

Depth patterns in Antarctic bryozoan skeletal Mg-calcite: Can they provide an analogue for future environmental changes?

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ABSTRACT: Factors related to depth have the potential to provide an analogue for future changes in the skeletal mineralogy of calcifying marine organisms and communities, given that oceanic pH decreases with depth, with a minimum pH of <7.7, which corresponds to the predicted pH of shallow waters in the next 85 yr. Antarctic bryozoans are often characterized by surprisingly broad bathymetrical ranges, and thus have potential for the study of depth-related environmental changes. This study addressed depth-related changes in the levels of magnesium (Mg)-calcite in Antarctic bryozoan skeletons for the first time in order to facilitate predictions of ocean acidification effects. Specimens (n = 103) belonging to 4 bryozoan species (3 cheilostomes and 1 cyclostome) were collected at various depths in East Antarctica (Terre Adelie and George V Land) during the CEAMARC cruise (December 2007 to January 2008), and Mg-calcite contents from their calcareous skeletons were studied using X-ray diffraction. A dataset was compiled from existing environmental data for both sampling and neighboring sites. All 4 species were found to be entirely calcitic with low or intermediate Mg-levels. The predicted negative correlation between pH and Mg-calcite was not evident. Higher Mg levels were found in *Fasciculipora ramosa* from the George V Basin, suggesting that high salinity shelf water creates favorable conditions for this species, although alternative environmental and biological factors influencing Mg-calcite in skeletons are also discussed for this species.

KEY WORDS: Skeletal chemistry · Magnesium · Spatial patterns · Ocean acidification

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INTRODUCTION

The observed increases in oceanic temperatures and acidification associated with global environmental change are major concerns worldwide (Doney et al. 2012). The uptake of CO₂ by the oceans, and the resulting decrease in pH, carbonate ion (CO₃²⁻) concentration and the calcium carbonate (CaCO₃) saturation states (Ω) in seawater may have a negative effect on the biomineralization of calcifying taxa (calcium-carbonate shell/skeleton-building organisms)

(Fabry 2008). In particular, the pH of surface oceans, with a current mean of ~8.2, is predicted to fall below pH 7.7–7.8 over the next 85 yr (Caldeira & Wickett 2005) due to exchange of CO₂ with the atmosphere. Moreover, most experimental studies demonstrate decreasing trends of calcification rate with a reduction in CaCO₃ Ω (e.g. Schneider & Erez 2006, Marubini et al. 2008). Ocean acidification (OA) will most likely impede biomineralization, weakening the skeletons of marine calcifiers and promoting skeletal dissolution (Goffredo et al. 2014). Given the essential

biological functions of these skeletons, notably in structural support and protection against predators, the survival of many marine organisms with calcified skeletons may become increasingly compromised as pH levels decline through the current century (Guinotte & Fabry 2008).

Carbonate saturation levels are lowest in the Southern Ocean due to the increase in solubility of calcium carbonate with decreasing temperature. Consequently, the Southern Ocean is likely to be one of the first regions to be affected by OA (Orr et al. 2005). This has prompted the rapid proliferation of studies to assess better how abundant Antarctic calcifiers, such as crustaceans, molluscs, echinoderms and bryozoans, will respond to global environmental change (e.g. McClintock et al. 2009). Unfortunately, knowledge of macrobenthic biodiversity and the environmental factors controlling communities in the Antarctic is poor, especially in some regions with high biodiversity and benthic abundance such as Terre Adélie and George V Land in East Antarctica (Stark 2000, Beaman & Harris 2005). Below the depths that are influenced by anchor ice and ice scour, Beaman & Harris (2005) found communities in East Antarctica to be dominated by highly diverse communities of sponges and bryozoans, as well as high abundances of epifauna within the bioconstructional bryozoans. The Mertz Polynya, an area of ice-free water, dominates the oceanography of the George V Shelf and consequently influences the distribution of these rich communities (Post et al. 2011). During the austral winter, sea-ice production in the polynya region increases water salinity and density, forming very saline high salinity shelf water (HSSW) that flows out of the George V Basin, where the seabed is below the 400 m isobath and bounded by the Mertz and Adélie Banks, via the Adélie Sill. During austral summers, the Adélie Sill is also a conduit for the inflow of warm and oxygen-depleted highly modified circumpolar deep water (HMCDW) into the basin, which promotes melting of sea-ice in the polynya region. Moreover, when the HMCDW is cooled by the atmosphere during winter, it forms winter water (WW) over the basin to depths of about 500 m in the Mertz Bank, with remnant WW filling most of the basin and overlying HSSW in the summer (Beaman & Harris 2005).

Coralline algae, corals, echinoderms, foraminifers, bryozoans and mollusks are among taxa that have been targeted for research on the impacts of OA (Kleypas et al. 2006). The biomineralized skeletons of these organisms are composed of CaCO_3 minerals,

especially aragonite and calcite, with magnesium (Mg) frequently replacing some of the calcium (Ca) ions in calcite (Weiner & Dove 2003). Their skeletons are categorized as low-Mg calcite (LMC; <4 mol% MgCO_3), intermediate-Mg calcite (IMC; 4–8 mol% MgCO_3) and high-Mg calcite (HMC; >8 mol% MgCO_3), following Rucker & Carver (1969). Echinoderms and bryozoans are among the most common marine invertebrates that secrete skeletal calcite containing significant amounts of Mg-calcite. Their HMC skeletons are more soluble than LMC, and consequently, more susceptible to OA, as the solubility of calcite increases with its Mg-calcite content (Brown & Elderfield 1996, Andersson et al. 2008). In particular, bryozoans also have potential for predicting the overall effects of OA on marine calcifiers (Bone & James 1993, Smith 2009). Bryozoan skeletons exhibit a wide range of carbonate mineralogies, from completely aragonitic to bimineralic to entirely calcitic, and from LMC (<1 mol% MgCO_3) to HMC (>12 mol% MgCO_3) (Gordon et al. 2006, Smith et al. 2006, Taylor et al. 2009).

