conescharallinids	Can be unilaminar or bilaminar Fenestrate is really just a sheet with holes in it Sabres are leaves that aren't very wide	Height Area = width of growing edge x height Number of zooids (5 zooids in illustration)
3 dimensions (volume)	Along the edge and on the surface		Encrusting multilaminar Mounds and nodules Spheres	Highly variable This is difficult to generalise Self-overgrowth is typical in this group, and can be very irregular	Volume of a sphere: $\frac{4}{3}\pi r^3$ Or a disc/cylinder: $H \pi r^2$ Or a prism: $H \times W \times L$ Number of zooids (6 zooids in illustration)

across the range of size and time, and possibly over the development of the colony. The most commonly used are: zooids added, linear increase (height, length, radius), and increase in area over time.

Bryozoans in cold waters sometimes stop growing, or slow down, during winter (Smith & Key, 2004). If calcification continues while linear extension does not, a thickened skeletal band, or growth check appears in the skeleton. While most growth checks occur in polar colonies, reflecting a lack of food availability

in winter (Brey *et al.* 1998; Smith 2007), temperate species can also slow their growth in the cold months, leaving a thickened layer as an annual marker (e.g., *Melicerita chathamensis*, Smith and Lawton 2010, Key *et al.* 2018), or just a gap in the record (*Adeonellopsis* sp., Smith *et al.* 2001, Smith and Key 2004).

A few colonial growth forms appear to have determinate growth, that is, they stop growing when they reach an optimal size (as some free-living forms do; Winston and Håkansson 1989), or they may shed

layers that are heavily fouled (Winston and Håkansson 1989). Some colonies, such as *Membranipora*, grow along with their macro-algal substrate (Winston and Hayward 2012). Others, such as *Pentapora*, seem as if they could grow forever (Cocito *et al.* 2004).

Growth has consequences – some biological activities do not happen until a colony reaches a critical size. For example, the onset and frequency of reproductive ovicells and degenerative brown bodies can be related to the overall size of the colony (or not, see Hayward and Ryland 1975). Some colonies may exert control over their shape as they grow, for example, by dropping unnecessary branches.

BRYOZOAN COLONIAL GROWTH RATES

As with the measurement of size, growth rates in various forms are also measured in different ways. A radial encrusting colony is generally measured in terms of increase in diameter or area. A branching colony, on the other hand, might be measured in terms of increased height, or the sum of branch lengths or even the number of branches. Smith's (2014) summary of growth rate measurements of bryozoan colonies (updated in Appendix Table) shows a range of units and approaches in reporting growth rates, including cm/y, mm²/y, zooids per month, specific growth rate, and doubling rate. These various measurements are difficult to compare against each other and make it nearly impossible to reach any conclusions about the range of normal growth rates in bryozoans.

Growth rate can translate, in most marine bryozoans, into calcification rate. Specimens can be weighed before and after, or the newly-added skeletal material can be separated and weighed (e.g., Smith *et al.* 2001), or the proportion of volume that is calcified (% calcimass) can be applied to the volume of the newly added colony. Calcification rate (in mg CaCO₃/y) offers a way to compare growth rate among different colonial forms which expand in different ways. If the carbonate per zooid is fairly constant (and it might be in a clonal organism, see Smith *et al.* 2001), it can be directly calculated from zooids/

time; conversely, measured calcification rates can be allocated to zooid number in order to determine mg CaCO₃ per zooid (Reid 2014). Although technically bryozoans should be bleached or ashed to remove organic material (ash-free dry weight) in order to calculate calcimass, in reality CaCO₃ is much heavier than dried organics and, at least among robustly calcified bryozoans, dry weight is not much different (Barnes *et al.* 2011)

Less intuitive growth measures (per Amui-Vedel *et al.* 2007) have been trialled, including: Specific Growth Rate $r = \ln(N/N_0)/t$ where N_0 = initial zooid number; N = final zooid number, t = time (days) elapsed, which ranges from 0.1 to 0.3; and doubling time $t_2 = 0.693/r$ in days, where r = radius.

Smith (2014) collated measured growth rates for 44 bryozoan species from the literature, and we have updated that table (by including additional references), resulting in measured growth rates for 84 bryozoan species (Appendix Table). The most commonly used measure of growth rate was linear extension, either as colony height or radius. We standardised these measures to mm/y (even though many species do not grow all year long); rates ranged from 0.1 to 1400 mm/y (mean 87 mm/y; standard deviation 245 mm/y; N = 54). Another common growth rate measure was increase in area; again, we standardised to annual growth in mm²/y. Colonial growth rate by area ranged from 44 to 193, 235 mm²/y (mean 20,998 mm²/y; SD 43, 897 mm²/y; N = 19). Calcification rate ranged from 9 to 23,700 mg CaCO₃/y (mean 1499 mg CaCO₃/y; SD 5247 mg CaCO₃/y; N = 20). All three measures of growth rate (Table 2) suggest either that growth rate varies among species by four orders of magnitude, or that growth rates measured by different researchers using different methods cannot be compared. In either case, the data do not lead to any useful generalisation about bryozoan colonial growth rates.

INFLUENCE OF METHODS ON RESULTS

It may be that there is so much variation in measured bryozoan colony growth rates because of the variety of methods that are used. To consider this possibility, we

**Table 2. Summary of data comprising 88 measurements of colony growth from 81 species of bryozoan (based on Appendix Table).**

	Maximum observed height or radius (mm)	Maximum observed area (mm ²)	Maximum known age (y)	Growth rate extension (mm/y)	Increase in area (mm ² /y)	Calcimass (% that is skeleton) (wt%)	Calcification rate (mg CaCO ₃ /y)	Calcification per zooid (mg CaCO ₃ /zz)
Min	2	97	0.1	0.1	44	0.4	9	0.1
Mean	114	4229	13	87	20988	85	1499	0.5
Max	1000	23400	86	1400	193235	230	23700	1.0
Range	998	23303	86	1400	193191	230	23691	1
StdDev	196	6288	16	245	43897	92	5247	0.4
N	28	20	42	54	19	4	20	3

have separated methods into seven categories (Table 3). Growth rate in bryozoan colonies can be measured by direct observation (in the laboratory or in the field), mark-and-recapture (both chemical and physical marks can be used) or by inference/proxy. Each of these methods has its strengths and weaknesses.

Direct Observation

Direct observation of growth rate can occur either in the sea (usually using settling plates) or in the lab. Settling plates that are simply empty substrate placed in the sea (e.g., Skerman 1958) provide only a minimum growth rate (as researchers don't know when each colony settled). On the other hand, early growth when colonies are just starting out can be the most rapid growth of the colony's life (Ryland 1976). Different substrates, flow rates, orientations, light regimes, and water depths may affect growth rate (e.g., Edmondson and Ingram 1939). And, of course, there is an element of random chance: researchers only catch the species that settle, which may be random or skewed towards first-colonising weedy r-selected species.

