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Skeletal magnesium content in Antarctic echinoderms along a latitudinal gradient

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ABSTRACT

Ocean warming and acidification driven by anthropogenic CO_2 emissions may impact the mineral composition of marine calcifiers. Species with high skeletal Mg content could be more susceptible in polar regions due to the increased solubility of CO_2 at lower temperatures. We aimed to assess the environmental influence on skeletal Mg content of Antarctic echinoderms belonging to Asteroidea, Ophiuroidea, Echinoidea and Holothuroidea classes, along a latitudinal gradient from the South Shetland Islands to Rothera (Adelaide Island). We found that all skeletal structures, except for echinoid spines, exhibited high Mg content, with asteroids showing the highest levels. Our results suggest that asteroids and holothuroids exert a higher biological capacity to regulate Mg incorporation into their skeletons. In contrast, the variability observed in the skeletal Mg content of ophiuroids and echinoids appears to be more influenced by local environmental conditions. Species-specific differences in how environmental factors affect the skeletal Mg content can thus be expected as a response to global climate change.

1. Introduction

Ocean warming (OW) and ocean acidification (OA) pose significant global threats to marine ecosystems worldwide, disrupting biological interactions (e.g., predator-prey relationships) and essential processes (e.g., synthesis of natural products or metabolism) and thus resulting in ecosystem shifts and biodiversity loss (Brierley and Kingsford, 2009; Bellard et al., 2012; Poloczanska et al., 2016; IPCC, 2022). Marine calcifiers, whose skeletons are primarily composed of calcium carbonate ($CaCO_3$), may be particularly susceptible to both stressors. This is because the combination of elevated seawater temperatures and reduced pH, along with changes in the $CaCO_3$ saturation state (Ω) could impair their biomineralization and eventually cause the dissolution of their skeletal structures (Orr et al., 2005; Figuerola et al., 2021, 2023). Moreover, the negative effects of OW and OA on marine calcifiers could be amplified in polar regions, where the solubility of CO_2 is greater at lower temperatures (Brasier et al., 2021).

Marine calcifiers form their skeletal structures from either calcite or aragonite, two primary carbonate polymorphs, with aragonite being more soluble than calcite. Calcite can also incorporate magnesium (Mg), which increases skeletal solubility due to its reduced structural stability (Morse et al., 2006; Dubois, 2014). Other factors, such as crystal size or the presence of impurities, may also contribute to higher solubility (Morse et al., 2007). Based on their solubility degree, the skeletal Mg content is typically classified as low-Mg calcite (LMC; <4 mol% $MgCO_3$), intermediate-Mg calcite (IMC; 4–8 mol% $MgCO_3$) or high-Mg calcite (HMC; >8 mol% $MgCO_3$) (Rucker and Carver, 1969). A higher skeletal Mg content is also linked to changes in physical skeletal properties. For instance, HMC structures tend to be harder than those composed of LMC (Ma et al., 2008; Kanold et al., 2015; Bianco-Stein et al., 2022; Gorzelak et al., 2024).

The skeletal Mg content may be influenced by environmental factors, such as seawater Mg^{2+}/Ca^{2+} ratio, temperature, salinity, $CaCO_3Ω$ and pH (Ries, 2010; Figuerola et al., 2015, 2019, 2023; Lebrato et al., 2016; Kołbuk et al., 2019, 2020, 2021). For instance, temperate marine calcifiers tend to form skeletons with higher Mg content compared to polar species, probably due to warmer seawater temperatures at lower latitudes (Andersson et al., 2008; Taylor et al., 2009; McClintock et al.,

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2011; Smith et al., 2013; Figuerola et al., 2023). Additionally, a higher seawater Mg^{2+}/Ca^{2+} ratio may result in increased Mg content in their skeletons (Ries, 2009, 2010; Kołbuk et al., 2019, 2020, 2021). However, the individual and combined effects of environmental factors on skeletal Mg content still remain unclear for most species (Byrne et al., 2014; Khalil et al., 2022). In addition, biological factors, such as diet, growth rate, genetic control or lifestyle (e.g., sessile or free movement) may also influence the skeletal Mg content, depending on the species (Weiner and Dove, 2003; Andersson et al., 2008; Asnaghi et al., 2014; Iglikowska et al., 2018; Figuerola et al., 2019, 2021).