Previous studies have suggested that environmental factors, notably temperature and seawater chemistry, as well as biological factors such as skeletal growth rate and the fractionation ability of the species concerned, play important roles in the incorporation of Mg into skeletons (Stanley 2006, Aranha et al. 2014). Furthermore, Ries (2011) predicted that the Mg-calcite in HMC-producing organisms may change in the future with an increase in atmospheric $p\text{CO}_2$. In particular, surface water pH is high because of photosynthetic uptake of inorganic carbon but decreases with depth to reach a minimum value of between pH 7.6–7.8 at ca. 200–600 m due to the oxidation of organic matter to CO_2 by microbial activity (Palmer 2009). Moreover, $\text{CaCO}_3 \Omega$ is known to decrease with depth, concurrent with increases in total dissolved CO_2 caused by biological respiration and cold temperatures in deep seawater, and is dependent on pressure which effects CaCO_3 solubility (Feely et al. 2009). Thus, depth patterns in carbonate skeletons can potentially provide analogues for future changes in seawater pH and chemistry (Borszcz et al. 2013).

Bryozoans are aquatic, colonial, suspension-feeding invertebrates that inhabit depths between the intertidal to abyssal plains, and at all latitudes in the oceans. They are often dominant skeletal-carbonate producers in temperate and polar waters, with a global species richness of around 5869 species (Bock & Gordon 2013). In particular, the estimated species richness of bryozoans in the Antarctic is

>390 (De Broyer & Danis 2011), and new Antarctic species continue to be found (Kuklinski & Barnes 2009, Figuerola et al. 2013a, Blauwe & Gordon 2014). These colonial invertebrates form the nuclei of many benthic communities, frequently creating patch reefs with high productivity, biodiversity and many ecosystem services and consequent economic benefits (Batson & Probert 2000, Wood et al. 2012, Prather et al. 2013, Wood & Probert 2013). They create microhabitats that are used as spawning, nursery, breeding and feeding areas for organisms of higher trophic levels with a commercial value (biotic services), provide protection from erosion by oceanic currents and waves (physical buffers), generate sediment derived from their skeletons (physical structure services), and promote tourism and fisheries (social/cultural services). Additionally, these organisms generate a variety of ecological products of interest in the constructional and pharmaceutical sectors (Prather et al. 2013). Thus, the negative impact of OA on marine calcifiers can spread across trophic levels of marine food webs and impact the quality and quantity of their ecological goods and services (Guinotte & Fabry 2008, Prather et al. 2013). Antarctic bryozoans, in particular, are often characterized as having circumpolar distributions and broad bathymetric ranges (Hayward 1995, Barnes & Kuklinski 2010, Figuerola et al. 2012). These characteristics give them potential for studying depth-related changes in skeletal Mg-calcite in the Antarctic. However, only 4 studies have assessed mineralogical changes in Antarctic bryozoans as a response to environmental parameters (Borisenko & Gontar 1991, Taylor et al. 2009, Loxton et al. 2013, Loxton et al. 2014a) and none has addressed depth-related changes in Mg-calcite in skeletons within species.

Considering the relatively high level of environmental stability in Antarctica below the limit of ice scour and anchor ice (Dayton et al. 1974), and the decrease in both $\text{CaCO}_3 \Omega$ and pH relative to increasing depth, we can predict a negative correlation between the Mg-calcite level in biomineralized skeletons and depth. Accordingly, Kroh & Nebelsick (2010) found a linear relationship between depth and Mg-calcite in skeletons in echinoderms, globally. In addition, several authors found a lower Mg-calcite content in skeletons of Pacific sea cucumbers and an Antarctic urchin species at greater depths, which was distinct from any temperature effect (Lowenstam 1973, Catarino et al. 2013). Moreover, global decreases in planktonic foraminiferal Mg/Ca ratios relative to increasing depth are due to lower $\text{CaCO}_3 \Omega$

in deeper waters (Lea et al. 2000, Dekens et al. 2002, Regenberg et al. 2014).

To improve our understanding of how Antarctic bryozoans might respond to OA, we investigated skeletal Mg-calcite in 4 common bryozoan species (3 cheilostomes and 1 cyclostome) collected over a range of depths (185–660 m) to (1) determine inter-specific variability in skeletal Mg-calcite, (2) test the prediction that skeletal Mg-calcite, which is a major determinant of mineralogical solubility, decreases along a depth gradient, and (3) investigate the potential influences of environmental and biological factors on bryozoan wt% MgCO_3 in calcite through geographical variability.

MATERIALS AND METHODS

Collection and identification of bryozoan samples

Samples ($n = 103$) of 4 targeted Antarctic bryozoan species were collected from East Antarctica using beam trawl during the CEAMARC cruise on the RSV 'Aurora Australis' (December 2007 to January 2008) (Fig. 1A). The study area covers part of the region Terre Adélie (Adélie Bank, a large plateau over 200 m in depth at 141–142° E) and George V Land (Commonwealth, Watt and Buchanan Bays, and Mertz Glacier; 142–145° E). Study sites were located on the Adélie Bank (Sites 1–5), Adélie Sill (Sites 6 and 7), and in the George V Basin (Sites 8–12) (Fig. 1B). Collection depths ranged from 185–660 m. Sampling sites were geo-referenced using GPS and depth was recorded at each site (Fig. 1, Table 1).