To overcome some of those difficulties, some researchers have settled larvae on glass slides, then grown them in the sea or in the laboratory (e.g., Jebram and Rummert 1978; Kitamura and Hirayama 1984). Others have mounted a piece of adult colony on a substrate (e.g., Sokolover *et al.* 2018). While this strategy ensures that the exact time of growth

is known, it still measures the earliest, most rapid growth of a colony, as it first spreads out.

Culturing bryozoans in the laboratory provides more environmental control, but it is notoriously difficult, particularly for large robustly-calcified species. Environmental variations, such as temperature (Amui-Vedel *et al.* 2007) or current speeds (Sokolover *et al.* 2018), can promote or retard growth. It appears that genetic variation in growth rates may also be considerable (Bayer and Todd 1996). Diet and feeding regime also affect growth rate (Winston 1976; Jebram and Rummert 1978). Lab culture of bryozoans is often over short time periods (e.g., 42 days in Winston 1976), possibly because bryozoans do not grow well in captivity. If conditions are suboptimal, growing bryozoans in culture may underestimate growth rate (see e.g., Smith *et al.* 2019).

Mark and Recapture

Mark-and-recapture techniques are well known in biology and have been applied to bryozoans as well as whales (e.g., Urian *et al.* 2015). Here an adult bryozoan colony is marked mechanically or chemically, and its size recorded. Then it is left in its natural habitat to grow. After time elapses, researchers revisit the colony and re-record its size. The bryozoan is photographed before and after marking (e.g., Okamura and Partridge 1999), or the bryozoan is immersed in a chemical marker dye such as calcein (Smith *et al.* 2019) and

Table 3. Methods used for the measurement of bryozoan colony growth.

	In the ocean (<i>in vivo</i>)	In the lab (<i>in vitro</i>)	In dead specimens (<i>post-mortem</i>)
Direct Observation	A. Settling plate placed empty in the sea, collecting whatever settles	C. Seeding a substrate, then growing it in the lab	
	B. Seeding a substrate, then returning it to the sea to grow		
Mark and Recapture	D. Marking colonies either with chemicals or tags, returning to the field, re-collecting or photographing after a time	E. Marking colonies with chemicals or tags, growing in the lab, then collecting or photographing them	
Inference			F. Counting annual growth checks or generations of ovicells
			G. Using chemical signals (such as stable isotopes) to track seasonal variations in environment

then recovered and the unmarked skeleton measured (e.g., Smith *et al.* 2001). These techniques have the advantage that growth is of adult colonies, beyond the initial flush of growth, and that growth is occurring in the natural habitat. It is not uncommon, however, to lose colonies or be unable to relocate them, not least because tagging itself can increase colony vulnerability to currents and waves.

Inference/Proxy

Direct observation and mark-and-recapture techniques measure growth over a short period of time. A better way to determine age and growth over the life of the whole colony is to utilize signals, physical and/or chemical, that indicate periods of time (like tree rings). For example, cross-time colony samples of oxygen isotope concentrations form a record of sea-water temperature and consequently document the passing of seasons (e.g., Pätzold *et al.* 1987; Bader and Schaefer 2005; Key *et al.* 2013, 2018). Colonies with measurable growth checks also allow annual growth to be measured from the annual bands of thicker skeleton that can be detected by x-rays or even just visually (e.g., Barnes 1995; Smith 2007). Using growth checks and isotopes simultaneously allows validation of the annual nature of the signal (Key *et al.* 2018).

Growth checks can lead to underestimation of the overall average growth rate (calculated as a simple size/time) (Key *et al.* 2018). Antarctic bryozoans grow at the same approximate rate as their temperate counterparts, but only for the few months of summer. So, a colony of the same size would be much older than its temperate or tropical cousin.

Comparison of Methodologies

We collated measured growth rates collected using all seven of these methods (see Table 4), grouped them according to method of measurement, and calculated basic descriptive statistics on them, to see if measurement method influences growth rate measured. In every case where there was a range, we chose the maximum growth rate. While there are very unequal sample numbers among methods, and the data were not designed for this test, nevertheless Table 4 shows that long-term measurements of growth over the life of the colony (annual growth checks and chemical proxies for growth) give much lower numbers than those which measure growth rate over periods of days to weeks. Settling plates *de novo* measure the fastest growth rates, which makes sense as they attract early settlers who grow fast to carve out space early.



Table 4. The influence of measurement technique on measured growth rate.

Method of measuring growth rate	Number of species measured this way	Mean annual growth rate											
		Linear extension (mm/y)				Increase in Area (mm ² /y)				Calcification Rate (mg CaCO ₃ /y)			
		Min	Max	Mean	Std Dev	Min	Max	Mean	Std Dev	Min	Max	Mean	Std Dev
A Settling Plates <i>in vivo, de novo</i>	38	1	1400	136	331	665	193235	30203	53183	220	736	478	258
B Substrate seeded, <i>in vivo</i>	2			220	0			73	0			730	0
C Substrate seeded, in lab	6			438	0	52	7300	3461	3327			48	0
D Mark and Recapture <i>in vivo</i>	4	7	730	368	362	44	37595	18820	18776			23700	0
E Mark and Recapture in lab	5	0	1	1	1								
F Annual growth checks (morphological)	23	1	36	9	8					9	1593	270	451
G Chemical proxies for annual growth	4	8	40	19	13			222	0	160	230	195	35
All Methods	81	0	1400	88	245	44	193235	20211	42853	9	23700	1467	5116

CONCLUSIONS

It is a little disappointing to have summarised data from dozens of papers and species and not to be able to answer the question: “How fast do bryozoan colonies grow?” Until we have a standardized methodology, we will be unable to do more than cite whichever paper is most relevant to our own species and growth form. Furthermore, it is currently impossible to compare growth rates among bryozoans, especially among those with different growth forms.

A study should be designed in which bryozoans of both encrusting and erect branching growth forms are cultured in the laboratory, grown at sea, and observed in the wild. *Post-mortem* analysis of oxygen isotopes or growth checks should also be carried out. The use of different techniques over the same season(s) in the same species should reduce variability and allow for selection of the best methods for ascertaining bryozoan growth rates.

In the meantime, we suggest that growth rate studies in bryozoans avoid methods that measure

only the first flush of rapid growth or rely on culture in the laboratory. Mark-and-recapture is effective over a short time, but the best picture of growth and growth rate in a bryozoan colony is achieved by the interpretation of physical or chemical annual markers, when present. In addition, we recommend that characterisations of growth in well-calcified bryozoans (whether linear, areal, or in number of zooids) include also the weight of the skeleton, so that calcification rate can be calculated. Calcification rate has real potential, among well-calcified bryozoans, to be a unit comparable among growth forms.

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REFERENCES

(includes references found in Appendix Table)

AMUI-VEDEL A.-M., HAYWARD, P.J. AND PORTER, J.S. 2007. Zooid size and growth rate of the bryozoan *Cryptosula pallasiana* Moll in relation to temperature, in culture and in its natural environment. *Journal of Experimental Marine Biology and Ecology* **353**, 1–12.