Echinoderms are benthic invertebrates distributed from temperate to polar regions and inhabiting environments ranging from the intertidal zone to the deep-sea (Jossart et al., 2023, 2024; Rahman and Zamora, 2024). This phylum consists of five extant classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins), Holothuroidea (sea cucumbers) and Crinoidea (sea lilies) (Arnone et al., 2015; Rahman and Zamora, 2024). Some of their representatives play keystone roles in ecosystems, influencing benthic community structures and also contributing to the marine carbon cycle (McClintock, 1994; Lebrato et al., 2010). In Antarctic benthic ecosystems, echinoderms are abundant and diverse, with some species acting as top-predators (Clarke and Johnston, 2003; Lockhart and Jones, 2008; McClintock et al., 2008). Echinoderms typically possess HMC skeletons, which may make them more susceptible to environmental changes (McClintock et al., 2011; Smith et al., 2016a). However, their skeletal structures are covered by an epidermis, which acts as a barrier from the seawater, potentially mitigating environmental impacts (Dery et al., 2014, 2017; Collard et al., 2016). While several studies have determined the skeletal Mg content across various echinoderm species (e.g., Clarke and Wheeler, 1922; Weber, 1973; Ries, 2011; McClintock et al., 2017; Duquette et al., 2018a), research specially focused on polar species remains limited (i.e., McClintock et al., 2011; Catarino et al., 2013; Iglikowska et al., 2017, 2018, 2020; Duquette et al., 2018b; Azcárate-García et al., 2024). In this context, studies conducted along latitudinal gradients, despite the significant logistical challenges in Antarctica, are particularly valuable for understanding species' mineralogical responses to different stressors associated with global change (e.g., McClintock et al., 2011; Figuerola et al., 2023; Piwoni-Piórewicz et al., 2024).

To investigate the impact of different environmental factors on the skeletal mineralogy of Antarctic echinoderms, we analyzed the skeletal Mg content in selected species belonging to the classes Asteroidea, Ophiuroidea, Echinoidea and Holothuroidea along a latitudinal gradient, ranging from the South Shetland Islands (62°) to Rothera (Adelaide Island; 67°). We hypothesized that populations from higher latitudes would display lower skeletal Mg content compared to those from lower latitudes due to colder seawater temperatures.

2. Material and methods

2.1. Environmental variables

Environmental variables (i.e., seawater temperature (°C), pH, conductivity (ms cm^{-1}) and oxygen saturation (%); Table 1) were measured using a HANNA HI98194 multiparameter probe ($n = 3$–9) at the same depth where the organisms were collected. Additionally, annual seawater temperature data, corresponding to sea surface temperature data (SST; °C; Supplementary Material Table S1), were extracted from ERDAP (NOAA; https://coastwatch.pfeg.noaa.gov/erddap/index.html) and compared to ensure reliability.

2.2. Sample collection

Echinoderm species belonging to the classes Asteroidea (i.e., *Odontaster validus* Koehler, 1906, *O. meridionalis* (E.A. Smith, 1876), *Perknaster* sp., *Diplasterias brucei* (Koehler, 1907), *Labidiaster annulatus* Sladen, 1889 and *Cuenotaster involutus* (Koehler, 1912); Supplementary Material Fig. S1), Ophiuroidea (i.e., *Ophionotus victoriae* Bell, 1902; Supplementary Material Fig. S2), Echinoidea (i.e., *Sterechinus neumayeri* (Meissner, 1900)) and Holothuroidea (i.e., *Heterocucumis steineni* (Ludwig, 1898)) were collected by SCUBA diving (up to 4 replicate specimens when possible from each species) at depths ranging from 7 to 25 m from the South Shetland Islands to Adelaide Island (Antarctica) from January to March 2023 (except for the specimen of *L. annulatus*, which was collected at Whaler's Bay South (Deception Island) in December 2008; Fig. 1; Supplementary Material Fig. S3; Supplementary Material Table S2). Individuals were then placed into plastic bottles filled with seawater and transported to the laboratory where they were taxonomically identified and then stored at −20 °C until dissection was conducted at the University of Barcelona.