On the research vessel, all bryozoan samples were preserved in similar solutions of 95% ethanol to ensure that any potential effects of the ethanol solution on skeletal Mg content were consistent between all samples. Bryozoan colonies were sorted and identified to species level in the laboratory using an optical microscope and a taxonomic reference guide (Hayward 1995). To confirm identification, a subset of specimens were bleached in sodium hypochlorite, rinsed in freshwater, air-dried, and examined using a LEO SEM at the Natural History Museum in London (Fig. 2).

The 4 abundant and widely distributed Antarctic bryozoan species selected for this study comprised 1 cyclostome (*Fasciculipora ramosa* d'Orbigny, 1839), 2 ascophoran cheilostomes (*Lageneschara lyrulata* (Calvet, 1909) and *Systemopora contracta* Waters, 1904), and 1 anascan cheilostome (*Melicerita obliqua* (Thornely, 1924)).

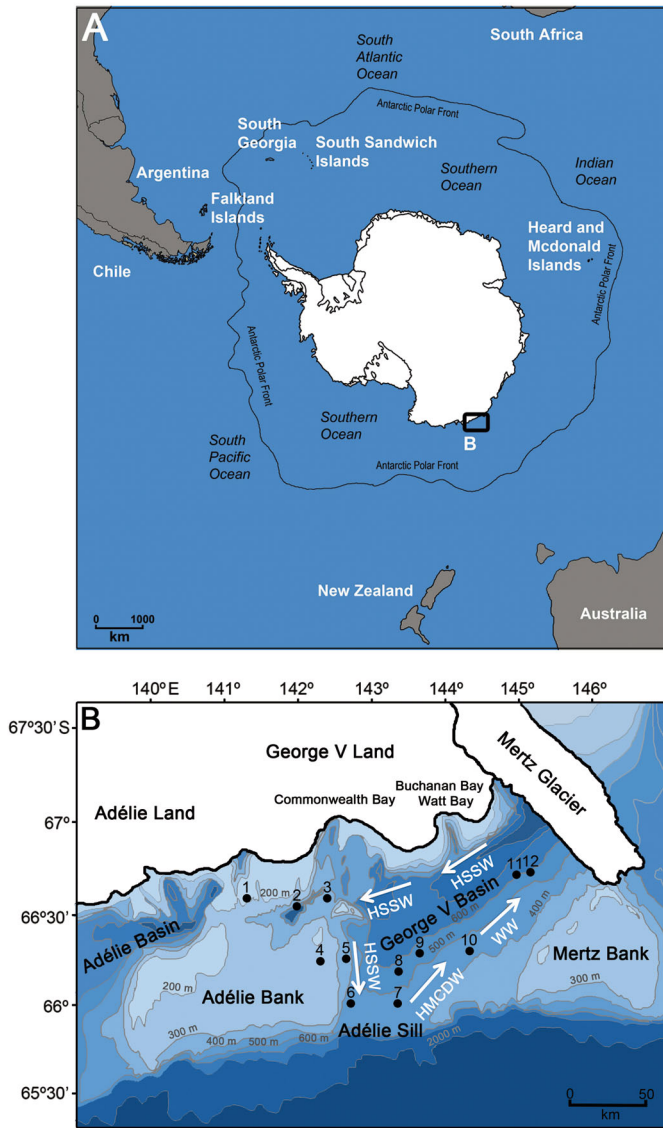


Fig. 1. Location of the study area (Terre Adélie and George V Land) in East Antarctica. (A) General map of Antarctica and neighboring regions, and (B) sampling sites (1–12) with bathymetry and simplified bottom water circulation of the George V Shelf, adapted from Beaman & Harris (2005) and Post et al. (2011). HMCDW = highly modified circumpolar deep water, WW = winter water, HSSW = high salinity shelf water

Environmental and biological data

Existing environmental and biological data for the sampling sites was obtained from Beaman & Harris (2005) (Table 1). Additionally, environmental data for neighboring sites that were of similar depth and close proximity to the CEAMARC cruise sampling sites, were compiled from Australian Antarctic Data Centre databases (Reeve 2010) (Table 2).

Table 1. Depth and coordinates of the sampling sites, environmental data (HMCDW = highly modified circumpolar deep water, WW = winter water, HSSW = high salinity shelf water), biotopes (DB = diverse bank, TS = transitional sill, DF = detritus-feeder basin, SF = suspension-feeder bank), and dominant macrofauna (B = Bryozoa, A = Ascidea) extracted from Beaman & Harris (2005). nd = no data

Site	Stn	Date (dd/mm/yy)	Latitude (S)	Longitude (E)	Depth (m)	Sand/mud (%)	Winter/summer water temp. (°C)	Winter/summer salinity (psu)	Winter/summer near-seabed water masses	Bio-topes	Dominant macrofauna
1	11-424-2527	13/01/08	66° 33' 42"	141° 15' 42"	185	nd	nd	nd	nd	nd	nd
2	9-117-710	26/12/07	66° 32' 5"	141° 58' 57"	520	40–60/40–60	nd/–1.6 to –1.4	nd/<34.55	nd/HMCDW	DB	B/A
3	8-126-761	27/12/07	66° 33' 51"	142° 23' 13"	385	40–60/40–60	nd/–1.8 to –1.6	nd/34.55–34.60	nd/HMCDW	DB	B/A
4	5-107-608	26/12/07	66° 18' 31"	142° 17' 38"	217	40–60/40–60	nd/–1.8 to –1.6	nd/34.55–34.60	nd/HMCDW	DB	B/A
5	6-99-513	26/12/07	66° 19' 52"	142° 40' 50"	390	40–60/40–60	nd/–1.8 to –1.6	nd/34.60–34.65	nd/HMCDW	DB	B/A
6a	27-46-132	22/12/07	66° 0' 50"	142° 42' 57"	443	40–60/40–60	nd/–1.6 to –1.4	nd/34.60–34.65	nd/remnant WW	TS	B
6b	27-33-34	23/12/07	66° 0' 29"	142° 41' 50"	461	40–60/40–60	nd/–1.6 to –1.4	nd/34.60–34.65	nd/remnant WW	TS	B
7	29-55-226	23/12/07	66° 0' 1"	143° 17' 49"	495	40–60/40–60	–1.8 to –1.6/–1.6 to –1.4	>34.65/>34.65	HSSW/remnant WW	TS	B
8	62-303-2003	04/01/08	66° 8' 36"	143° 17' 43"	544	20–60/60–80	<–1.8/–1.8 to –1.6	>34.65/>34.65	HSSW/remnant WW	DF	B
9	36-297-1947	04/01/08	66° 19' 7"	143° 37' 55"	566	20–60/60–80	–1.8 to –1.6/–1.8 to –1.6	>34.65/>34.65	HSSW/remnant WW	DF	B
10	34-288-1849	03/01/08	66° 19' 16"	144° 18' 31"	459	40–60/40–60	–1.8 to –1.6/–1.6 to –1.4	34.60–34.65/34.60–34.65	WW/remnant WW	SF	B/A
11	57-225-1436	31/12/07	66° 44' 43"	144° 57' 44"	660	20–60/60–80	<–1.8/<–1.8	>34.65/>34.65	HSSW/HSSW	DF	B
12	50-220-1393	30/12/07	66° 45' 12"	145° 12' 30"	597	40–60/40–60	<–1.8/<–1.8	>34.65/>34.65	HSSW/HSSW	DF	B