BADER, B. 2000. Life cycle, growth rate and carbonate production of *Cellaria sinuosa*. In: A. Herrera Cubilla and J.B.C. Jackson (eds), *Proceedings of the 11th International Bryozoology Association Conference*. Balboa, Smithsonian Tropical Research Institute, pp. 136–144

BADER, B. AND P. SCHÄFER. 2004. Skeletal morphogenesis and growth check lines in the Antarctic bryozoan *Melicerita obliqua*. *Journal of Natural History* **38**, 2901–2922.

BADER, B. AND P. SCHÄFER. 2005. Impact of environmental seasonality on stable isotope composition of skeletons of the temperate bryozoan *Cellaria sinuosa*. *Palaeogeography Palaeoclimatology Palaeoecology* **226**, 58–71.

BARNES, D.K.A. 1995. Seasonal and annual growth in erect species of Antarctic bryozoans. *Journal of Experimental Marine Biology and Ecology* **188**, 181–198.

BARNES, D.K.A., WEBB, K.E. AND LINSE, K. 2007. Growth rate and its variability in erect Antarctic bryozoans. *Polar Biology* **30**, 1069–1081.

BARNES, D.K.A., KUKLINSKI, P., JACKSON, J.A., KEEL, G.W., MORLEY, S.A. AND WINSTON, J.A. 2011. Scott's collections help reveal accelerating marine life growth in Antarctica. *Current Biology* **21**, R147–R148.

BAYER, M.M. AND TODD, C.D. 1996. Effect of polypide regression and other parameters on colony growth in the cheilostomate *Electra pilosa* (L.). In: D.P. Gordon, A.M. Smith and J.A. Grant-Mackie (eds), *Bryozoans in Space and Time. Proceedings of the 10th International Bryozoology Conference*. Wellington, Wilson and Horton, pp. 29–45.

BAYER, M.M., CORMACK, R.M., AND TODD, C.D. 1994. Influence of food concentration on polypide regression in the marine bryozoan *Electra pilosa* (L.) (Bryozoa: Cheilostomata). *Journal of Experimental Marine Biology and Ecology* **178**, 35–50.

BONE, Y. 1991. Population explosion of the bryozoan *Membranipora aciculata* in the Coorong Lagoon in late 1989. *Australian Journal of Earth Sciences* **38**, 121–123.

BONE Y. AND JAMES N.P. 1993. Bryozoans as carbonate sediment producers on the cool-water Lacedpede shelf, southern Australia. *Sedimentary Geology* **86**, 247–271.

BREY, T., GUTT, J., MACKENSEN, A. AND STARMANS, A. 1998. Growth and productivity of the high Antarctic bryozoan *Melicerita obliqua*. *Marine Biology* **132**, 327–333.

BREY, T., GERDES, D., GUTT, J., MACKENSEN, A. AND STARMANS, A. 1999. Growth and age of the Antarctic bryozoan *Cellaria incula* on the Weddell Sea shelf. *Antarctic Science* **11**, 408–414.

COCITO, S. AND FERDEGHINI, F. 2001. Carbonate standing stock and carbonate production of the bryozoan *Pentapora fascialis* in the north-western Mediterranean. *Facies* **45**, 25–30.

COCITO S., NOVOSEL M. AND NOVOSEL A. 2004. Carbonate bioformations around underwater freshwater springs in the northeastern Adriatic Sea. *Facies* **50**, 13–17.

COCINO, S., NOVOSEL M., PASARIĆ, Z. AND KEY, M.M. JR. 2006. Growth of the bryozoan *Pentapora fascialis* (Cheilostomata, Ascophora) around submarine freshwater springs in the Adriatic Sea. *Linzer Biologische Beiträge* **38**, 15–24.

CUFFEY, R.J. AND FINE, R.L. 2006. Reassembled trepostomes and the search for the largest bryozoan colonies. *International Bryozoology Association Bulletin* **2**, 13–15.

ECKMAN, J.E. AND DUGGINS, D.O., 1993. Effects of flow speed on growth of benthic suspension feeders. *Biological Bulletin* **185**, 28–41.

EDMONDSON, C.H. AND INGRAM, W.M. 1939. Fouling organisms in Hawaii. *Occasional Papers of Bernice P Bishop Museum, Honolulu Hawaii* **XIV**, 251–300.

FORTUNATO, H., SCHÄFER, P. AND BLASCHEK, H. 2013. Growth rates, age determination, and calcification levels in *Flustra foliacea* (L.) (Bryozoa: Cheilostomata): preliminary assessment. In: A. Ernst, P. Schäfer and J. Scholz (eds) *Bryozoan Studies 2010, Lecture Notes in Earth System Sciences* **143**, 59–74.

GERACI, S. AND RELINI, G. 1970. Osservazioni sistematico-ecologiche sui briozoi del fouling Portuale di Genova. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova* **38**, 103–139.

HAGEMAN, S.J. 2003. Complexity generated by iteration of hierarchical modules in Bryozoa. *Integrative and Comparative Biology* **43**, 87–98.

HAGEMAN, S.J., BOCK, P.E., BONE, Y., AND MCGOWRAN, B. 1998. Bryozoan Growth Habits: Classification and Analysis. *Journal of Paleontology* **72**, 418–436.

HAGEMAN, S.J., BONE, Y., MCGOWRAN, B. AND JAMES, N.P. 1997. Bryozoan colonial growth forms as paleoenvironmental indicators: Evaluation of methodology. *Palaios* **12**, 406–419.

HAYWARD P.J. AND HARVEY, P.H. 1974. Growth and mortality of the bryozoan *Alcyonidium hirsutum* (Fleming) on *Fucus serratus* L. *Journal of the Marine Biological Association of the UK* **54**, 677–684.

HAYWARD, P.J. AND RYLAND, J.S. 1975. Growth, reproduction and larval dispersal in *Alcyonidium hirsutum* (Fleming) and some other Bryozoa. VIII European Marine Biology Symposium. *Pubblicazioni della Stazione Zoologica de Napoli* **39** Suppl: 226–241.



- HERMANSEN, P., LARSEN, P.S. AND RIISGÅRD H.U. 2001. Colony growth rate of encrusting marine bryozoans (*Electra pilosa* and *Celleporella hyalina*). *Journal of Experimental Marine Biology and Ecology* **263**, 1–23.
- HUNTER E. AND HUGHES, R.N. 1993. Effects of diet on life-history parameters of the marine bryozoan *Celleporella hyalina* (L.). *Journal of Experimental Marine Biology and Ecology* **167**, 163–177.
- JACKSON J.B.C. AND WERTHEIMER S.P. 1985. Patterns of reproduction in five common species of Jamaican reef-associated bryozoans. In: C. Nielsen and G.P. Larwood (eds), *Bryozoa: Ordovician to Recent*. Fredensborg, Olsen and Olsen, pp. 161–168.
- JACKSON, J.B.C. AND J.E. WINSTON. 1981. Modular growth and longevity in bryozoans. In: G.P. Larwood and C. Nielsen (eds), *Recent and Fossil Bryozoa*. Fredensborg, Olsen and Olsen, pp. 121–126.
- JEBRAM, D. AND RUMMERT, H.-D. 1978. Influences of different diets on growth and forms of *Conopeum seurati* (CANU) (Bryozoa, Cheilostomata). *Zoologische Jahrbücher Abteilun für Systematik, Geographie, und Biologie der Teire* **105**, 502–514.
- KAHLE, J., LIEBEZEIT, G. AND GERDES, G. 2003. Growth aspects of *Flustra foliacea* (Bryozoa, Cheilostomata) in laboratory culture. *Hydrobiology* **503**, 237–244.
- KEY, M.M., JR., HOLLENBECK, P.M., O'DEA, A. AND PATTERSON, W.P. 2013. Stable isotope profiling in modern marine bryozoan colonies across the Isthmus of Panama. *Bulletin of Marine Science* **89**, 837–856.
- KEY, M.M., JR., ROSSI, R.K., SMITH, A.M., HAGEMAN, S.J. AND PATTERSON, W.P. 2018. Stable isotope profiles of skeletal carbonate validate annually-produced growth checks in the bryozoan *Melicerita chathamensis* from Snares Platform, New Zealand. *Bulletin of Marine Science* **94**, 1447–1464.
- KITAMURA, H. AND HIRAYAMA, K. 1984. Growth of the bryozoan *Bugula neritina* in the sea at various water temperatures. *Bulletin of the Japanese Society of Scientific Fisheries* **50**, 1–5.
- KUKLINSKI, P. AND P.D. TAYLOR. 2006. Unique life history strategy in a successful Arctic bryozoan, *Harmeria scutulata*. *Journal of the Marine Biological Association of the UK* **86**, 1305–1314.
- KUKLINSKI, P., SOKOLOWSKI, A., ZIOLKOWSKA, M., BALAZY, P., NOVOSEL, M. AND BARNES, D.K.A. 2013. Growth rate of selected sheet-encrusting bryozoan colonies along a latitudinal transect: preliminary results. In: A. Ernst, P. Schäfer and J. Scholz (eds) *Bryozoan Studies 2010, A. Lecture Notes in Earth System Sciences* **143**, pp. 155–167
- LAGAAIJ, R. AND GAUTIER, Y.V. 1965. Bryozoan assemblages from marine sediments of the Rhone delta, France. *Micropaleontology* **11**, 39–58.
- LIDGARD, S. AND JACKSON, J.B.C. 1989. Growth in encrusting cheilostome bryozoans: I. Evolutionary trends. *Paleobiology* **15**, 255–282.
- LIUZZI, M.G., LÓPEZ-GAPPA J. AND SALGADO, L. 2018. Bryozoa from the continental shelf off Tierra del Fuego (Argentina): Species richness, colonial growth-forms, and their relationship with water depth. *Estuarine, Coastal and Shelf Science* **214**, 48–56.
- LOMBARDI, C., COCITO, S., HISCOCK, K., OCCHIPINTI-AMBROGI, A., SETTI, M. AND TAYLOR, P.D. 2008. Influence of seawater temperature on growth bands, mineralogy and carbonate production in a bioconstructional bryozoan. *Facies* **54**, 333–342.
- MCCLELLAND, H.L.O., TAYLOR, P.D., O'DEA, A. AND OKAMURA, B. 2014. Revising and refining the bryozoan zs-MART seasonality proxy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **410**, 412–420.
- MCKINNEY F.K. AND JACKSON, J.B.C. 1989. *Bryozoan Evolution*. Boston, Unwin-Hyman, Boston.
- MENON, N.R. 1975. Observations on growth of *Flustra foliacea* (Bryozoa) from Helgoland waters. *Helgoländer wiss Meeresunters* **27**, 263–267.
- MENON, N.R. AND NAIR, N.B. 1972. The growth rates of four species of intertidal bryozoans in Cochin backwaters. *Proceedings Indian National Science Academy* **38**, 397–402.
- NELSON, C.S., HYDEN, F.M., KEANE, S.L., LEASK, W.L. AND GORDON, D.P. 1988. Application of bryozoan zoarial growth form studies in facies analysis of non-tropical carbonate deposits in New Zealand. *Sedimentary Geology* **60**, 301–322.
- NEKLIUDOVA U.A., SHUNKINA K.V., GRISHANKOV A.V., VARFOLOMEEVA M.N., GRANOVITCH A.I. AND OSTROVSKY A.N. 2019. Colonies as dynamic systems: reconstructing the life history of *Cribrilina annulata* (Bryozoa) on two algal substrates. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1–15.
- O'DEA, A. AND OKAMURA, B. 2000. Cheilostome bryozoans as indicators of seasonality in the Neogene epicontinental seas of Western Europe. In: A. Herrera-Cubilla and J.B.C. Jackson (eds.), *Proceedings of the 11th International Bryozoology Association Conference*. Balboa, Smithsonian Tropical Research Institute, pp. 74–86.
- OKAMURA, B. AND PARTRIDGE, J.C. 1999. Suspension feeding adaptations to extreme flow environments in a marine bryozoan. *Biological Bulletin* **196**, 205–215.
- PÄTZOLD, J., RISTEDT H. AND WEFER G. 1987. Rate of growth and longevity of a large colony of *Pentapora foliacea* (Bryozoa) recorded in their oxygen isotope profiles. *Marine Biology* **96**, 535–538.
- REID CM. 2014. Growth and calcification rates in polar bryozoans from the Permian of Tasmania, Australia. In:

- A. Rosso, P.N. Wyse Jackson and J. Porter (eds) *Bryozoan Studies 2013*, Proceedings of the 16th International Bryozoology Association Conference, Catania, Sicily, *Studi Trentini di Scienze Naturali* **94**, 189–197.
- RYLAND, J.S. 1976. Physiology and ecology of marine bryozoans. *Advances in Marine Biology* **14**, 285–443.
- RYLAND, J.S. AND WARNER, G.F. 1986. Growth and form in modular animals: ideas on the size and arrangement of zooids. *Philosophical Transactions of the Royal Society of London B*. **313**, 53–76.
- SAUNDERS, M. AND METAXAS, A. 2009. Effects of temperature, size, and food on the growth of *Membranipora membranacea* in laboratory and field studies. *Marine Biology* **156**, 2267–2276.
- SCHOPF, T.J.M. 1969. Paleocology of ectoprocts (bryozoans). *Journal of Paleontology* **43**, 234–244.
- SKERMAN, T.M. 1958. Marine fouling at the port of Lyttelton. *New Zealand Journal of Science* **1**, 224–257.
- SMITH, A.M. 1995. Palaeoenvironmental interpretation using bryozoans: a review. In: D. Bosence and P. Allison (eds), *Marine Palaeoenvironmental Analysis from Fossils. Geological Society Special Publication* **83**, 231–243.
- SMITH, A.M. 2007. Age, growth and carbonate production by erect rigid bryozoans in Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **256**, 86–98.
- SMITH, A.M. 2014. Growth and calcification of marine bryozoans in a change ocean. *Biological Bulletin* **226**, 203–210.
- SMITH, A.M. AND KEY, M.M., JR. 2004. Controls, variation and a record of climate change in detailed stable isotope record in a single bryozoan skeleton. *Quaternary Research* **61**, 123–133.
- SMITH, A.M., KEY, M.M., JR. AND WOOD, A.C.L. 2019. Culturing large erect shelf bryozoans: skeletal growth measured using calcein staining in culture. In: R. Schmidt, C.M. Reid, D.P. Gordon, G. Walker-Smith, S. Martin and I. Percival (eds), *Bryozoan Studies 2016*. Proceedings of the Seventeenth International Bryozoology Association Conference, 10–15 April 2016, Melbourne, Australia. *Memoirs of the Australasian Association of Palaeontologists* **52**, 131–138.
- SMITH, A.M. AND LAWTON, E.I. 2010. Growing up in the temperate zone: age, growth, calcification and carbonate mineralogy of *Melicerita chathamensis* (Bryozoa) in southern New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology* **298**, 271–277.
- SMITH, A.M. AND NELSON, C.S. 1994. Calcification rates of rapidly colonising bryozoans in Hauraki Gulf, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **28**, 227–234.
- SMITH, A.M., STEWART, B., KEY, M.M., JR. AND JAMET, C.M. 2001. Growth and carbonate production by *Adeonellopsis* (Bryozoa: Cheilostomata) in Doubtful Sound, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology* **175**, 201–210.
- SOBICH, A. 1996. Analyse von stabilen Isotopen und Wachstumsstrukturen der Bryozoe *Celleporaria fusca* zur Rekonstruktion der Umweltbedingungen im nördlichen Golf von Aqaba. Diplomarbeit (Thesis), University of Bremen, 64 pp.
- SOKOLOVER N., OSTROVSKY A.N. AND ILAN, M. 2018. *Schizoporella errata* (Bryozoa, Cheilostomata) in the Mediterranean Sea: abundance, growth rate, and reproductive strategy, *Marine Biology Research*, DOI: 10.1080/17451000.2018.1526385
- STACH, L.W. 1935. Growth variation in Bryozoa Cheilostomata. *The Annals and Magazine of Natural History* **16**, ser 10, 645–647.
- STEBBING, A.R.D. 1971. Growth of *Flustra foliacea* (Bryozoa). *Marine Biology* **9**, 267–272.
- TAYLOR, P.D. AND JAMES, N.P. 2013. Secular changes in colony-forms and bryozoan carbonate sediments through geological history. *Sedimentology* **60**, 1184–1212.
- TAYLOR, P.D. AND E. VOIGT. 1999. An unusually large cyclostome bryozoan (*Pennipora anomalopora*) from the Upper Cretaceous of Maastricht. *Bulletin de L'Institut Royal des Sciences Naturelle de Belgique Sciences de la Terre* **69**, 165–171.
- URIAN, K., GORGONE, A., READ, A., BALMER, B., WELLS, R. S., BERGGREN, P., DURBAN, J., EGUCHI, T., RAYMENT, W., AND HAMMOND, P. S. (2015). Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science*, **31**, 298–321
- WASS, R.E., VAIL, L.L. AND BOARDMAN, R.S. 1981. Early growth of Bryozoa at Lizard Island, Great Barrier Reef. In: G.P. Larwood and C. Nielsen (eds), *Recent and Fossil Bryozoa*, Fredensborg, Olsen and Olsen, 299–303.
- WINSTON, J.E. 1976. Experimental culture of the estuarine ectoproct *Conopeum tenuissimum* from Chesapeake Bay. *Biological Bulletin* **150**, 318–335.
- WINSTON, J.E. 1983. Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica. *Bulletin of Marine Science* **33**, 688–702.
- WINSTON J.E. AND HÅKANSSON, E. 1989. Molting by *Cupuladria doma*, a free-living bryozoan. *Bulletin of Marine Science* **44**, 1152–1158.
- WINSTON, J.E. AND HAYWARD, P.J. 2012. The marine bryozoans of the northeast coast of the United States: Maine to Virginia. *Virginia Museum of Natural History Memoir* **11**, 1–180.
- WOOD, A.C.L. AND PROBERT, P.K. 2013. Bryozoan-dominated benthos of Otago shelf, New Zealand: its associated fauna, environmental setting and anthropogenic threats. *Journal of the Royal Society of New Zealand* **43**, 231–249.



Appendix Table: Summary of published literature on size, age, growth and calcification in 83 species of bryozoans.