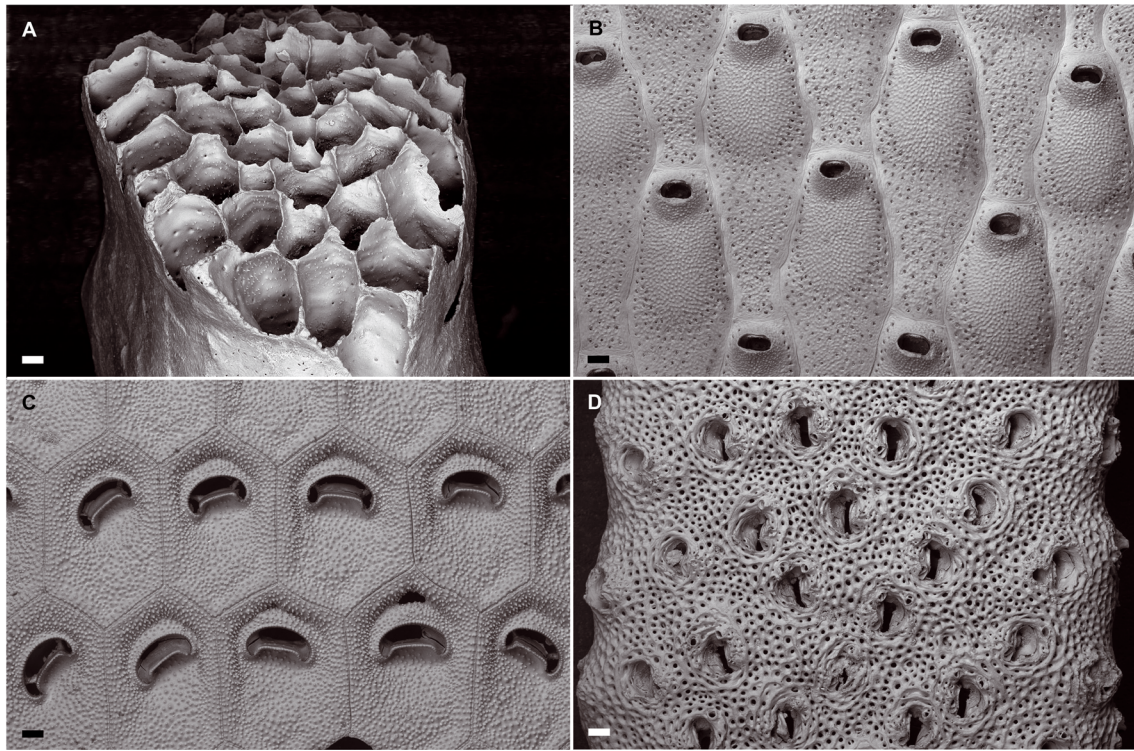


Fig. 2. SEM images of the 4 Antarctic bryozoan species studied: (A) *Fasciculipora ramosa* branch tip (scale bar = 100 μm), (B) *Lageneschara lyrulata*, group of zooids (scale bar = 200 μm), (C) *Melicerita obliqua*, zooids from near centre of branch (scale bar = 100 μm), and (D) *Systemopora contracta*, zooids on branch surface (scale bar = 200 μm)

Mineralogical analysis

For the mineralogical analysis, we used a minimum of 3 replicates, and up to 5 replicate individuals when possible from each species and site. Selected specimens were cleaned carefully of epibionts to avoid mineralogical contamination. From the growing edge of each specimen, a piece (2 mm²) was cut and air-dried as described in previous studies (Kuklinski & Taylor 2009, Loxton et al. 2014a,b). In the case of *M. obliqua* (the only species used in this study for which growth rates have been published and which forms growth check lines), branches grow in colony length by 4.5 mm yr⁻¹ on average (Brey et al. 1998). Therefore, the excised pieces are estimated to have been formed within a period of approximately 9 mo prior to the date of collection; although food supply and growth at these latitudes are highly seasonally variable, the growth check lines are formed annually (Brey et al. 1998). The pieces were powdered using a quartz pestle and mortar and

affixed to single quartz crystal substrates using acetone. Mineralogical analyses were carried out at the Natural History Museum using a high-precision Enraf-Nonius X-ray diffractometer (XRD) equipped with an INEL CPS-120 Curved Position Sensitive detector (-120° , 2-theta) and a cobalt X-ray source. Operating conditions of the cobalt source were 40 kV and 40 mA. The tilt angle between source and sample was 5.9°. The horizontal slit system was set to 0.14 mm to con-