Species	Location	Growth form	Reported growth rate	Max observed size (height or radius in mm)	Max observed area (in mm ²)	Max age (y)	Growth rate (extension in mm/y)	Growth rate (area in mm ² /y)	Calcimass (wt% skeleton)	Calcification rate (mg CaCO ₃ /y)	Calcification per zooid (mg CaCO ₃ /zo)	Method	Method Code (Table 4)	Sources
<i>Adomellopsis</i> sp.	Doubtful Sound, Otago shelf, New Zealand	Erect rigid branching	6.9 mm/y branch length, 24g CaCO ₃ /y	300		20	6.9			23700	0.13	Calcein marked in vivo	D	Smith et al., 2001
<i>Adomellopsis</i> sp.	Otago shelf, New Zealand	Erect rigid branching	1 mm/y				1					Calcein marked in culture	E	Smith et al., 2019
<i>Alcyonidium hirsutum</i>	South Wales, UK	Encrusting unilaminar	up to 100 mm ² in 160 days		100	0.4		44				Observation in vivo	D	Hayward & Ryland, 1975
<i>Alderina arabianensis</i>	Cochin, India	Encrusting unilaminar	1964-3020 mm ² /mo in spring		3020			36240				Setting plates	A	Menon & Nair 1972
<i>Alloflustra tenuis</i>	Signy Is	Erect flexible branching	max age 26 y, 63mg ash free dry wty			26				63		Annual growth checks	F	Barnes, 1995
<i>Arachnopusia inchoata</i>	Ryder Bay, Antarctica	Encrusting	mean increase 100 mm ² /y on artificial panels, n = 10; up to 0.4 mm/d radial extension in summer	2.8			5.6					Setting plates	A	Bowden et al., 2006
<i>Bugula neritina</i>	Kaneohe Bay, Hawaii	Erect flexible branching	3 inches in 3 mo, 65mm height in 156 days				152					Setting plates	A	Edmondson & Ingram 1939
<i>Bugula neritina</i>	Nagasaki, Japan	Erect flexible branching	270 zooids, 28mg, in 14 days						730			Larvae sceded then in vivo	B	Kitamura & Hirayama 1984
<i>Bugula</i> sp. (aff. <i>neritina</i>)	Lyttelton, NZ	Erect flexible articulated	7 cm in 2 mo	70		0.2	420					Setting plates	A	Skerman 1958
<i>Caberea zelandica</i>	Lyttelton, NZ	Erect flexible articulated	1-3 cm in 6 mo	30		0.5	60					Setting plates	A	Skerman 1958
<i>Callopora dumerilii</i>	Adriatic Sea	Encrusting unilaminar	52-210 mm ² in 18 mo (mean = 13.1, n=2)				5.5					Setting plates	A	Kuklinski et al., 2013
<i>Cellaria incala</i>	Weddell Sea	Erect flexible articulated	one branchy, 8 mm/y, max age 14 y	100		14	8					Stable isotope profiles	G	Brey et al., 1999
<i>Cellaria sinuosa</i>	English Channel	Erect flexible articulated	max age 1.5-2 y, growth 32-40 mm/y, 12-57 g/m ² /y			2	40			160		Stable isotope profiles	G	Bader, 2000; Bader & Schaefer, 2005
<i>Cellarinella foveolata</i>	Ross Sea	erect branching, flexible base	max size 6cm, 12 internodes (assumed annual)	60		12	5					Annual growth checks	F	Winston, 1983
<i>Cellarinella margueritae</i>	Ross Sea, Weddell Sea	erect branching, flexible base	max size 5.6cm, max 10 internodes; 3.4 mm/y, 24mg CaCO ₃ /y	56		15	4.4			24		Annual growth checks	F	Winston, 1983; Barnes et al. 2007
<i>Cellarinella megovanae</i>	Ross Sea	erect branching, flexible base	max size 8cm, max 18 internodes	80		18	4.4					Annual growth checks	F	Winston, 1983
<i>Cellarinella nodulata</i>	Ross Sea, Weddell Sea	erect branching, flexible base	1.3 to 5.6, mm/y, 5-33 mg/y, max age 18 y, max size 4.8 cm, max 11 internodes; 3.9 mm/y, 55mg CaCO ₃ /y	48		18	5.6			55		Annual growth checks	F	Winston, 1983; Smith, 2007; Barnes et al., 2007
<i>Cellarinella nutti</i>	Ross Sea	erect branching, flexible base	1.0 to 7.1 mm/y, 3-57 mg/y, max age 14 y, max size 5.7cm, max 11 internodes; 3.9 mm/y, 30 mg CaCO ₃ /y	57		14	7.1			57		Annual growth checks	F	Winston, 1983; Barnes et al., 1995; Smith, 2007; Barnes et al., 2011
<i>Cellarinella ogckuae</i>	Weddell Sea	erect branching, flexible base	4.6 mm/y, 45mg CaCO ₃ /y			15	4.6			45		Annual growth checks	F	Barnes et al., 2007
<i>Cellarinella rossi</i>	Ross Sea	erect branching, flexible base	max size 6.0 cm, max 14 internodes	60		14	4.3					Annual growth checks	F	Winston, 1983
<i>Cellarinella roysdi</i>	Antarctica	erect branching, flexible base	7 yrs age			7						Annual growth checks	F	Ryland, 1976
<i>Cellarinella</i> sp. M	Ross Sea	erect branching, flexible base	max age 20 y, 5.4 mm/y			20	5.4					Annual growth checks	F	Winston, 1983

<i>Cellarinella watersi</i>	Signy Is, Weddell Sea	erect branching, flexible base	max age 9 y, max ht 5 cm, 4.1 mm ³ /y, 176 mg CaCO ₃ /y	50	11	4.1													Barnes, 1995; Barnes et al., 2007
<i>Celleporaria fiasca</i>	Gulf of Aqaba	multilaminar	max age 86 y, avg growth 750 μm ³ /y, up to 6.5 cm tall from 1 to 40 mm ² /56 days; from 6 to 591 zooids/56 days (depending on diet)	65	86	0.75													Sobich, 1996
<i>Celleporella hyalina</i>	Wales, UK	Encrusting unilaminar	mean increase 50 mm ² /y on artificial panels, n = 20; up to 0.3 mm/day radial extension in summer	2		4													Hunter & Hughes 1993 and many others
<i>Chaperopsis protecta</i>	Ryder Bay, Antarctica	Encrusting	1.15 mm ³ /y																Bowden et al., 2006
<i>Cinctipora elegans</i>	Otago shelf, New Zealand	Erect rigid branching	up to about 800 zooids in 25-31 days			1.15													Smith et al 2019
<i>Conopeum seurati</i>	Kiel Canal, Germany																		Jehram & Rummert, 1978
<i>Conopeum tenuissimum</i>	Chesapeake Bay USA	Encrusting unilaminar	up to 1629 zooids and 8 generations in 42 days		0.12														Winston 1976
<i>Cribrella annulata</i>	Spitsbergen	Encrusting unilaminar	53 to 88 mm ² in 4 y (n = 4)			1.3													Kuklinski et al., 2013
<i>Cribrella annulata</i>	Kandalaksha Bay, White Sea	Encrusting unilaminar	mean max of 155 zooids in July; radius of about 3 mm (measured off photo), max age 17 mo	3	1.5														Nekhludova et al., 2019
<i>Cristia</i> sp.		Erect flexible braching	180x100 mm in 34 days				18 000												Paul 1942 reported in Menon & Nair
<i>Cryptosula pallasiana</i>	Swansea UK	Encrusting unilaminar	14°C: 100 zooids in 4 weeks; 18C: 300 zooids in 4 weeks																Amri-Vedel et al., 2007
<i>Cryptosula pallasiana</i>	Lytleton, NZ	Encrusting unilaminar	12 cm ² in 6 mo		0.5		1200												Skerman 1958
<i>Cupuladria exfragminis</i>	Gulf of Panama	Encrusting unilaminar	GPI: 16.8 mm diameter, 0.23 g in 1.0 y GP2: 16.6 mm diameter, 0.31 g in 1.5 y GP3: 15.6 mm diameter, 0.20 g in 2.5 y	8.4	2.5	8.4	222	222	230	230									Key et al., 2013
<i>Diplosolen cf obelia</i>	Adriatic Sea	Encrusting unilaminar	82-98 mm ² in 18 mo (mean = 92, n = 3)			3.7													Kuklinski et al., 2013
<i>Diplosolen arctica</i>	Spitsbergen	Encrusting unilaminar	81 to 234 mm ² in 2 y			4.3													Kuklinski et al., 2013
<i>Disporella gordoni</i>	Hauraki Gulf, NZ	Encrusting multilaminar	736 mg CaCO ₃ in one year		1														Smith & Nelson, 1994
<i>Drepanophora tuberculatum</i>	Rio Bueno Harbour, Jamaica	Encrusting unilaminar	median colony area = 0.6 cm ² , smallest reproductive colony = 0.1 cm ² , max colony area 1.4 cm ²				140												Jackson & Wertheimer, 1985
<i>Einhornia crustulenta</i>	Baltic Sea	Encrusting unilaminar	2376 to 8290 mm ² in 8 mo (mean = 4951, n = 4)			77.1													Kuklinski et al., 2013
<i>Electra bengalensis</i>	Cochin, India	Encrusting unilaminar	2213-2828 mm ² /mo in spring				2828												Menon & Nair 1972
<i>Electra crustulenta</i>	Cochin, India	Encrusting unilaminar	314-707 mm ² /mo (June-Jan)				707												Menon & Nair 1972
<i>Electra pilosa</i>	Scotland, Wales, UK	Encrusting unilaminar	311-1758 mm ² in 103 d, lifespan >2 y, 2-15 mm ² /14 days; 15-100 zz/14 days		>2y														Bayer et al., 1994; Bayer & Todd 1996; Hermansen et al., 2001



Summary of published literature on size, age, growth and calcification in 83 species of bryozoans (continuation).

Species	Location	Growth form	Reported growth rate	Max observed size (height or radius in mm)	Max observed area (in mm ²)	Max age (y)	Growth rate (extension in mm/y)	Growth rate (area in mm ² /y)	Calcimass (wt% skeleton)	Calcification rate (mg CaCO ₃ /y)	Calcification per zooid (mg CaCO ₃ /zo)	Method	Method Code (Table 4)	Sources
Encrusting bryozoans (18 spp.)	Hauraki Gulf, NZ	Encrusting, mostly unilaminar	25 to 220 mg CaCO ₃ in one year			1				220		Settling plates	A	Smith & Nelson, 1994
<i>Escharella immersa</i>	Norwegian Sea	Encrusting unilaminar	137 to 175 mm ² in 3 y (n = 4)		400	1.7	2.5	665				Settling plates	A	Kuklinski et al., 2013
<i>Escharoides angela</i>	Lytelton, NZ	Encrusting unilaminar	4 cm ² in 20 mo									Settling plates	A	Skerman 1958
<i>Fenestrulina rugula</i>	Ryder Bay, Antarctica	Encrusting unilaminar	mean increase 50 mm ² /y on artificial panels, n = 50; up to 0.3 mm/day radial extension in summer	2			4					Settling plates	A	Bowden et al., 2006
<i>Figularia</i> sp.	Otago shelf, New Zealand	Encrusting unilaminar	1.38 mm ² /y				1.38					Calcium marked in culture	E	Smith et al., 2019
<i>Filustra foliacea</i>	North Sea	Erect flexible branching	1-1.3 mm ² area of front of branches in 92 days, 80-248 Z in 92 days, 3-12 mg in 92 days		97	3		52		48		Lab Culture	C	Kahle et al., 2003
<i>Filustra foliacea</i>	Wales, North Sea, Baltic Sea, Helgoland, Scotland	Erect flexible branching	12 y age, 15 mm ² , 25 - 220 mg CaCO ₃ /y, lit of 7.93 cm in 8 y, annual growth rates up to 2.65 cm/y			12	10 to 26			about 850		Annual growth checks	F	Stebbing, 1971; Menon 1975; O'Dea & Okamura 2000; Fortunato et al., 2013
<i>Harmeria scutulata</i>	Arctic	Encrusting unilaminar	max diameter of 5.1 mm, less than a year's growth	5.1			2.5					Settling plates	A	Kuklinski & Taylor, 2006
<i>Hornera foliacea</i>	Otago shelf, New Zealand	Erect rigid fenestrate	0.05 mm ² /y				0.05					Calcium marked in culture	E	Smith et al., 2019
<i>Hornera robusta</i>	Otago shelf, New Zealand	Erect rigid branching	0.05 mm ² /y				0.05					Calcium marked in culture	E	Smith et al., 2019
<i>Melicertia chathamensis</i>	Snares Platform, S New Zealand	Blade with flexible base	max size 4 cm, 9 segments, 1.3 to 13.7 mm ² /y, 9 mg CaCO ₃ /y	40		9	13.7			9		Annual growth checks	F	Smith & Lawton, 2010
<i>Melicertia obliqua</i>	Weddell Sea, Ross Sea	Blade with flexible base	max size 6.6 cm, max 22 segments, 4.9 mm ² /y; 34 mg CaCO ₃ /y, max age 32	200		50	8.1			34		Annual growth checks	F	Winston, 1983; Brey et al., 1998; Bader & Schaefer, 2004; Barnes et al., 2007
<i>Membranipora aciculata</i>	Coorong Lagoon, S Australia	Encrusting unilaminar	2 mm/day, max diameter 6 cm	30			730					Observation in vivo	D	Bone 1991
<i>Membranipora membranacea</i>	Nova Scotia & Washington State	Encrusting unilaminar	0.1 to 1.2 mm/day linear extension				438					Lab Culture	C	Saunders & Metaxas 2009
<i>Membranipora membranacea</i>	Friday Harbour, Washington, USA	Encrusting unilaminar	19 days in pipes with different flows: growth rates from 5 to 20 mm ² /day					7300				Larvae seeded then in vitro	C	Eckman & Duggins 1993
<i>Membranipora membranacea</i>	Lough Hyne, Ireland	Encrusting unilaminar	10 days, added 800-900 mm ² mean, 1400 mm ² max, mean growth rate 86-103 mm ² /d					37595				Mark and photograph in situ	D	Okamura & Partridge 1999
<i>Membranipora nitida</i>	Norwegian Sea	Encrusting unilaminar	92 mm ² in 4 y				1.4					Settling plates	A	Kuklinski et al., 2013