Table 2. Environmental data for the sites close to the sampling sites. Sourced from Australian Antarctic Data Centre databases (Reeve 2010)

Near sites	Date (dd/mm/yy)	Latitude (S)	Longitude (E)	Depth (m)	Water temp. (°C)	Salinity (psu)	Alkalinity ($\mu\text{mol kg}^{-1}$)
1	13/01/08	66° 33' 53"	141° 18' 26"	197	0.05	34.31	2333.12
2, 3	27/12/07	66° 33' 26"	142° 17' 45"	368	-0.83	34.35	2333.55
4, 5	26/12/07	66° 20' 8"	142° 16' 27"	207	-1.22	34.34	2331.09
6a	23/12/07	66° 0' 52"	142° 43' 41"	433	-0.20	34.11	2322.86
6b	23/12/07	66° 0' 49"	142° 39' 43"	443	-0.36	34.13	2319.74
7	24/12/07	66° 1' 29"	143° 18' 46"	478	-0.90	34.06	2310.63
8	04/01/08	66° 11' 4"	142° 57' 13"	581	-0.20	34.13	2318.60
9	04/01/08	66° 18' 33"	143° 18' 40"	701	-0.59	34.19	2320.33
10	04/01/08	66° 19' 10"	143° 58' 25"	505	-0.53	34.19	2322.61
11	31/12/07	66° 44' 42"	144° 58' 21"	668	-0.36	34.21	2325.56
12	31/12/07	66° 45' 10"	145° 15' 28"	599	-0.16	34.21	2322.95

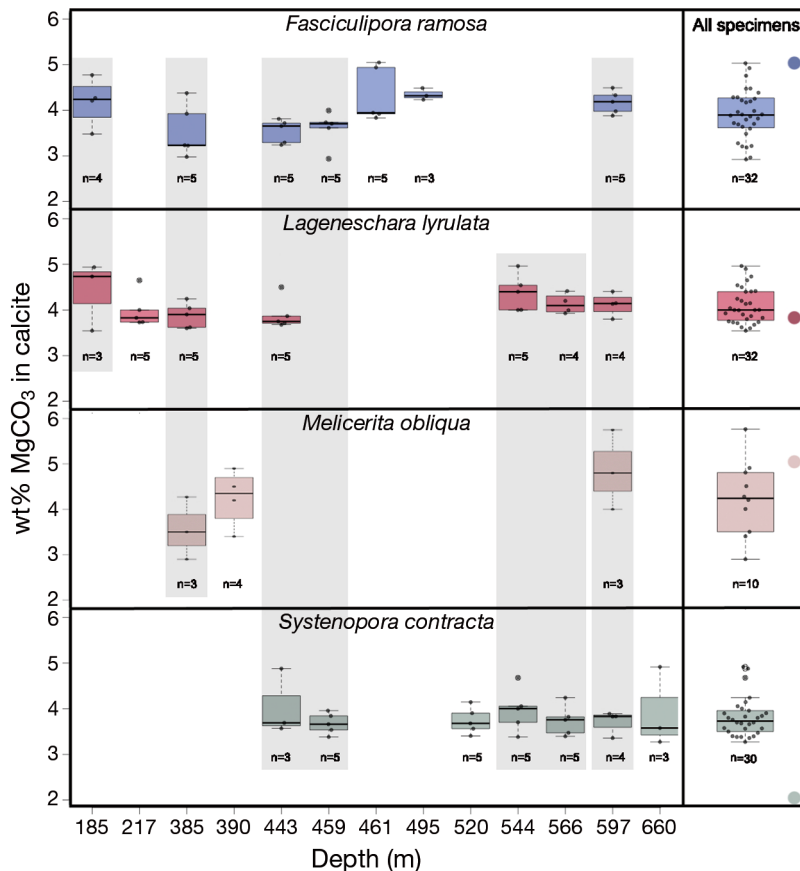


Fig. 3. Mean values (\pm SD) of wt% MgCO₃ in skeletal calcite in the 4 Antarctic bryozoan species among different depths (left panel), and summed mean values (\pm SD) of wt% MgCO₃ in calcite for each species (right panel). Boxes show standard deviation around mean (mid-line), tail indicates range, and scatterplot shows spread of samples (dark grey dots), larger grey dots are outliers. Background shading indicates the samples in the same depth. Large coloured dots in right panel show previous mean values of wt% MgCO₃ in calcite from Borisenko & Gontar (1991) and Taylor et al. (2009)

fine the X-ray beam to pure cobalt $K\alpha_1$. The samples were rotated during the measurements to improve the randomness of grain orientations in the X-ray beam. The 2-theta linearity of the detector was calibrated with silver behenate ($\text{AgC}_{22}\text{H}_{43}\text{O}_2$) and SRM 640 silicon powder (NIST) and the calibration curve was fitted using a least-squares cubic spline function.

The wt% MgCO₃ in calcite was calculated by measuring the position of the d104 peak, assuming a linear interpolation between CaCO₃ and MgCO₃ (Chave 1952, Mackenzie et al. 1983). A linear trend of d104 vs. mol% MgCO₃ can be observed in the range between 0 and 17 mol% MgCO₃ (Mackenzie et al. 1983); all data from the present study fall into this range. This composition information is accurate to within 2% on a well-calibrated instrument (Kuklinski & Taylor 2009).

Data analysis

All variables were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test). Since the data did not meet basic assumptions of parametric ANOVA, significant effects in the skeletal Mg-calcite among depths were further explored with the non-parametric Kruskal-Wallis one-way ANOVA followed by the post-hoc Mann-Whitney *U*-test. In order to determine if a relationship existed between the skeletal Mg-calcite with various environmental variables, non-parametric correlations were calculated (Kendall's tau) (Sokal & Rohlf 1981). Statistical analyses and graphical displays were produced using R version 3.1.2 (R Core Development Team 2014).

RESULTS

Mineralogy and interspecific variability in Mg-calcite

Mineralogies determined for 103 samples revealed that all bryozoan species used in this study were entirely calcitic. *Lageneschara lyrulata* (n = 32) and *Melicerita obliqua* (n = 10) comprised IMC-level skeletons (4–8 wt% MgCO₃ in calcite) with a Mg-calcite content of 4.0 ± 0.39 and 4.2 ± 0.82 wt% MgCO₃ (mean \pm SD), respectively (Fig. 3). Skeletons in the remaining species, *Fasciculipora ramosa* (n = 32) and *Systemopora contracta* (n = 30), consisted of LMC (2–4 wt% MgCO₃ in calcite) with a mean Mg-calcite content of 3.9 ± 0.53 and 3.8 ± 0.42 wt% MgCO₃, respectively (Fig. 3). Both the highest (5.7) and lowest (2.9) values of wt% MgCO₃ in calcite were found in *M. obliqua*.

The ANOVA analysis showed that there is a statistically significant difference in the mean wt% MgCO₃ in calcite among the 4 species (Kruskal-Wallis; $\chi^2 = 8.81$, df = 3, p = 0.031). However, post-hoc testing revealed a statistically significant difference in the mean wt% MgCO₃ in calcite only between *L. lyrulata* and *S. contracta* (Mann-Whitney *U*-test; p = 0.003) (Fig. 3).

Bathymetric variability in Mg-calcite

Kruskall-Wallis 1-way ANOVA analysis showed significant differences in the mean wt% MgCO₃ in calcite among depths in the cyclostome *F. ramosa* ($\chi^2 = 14.64$, df = 6, p = 0.023) (Fig. 3). In contrast, mean wt% MgCO₃ in calcite was not significantly different among depths in the cheilostomes *L. lyrulata* ($\chi^2 = 7.09$, df = 6, p = 0.312), *M. obliqua* ($\chi^2 = 2.66$, df = 2, p = 0.264), and *S. contracta* ($\chi^2 = 1.54$, df = 6, p = 0.956).

Post-hoc Mann-Whitney *U*-tests showed that wt% MgCO₃ in calcite in *F. ramosa* was significantly different between the depth 443 m (Site 6a) and the depths 461 m (Site 6b) (Mann-Whitney *U*-test; p = 0.007), 495 m (Site 7) (p = 0.035) and 597 m (Site 12) (p = 0.007), as well as between the depth 459 m (Site 10) and the depths 495 m (Site 7) (p = 0.035) and 597 m (Site 12) (p = 0.031).

The cyclostome *F. ramosa* did not show a significant positive correlation between depth and wt% MgCO₃ in calcite (Kendall's correlation; p > 0.05). Furthermore, no significant relationships were detected between *F. ramosa* wt% MgCO₃ in calcite and any other environmental variables measured (water temperature, salinity, and alkalinity).

DISCUSSION

Interspecific variability in Mg-calcite

To our knowledge, this is the first study to address depth-related variability in Mg-calcite in skeletons of Antarctic bryozoans in order to assess the potential influences of environmental and biological factors on bryozoan skeletal mineralogy and gain insights into the potential effects of future ocean acidification. All species were found to have entirely calcitic skeletons, thus supporting findings from previous studies which have reported bryozoan skeletons at high latitudes to be mostly calcitic (Smith et al. 2006, Kuklinski & Taylor 2009, Taylor et al. 2009, Loxton et al. 2013). Differences in the mean values of skeletal Mg-calcite were found between *Lageneschara lyrulata* and *Systemopora contracta*. Although these species are both ascophoran cheilostomes, they belong to different families (Romancheinidae and Sclerodomidae, respectively), and some samples from our study were collected from different sites. Therefore, their skeletal Mg-calcite levels could be both biologically and environmentally influenced, as suggested for bryozoans by previous authors (see Taylor et al. 2014).

Moreover, Mg-calcite levels in bryozoan skeletal calcite are apparently biologically controlled at intra- and interspecific levels as well as within individual colonies (Gordon et al. 2006, Smith et al. 2006, Schäfer & Bader 2008, Taylor et al. 2009). In contrast, neither the anascan cheilostome *Melicerita obliqua* nor the cyclostome *Fasciculipora ramosa* showed significant differences in the mean wt% MgCO₃ in calcite with respect to the other 2 species. However, our study only analyzed the mineralogy of *M. obliqua* from 3 sites. The composition of skeletons was categorized as IMC in *M. obliqua* and *L. lyrulata*, and LMC in *S. contracta*, corresponding with the mean wt% MgCO₃ in calcite of these species (5, 3.8 and 1.7, respectively) reported from other Antarctic regions (Borisenko & Gontar 1991, Taylor et al. 2009). The lack of geographical differences in skeletal Mg-calcite levels between several Antarctic regions suggests strong biological control. Although the IMC reported by Borisenko & Gontar (1991) for *F. ramosa* (mean = 5 wt% MgCO₃ in calcite) contrasts with the LMC detected in our study (mean = 3.9 wt% MgCO₃ in calcite), our value is close to the 4 wt% MgCO₃ in calcite upper limit between LMC and IMC.

Kuklinski & Taylor (2009) observed a higher proportion of bryozoan species from higher latitude, colder waters to have LMC skeletons compared to species living in warm waters. Given that aragonite and high Mg-calcite contents in skeletons are more vulnerable to dissolution than calcite (Morse et al. 1980), the lack of aragonite and the IMC or LMC skeletons found in our study could be interpreted as adaptations to cold waters, as suggested by Kuklinski & Taylor (2009). These results thus also support the idea that temperature is an important factor in bryozoan skeletal mineralogy (Taylor et al. 2009).