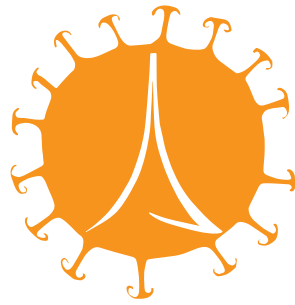
<i>Membranipora</i> sp.		Emerusting unilaminar	41x40mm in 34 days	1640			17605		Settling plates	A	Paul 1942 reported in Menon & Nair 1972
<i>Membranipora</i> sp.	Visakhapatnam Harbour	Emerusting unilaminar	50x50 mm in 30 days	2500			30415		Settling plates	A	Ganapati et al 1958 reported in Menon & Nair 1972
<i>Menipea</i> sp.	Lyttelton, NZ	Erect flexible articulated	8-10mm		10				Settling plates	A	Skerman 1958
<i>Microporoella arctica</i>	Norwegian Sea	Emerusting unilaminar	109 to 139 mm ² in 3 y (n=4); 89 to 192 mm ² in 4 y			2.2			Settling plates	A	Kuklinski et al., 2013
<i>Microporoella</i> sp.	Lizard Island, Queensland, Australia	Emerusting unilaminar	5 mm diameter in 3 months		2.5	0.25	10		Settling plates	A	Wass et al., 1981
<i>Nematofusira flagellata</i>	Signy Is	Erect flexible branching	max age 26 y			26			Annual growth checks	F	Barnes, 1995
<i>Parasmitina</i> sp.	Rio Bueno Harbour, Jamaica	Emerusting unilaminar	median colony area = 5 cm ² , smallest reproductive colony = 0.4 cm ² ; max colony area 46 cm ²	4600							Jackson & Wertheimer, 1985
<i>Patinella</i> sp.	Norwegian Sea	Emerusting unilaminar	8 to 89 mm ² in 2 y; 44.6 in 4 y				1.3		Settling plates	A	Kuklinski et al., 2013
<i>Pennipora anomalopora</i>	Upper Cretaceous; Maasricht, Netherlands	Erect branching	one large fossil colony with dark bands 3 mm apart		105	35	2.9		Annual growth checks	F	Taylor & Voigt, 1999
<i>Pentapora fascialis</i>	UK, NW Europe, Mediterranean	Erect rigid branching	max size 42 cm tall, 82 cm diameter, 358 to 1214 g/m ² /y; 3.6 cm/y, max skeletal mass 35-1098 g. Up to 1m tall, 3 cm/y		1000	11	36	97	Annual growth checks	F	Cocito & Ferdeghini, 2001; Lombardi et al. 2006
<i>Pentapora foliacea</i>	Irish Sea	Erect rigid branching	60 mm in 3 yrs			3	20		Stable isotope profiles	G	Pätzold et al., 1987
<i>Pentapora</i> spp.	Plymouth and Italian Mediterranean	Erect rigid branching	6-7 mm in winter; 12-21 mm in summer; 125 to 889 g/m ² /y, largest branch length 232 mm		116				Annual growth checks	F	Lombardi et al., 2008
<i>Pentellina hincski</i>	Adriatic Sea	Emerusting unilaminar	100 mm ² in 18 mo				3.8		Settling plates	A	Kuklinski et al., 2013
<i>Repaconella 'plagiopora'</i>	Rio Bueno Harbour, Jamaica	Emerusting unilaminar	median colony area = 27 cm ² , smallest reproductive colony = 8 cm ² , max colony area 234 cm ²	23400							Jackson & Wertheimer, 1985
<i>Schizoporella cochranensis</i>	Cochin, India	Emerusting multilaminar	122-260 mm ² /mo in spring	260			3120		Settling plates	A	Menon & Nair 1972
<i>Schizoporella errata</i>	Israeli coast of Mediterranean, Ligurian Sea	Emerusting multilaminar	0.73 cm ² /day; mean max 37 cm ² after 6 weeks; 5.5 cm diam after 3 mo	3700			220	73	Seeding	B	Geraci & Relini 1970; Sokolover et al 2018
<i>Schizoporella sanguinensis</i>		Emerusting multilaminar	30,000 zooids in 5 mo						Settling plates	A	Friedle 1952, reported in Menon & Nair
<i>Schizoporella unicornis</i>	Kaneohe Bay, Hawaii	Emerusting unilaminar	1 mm/d in diameter; 50-70mm in diameter after 3 mo; 132 mm after 60 d				803		Settling plates	A	Edmondson & Ingram 1939
<i>Stegitoporella</i> sp. nov.	Rio Bueno Harbour, Jamaica	Emerusting unilaminar	median colony area = 55 cm ² , smallest reproductive colony = 22 cm ² , max colony area 114 cm ²	11400							Jackson & Wertheimer, 1985



Summary of published literature on size, age, growth and calcification in 83 species of bryozoans (continuation).

Species	Location	Growth form	Reported growth rate	Max observed size (height or radius in mm)	Max observed area (in mm ²)	Max age (y)	Growth rate (extension in mm/y)	Growth rate (area in mm ² /y)	Calcimass (wt% skeleton)	Calcification rate (mg CaCO ₃ /y)	Calcification per zooid (mg CaCO ₃ /zo)	Method	Method Code (Table 4)	Sources				
<i>Stenopora spiculata</i>	Permian of Maria Island, Tasmania, Australia	Erect branching	8.2 to 16 mm/y, max age 25 y; 12% calcimass, 528 mg CaCO ₃ /y, 0.19 mg/zooid			25	16		12	528	0.19	Annual growth checks	F	Reid, 2019				
<i>Stenopora tasmaniensis</i>	Permian of Maria Island, Tasmania, Australia	Erect foliose	35 cm tall, 50 cm wide bilamellar, 12.5 mm thick, 28 y old, 6 mm/y, 1593 mg CaCO ₃ /y, 1.03 mg/zooid	350		28	6		38	1593	1.03	Annual growth checks	F	Reid, 2014				
<i>Stomhyxselosaria watersi</i>	Weddell Sea	erect branching, flexible base	4.5 mm/y, 46 mg CaCO ₃ /y, 11-15 y max age			15	4.5			46		Annual growth checks	F	Barnes et al., 2007				
<i>Sytopoma spongites</i>	Rio Bueno Harbour, Jamaica	Enercusting unilaminar	median colony area = 16 cm ² , smallest reproductive colony = 4 cm ² , max colony area 91 cm ²		9100									Jackson & Wertheimer, 1985				
<i>Swanomia belgica</i>	Ross Sea	erect branching, flexible base	0.6 to 9.7 mm/y, 1-27 mg/y, max age 23 y			23	9.7			27		Annual growth checks	F	Smith, 2007				
<i>Tegella arctica</i>	Spitsbergen	Enercusting unilaminar	276 to 495 mm ² in 3 y (n = 5)				4.2					Settling plates	A	Kuklinski et al., 2013				
<i>Thalamoporella</i> sp.	Lizard Island, Queensland, NSW, Australia	Enercusting unilaminar	4.5x1.5 cm in 3 months		675	0.25		2700				Settling plates	A	Wass et al., 1981				
<i>Taldemunitella vildemunita</i>	Port Hacking, NSW, Australia	Enercusting unilaminar	Six colonies, 148 to 584 mm ² after 9 weeks		584	0.17		3435				Settling plates	A	Wass & Yail 1978				
<i>Vitaticella</i> sp	Lizard Island, Queensland, Australia	Erect flexible articulated	4 cm wide, 3.5 cm tall in 3 months	350		0.25	1400					Settling plates	A	Wass et al., 1981				
<i>Zoobotryon pellicidius</i>	Kaneohe Bay, Hawaii	Erect flexible branching	5 mm in 56 days				33					Settling plates	A	Edmondson & Ingram 1939				
Mean											114	4229	13	87	20988	85	1499	0.45
Min											2	97	0.12	0.05	44	0.38	9	0.13
Max											1000	23400	86	1400	193235	230	23700	1.03
Range											998	23303	85.88	1399.95	193191	229.62	23691	0.9
StdDev											196	6288	16	245	43897	92	5247	0.41
N											28	20	42	54	19	4	20	3

List above = 89
 duplicates = 5
 So N species = 84



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