M. obliqua displayed the greatest variation in skeletal Mg-calcite, suggesting that secondary calcification might be occurring in the sample with the highest Mg-calcite content. During later astogeny, secondary calcification may occur in *Melicerita* spp., resulting in greater amounts of HMC in older parts of the colonies, which could be especially vulnerable to dissolution (Smith & Lawton 2010).

Bathymetric variability in Mg-calcite

The predicted correlation between depth and skeletal Mg-calcite was not found in any of the 4 Antarctic bryozoan species studied here. Similarly, the only other study evaluating this relationship, using data from 52 Arctic bryozoan species, failed to

find a correlation (Borszcz et al. 2013), despite the fact that the Arctic data included a smaller depth range (from <50 to >200 m) than our data from the Antarctic, and that the minimum pH value can vary between 200 and 600 m (Palmer 2009). Borszcz et al. (2013) suggested that Arctic communities may be too young to have adapted to present-day seawater conditions. Moreover, the Antarctic benthos is more ancient than the Arctic (Sirenko 2009). The results from both of these polar bryozoan studies contrast with the positive relationship found globally between depth and skeletal Mg-calcite in echinoderms (Kroh & Nebelsick 2010). Although oceanic pH decreases with depth, reaching a minimum value at ~200–600 m (Palmer 2009), most of our samples were from relatively deep (~400–600 m) locations, where conditions are stable (Dayton et al. 1974). In agreement with a potential positive correlation between pH and Mg-calcite in bryozoan skeletons, a decrease in Mg-calcite was observed at lower pH levels in the temperate bryozoan species *Myriapora truncata* (Pallas, 1766) by Lombardi et al. (2011), although this may reflect the dissolution of Mg-calcite-rich outer walls in the extremely low pH conditions found in their study rather than a reduction in the skeleton as a whole. Although trends of decreasing skeletal Mg-calcite have been observed in some species with a depth-related reduction in $\text{CaCO}_3 \Omega$ (Lowenstam 1973, Catarino et al. 2013, Regenberget al. 2014), further studies should consider a wider depth range to test the effect of the lower $\text{CaCO}_3 \Omega$.

Potential influences of environmental and biological factors on *F. ramosa*

We only observed a response in skeletal composition to changes in the environment in 1 species (*F. ramosa*), suggesting that environmental and biological factors have a variable influence on different species. Several studies using diverse calcifying taxa (e.g. bryozoans, coccoliths, foraminifera and sea stars) have demonstrated that different factors such as alkalinity, water temperature, salinity and the Mg/Ca ratio of seawater can influence Mg-calcite in skeletons (Stoll et al. 2001, Russell et al. 2004, Stanley et al. 2005, Borremans et al. 2009, Loxton et al. 2014a,b). However, although mean values of Mg-calcite in the skeletons of *F. ramosa* differed significantly in several sites, relationships between Mg-calcite and available data on environmental variables from sites nearby were inconsistent. The relatively stable environment below the limit of ice scour and anchor ice (Dayton et al.

1974) may have supported the development of fine-tuned adaptations in Antarctic continental shelf benthic communities to environmental variables. Moreover, the variation detected in these environmental values is probably too low to significantly affect skeletal Mg-calcite in these 4 species. Given the constantly low seawater temperatures in Antarctica, temperature should have little influence on the Mg-calcite in Antarctic bryozoan skeletons (Loxton et al. 2014a). Seawater temperature ranged from -1 to 0°C in our study, which is smaller than the range (-2 to 0.2°C) in the study of Rathburn & De Deckker (1997) who found no significant relationship between temperature and skeletal Mg-calcite in benthic Foraminifera. In the study area, salinity varied by ~ 0.1 psu in regions without the influence of the HSSW; Hermans et al. (2010) reported that minor changes of salinity (3 psu) had no effect on Mg-calcite in skeletons in the temperate sea urchin *Paracentrotus lividus* (Lamarck, 1816). In contrast, Loxton et al. (2014b) found significant correlations between the environmental variables (temperature, salinity and alkalinity) and wt% MgCO_3 in calcite in the temperate bryozoan *Escharella immersa* (Fleming, 1828), and between salinity and pH with wt% MgCO_3 in calcite in the bryozoan *Membraniporella nitida* (Johnston, 1838) despite the narrow ranges of variation in temperature (0.2°C), salinity (1 psu), alkalinity ($200 \mu\text{mol kg}^{-1}$) and pH (0.1) in their study. Stanley et al. (2005) demonstrated that some coccolithophore species incorporated less Mg in their skeletons as the ambient Mg/Ca ratio was reduced under controlled conditions. Furthermore, Segev & Erez (2006) also found a positive correlation between shell Mg-calcite and Mg/Ca in the culturing media in benthic foraminifera. Although no data concerning the variability of Mg/Ca in seawater exist for the Antarctic region, the oceanic Mg/Ca is constant over shorter time scales (Mewes et al. 2014).

Although this study could not detect any relationship between variations in skeletal Mg-calcite of *F. ramosa* and environmental variables measured from nearby sites, these values may vary through the year, especially in this region, given the influence of various water masses with different salinities and temperatures close to the sea-bed (Beaman & Harris 2005). The HSSW could account for some of the differences found in this study between Site 6 and Sites 7 and 12, and between Site 10 and Sites 7 and 12. Although Sites 6 and 7 are both located on the Adélie Sill, Site 7 is influenced by HSSW (>34.66 psu) in winter. Similarly, Sites 10 and 12 are located in the George V Basin but HSSW flows only at Site 12 throughout the entire year (Beaman & Harris 2005).

In contrast, WW (34.66–34.63 psu) encloses Sites 6 and 10. Thus, the higher skeletal Mg-calcite levels at Sites 7 and 12 suggest that *F. ramosa* could be more adapted to conditions of high salinity under the influence of HSSW. Correspondingly, Loxton et al. (2014b) reported that *E. immersa* exhibited a decrease in skeletal Mg-calcite at lower salinities, suggesting this species can suffer some physiological and metabolic stress in these conditions. However, these differences in salinity seem not to affect the abundance of bryozoans, which are the dominant sessile macrofauna at Sites 6, 7 and 12 (Beaman & Harris 2005). Although HMCDW (<34.63 psu) (Beaman & Harris 2005) is found over the Adélie Bank (Site 3) in the summer, Mg-calcite in skeletons did not differ from other sites in our study. The intermediate value in *F. ramosa* wt% MgCO₃ in calcite may be a result of water mass conditions, i.e. a combination of lower salinity than HSSW and WW and warmer water. However, the variability in skeletal Mg-calcite in *F. ramosa* could also be influenced by other environmental variables not evaluated here.

Various biological processes could mask any signal of the environmental effects on mineralogy in bryozoans (Kuklinski & Taylor 2009, Taylor et al. 2009, Loxton et al. 2014b), a phenomenon known as a 'vital effect' (Weiner & Dove 2003). The significant differences found in skeletal Mg-calcite in *F. ramosa* between Site 6 (close to the Adélie Bank zone) and Site 12 (close to the Mertz Glacier zone) could also be partly explained by biological factors, such as food availability (which is known to be important for the incorporation of Mg in calcium carbonate), competition for food, and predation (e.g. Stanley 2006, Aranha et al. 2014). Minimum pH can vary in depth (~200–600 m) among sites, according to the rate of supply of organic matter from the surface and the physical oceanography of the water column (Palmer 2009). Accordingly, the near-seabed water masses create spatial contrasts in nutrient supply in this region (Post et al. 2011). Moreover, Mg-calcite levels in skeletons correlate with skeletal growth rate (kinetic effect), with the expectation that higher food availability would lead to faster growth and a greater amount of Mg-calcite in the skeleton (Ford et al. 2010). Consistent with this, Beans et al. (2008) found differences between these 2 zones with respect to species composition and biomass of the microplankton. The highest values of the phytoplankton biomass and diatom abundance were reported closer to the west of the Mertz Glacier zone, characterized by the presence of a polynya, which is open from September to October, allowing for a phytoplankton bloom.

In addition, the Adélie Bank zone is characterized by an abundant macrofauna whereas the Mertz Glacier Tongue has reduced macrobenthic diversity. Thus, greater predation pressure could exist in several areas of Adélie Bank, potentially affecting mineralogical composition (Beaman & Harris 2005, Beans et al. 2008, Post et al. 2011). Given that the maintenance of skeletons in marine invertebrates is important for protection against predators, and that the HMC skeletons are more soluble than LMC, especially in cold waters (Andersson et al. 2008), predation may have influenced Mg-calcite levels in skeletons during their evolution. In contrast with other geographical regions, generalist echinoderm and crustacean predators, which may exert a higher localized predation pressure than echinoderms, occupy high trophic levels in the Southern Ocean (Dearborn et al. 1983, Huang et al. 2007), which could lead to the development of a greater proportion of LMC skeletons, which are less susceptible to dissolution. Consistent with the high predation pressure on Antarctic bryozoans, recent studies have demonstrated the presence of physical and chemical defences in this taxa against some main predators (Figuerola et al. 2013b, 2014). However, more studies are needed to confirm this hypothesis for LMC skeletons in bryozoans.

CONCLUSIONS

Knowledge of biological responses and tolerances of calcifying organisms to changes in environmental conditions are essential to predict the potential effects of future ocean acidification scenarios and to make management decisions. Mineralogy and geochemistry, especially the Mg contents of skeletal calcite, vary among calcifying species and these variations affect both the solubility and mechanical strength of the skeleton. However, data is sparse on the spatial patterns of Mg-calcite in the skeletons of calcifying organisms in general and bryozoans in particular. Antarctic bryozoans are a potential taxon for studying the depth-related variations in skeletal Mg-calcite, expected as a result of decreasing seawater pH with depth and greater solubility of skeletons with high Mg-calcite contents. However, our results failed to find the expected correlation in the 4 studied species, suggesting that other environmental and biological variables may play more important roles in the incorporation of Mg-calcite into their skeletons. Among the bryozoans in this study, only the single cyclostome species (*Fasciculipora ramosa*)

responds to environmental and biological factors. Further studies are required to ascertain which factors or combination of factors are responsible for determining the geochemistry of bryozoan skeletons and how they might be impacted by global change.

Acknowledgements. The authors thank Jens Najorka (Natural History Museum, UK) for help with XRD analyses and Mary Spencer-Jones for her valuable support at the Natural History Museum and for facilitating the SYNTHESYS visit. We are also very grateful for the helpful suggestions of the anonymous reviewers. We acknowledge the voyage leader, Martin Riddle, the crew and the captain of the RV Aurora Australis. The CAML-CEAMARC cruise of RV 'Aurora Australis' (IPY project no. 53) was supported by the Australian Antarctic Division, the Japanese Science Foundation, the French Polar Institute IPEV and the Muséum National d'Histoire Naturelle. The research stay of B.F. at the Natural History Museum received support from the SYNTHESYS Project www.synthesys.info, which is financed by European Community Research Infrastructure Action under the FP7 'Capacities' Program. The study was completed thanks to the financial support to P.K. from the Polish-Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the frame of Project Contract No. Pol-Nor/196260/81/2013.

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Editorial responsibility: James McClintock, Birmingham, Alabama, USA

*Submitted: July 3, 2015; Accepted: October 6, 2015
Proofs received from author(s): November 11, 2015*