2.3. Dissection protocol

Skeletal structures of collected specimens were dissected in the laboratory following the protocol described by McClintock et al. (2011). For asteroid species (i.e., *O. validus*, *O. meridionalis*, *Perknaster* sp., *D. brucei*, *L. annulatus* and *C. involutus*), one random selected arm was excised. For the ophiuroid specimen (i.e., *O. victoriae*), one random selected arm and a segment of the central disk were excised. For the echinoid specimen (i.e., *S. neumayeri*), a segment of the test and the Aristotle's lantern were excised, and spines were scraped with a dissecting blade. Finally, for the holothuroid specimen (i.e., *H. steineni*), the calcareous ring surrounding the pharynx was extracted. After dissection, soft body tissues were carefully removed by hand without the application of bleaching techniques (Smith et al., 2016b) and the skeletal body components were dried at 60 °C for 48 h and stored until mineralogical analyses were conducted.

Table 1

Details of the sampling stations, latitude and longitude, depth (m) and environmental variables (seawater temperature (°C), pH, conductivity (ms cm^{-1}), and oxygen saturation (O_2; %)), where the echinoderm specimens were collected. Environmental variables data represent mean ± standard deviation (SD). ^{1}n = 1; ^{2}Data measured in the intertidal; ^{3}Mean sea surface temperature data for February 2023 extracted from ERDAP (NOAA; https://coastwatch.pfeg.noaa.gov/erddap/index.html).

Island	Station	Latitude	Longitude	Depth (m)	Temperature (°C)	pH	Conductivity (ms cm^{-1})	O_2 (%)
King George Is.	Fildes Bay	−62.18348	−58.85438	25	1.97 ± 0.27^3	7.93^1	52.44^1	102.95^1
Livingston Is.	Hesperides Point	−62.64475	−60.37770	15–20	2.11 ± 0.29^3	8.04^1	52.46^1	100.50^1
	Antarctic Spanish Base	−62.66143	−60.38522	7	2.14 ± 0.31^3	8.10^1	52.47^1	90.50^1
Deception Is.	Bidones East	−62.99144	−60.62867	15–20	2.58 ± 0.02	7.79 ± 0.01	52.13 ± 0.20	110.20 ± 5.47
	Whaler's Bay South	−62.99244	−60.56422	15	2.38 ± 0.01	7.90 ± 0.01	52.70 ± 0.01	108.93 ± 3.75
Rongé Is.	Rongé	−64.68980	−62.62997	25	1.34 ± 0.17^3	8.05 ± 0.03^2	52.37 ± 0.02^2	98.37 ± 1.00^2
Anvers Is.	Palmer	−64.76162	−64.08278	15–20	1.17 ± 0.24	7.97 ± 0.01	52.69 ± 0.03	96.57 ± 2.76
Goudier Is.	Port Lockroy	−64.82590	−63.49415	15–20	1.20 ± 0.16	7.96 ± 0.03	52.50 ± 0.03	96.57 ± 2.94
Irizar Is.	Irizar	−65.22505	−64.20207	25	0.85 ± 0.21	8.01 ± 0.03	52.40 ± 0.60	99.67 ± 4.79
Adelaide Is.	Rothera	−67.55450	−68.19717	15–20	0.82 ± 0.23	7.97 ± 0.04	52.10 ± 0.52	100.73 ± 3.01

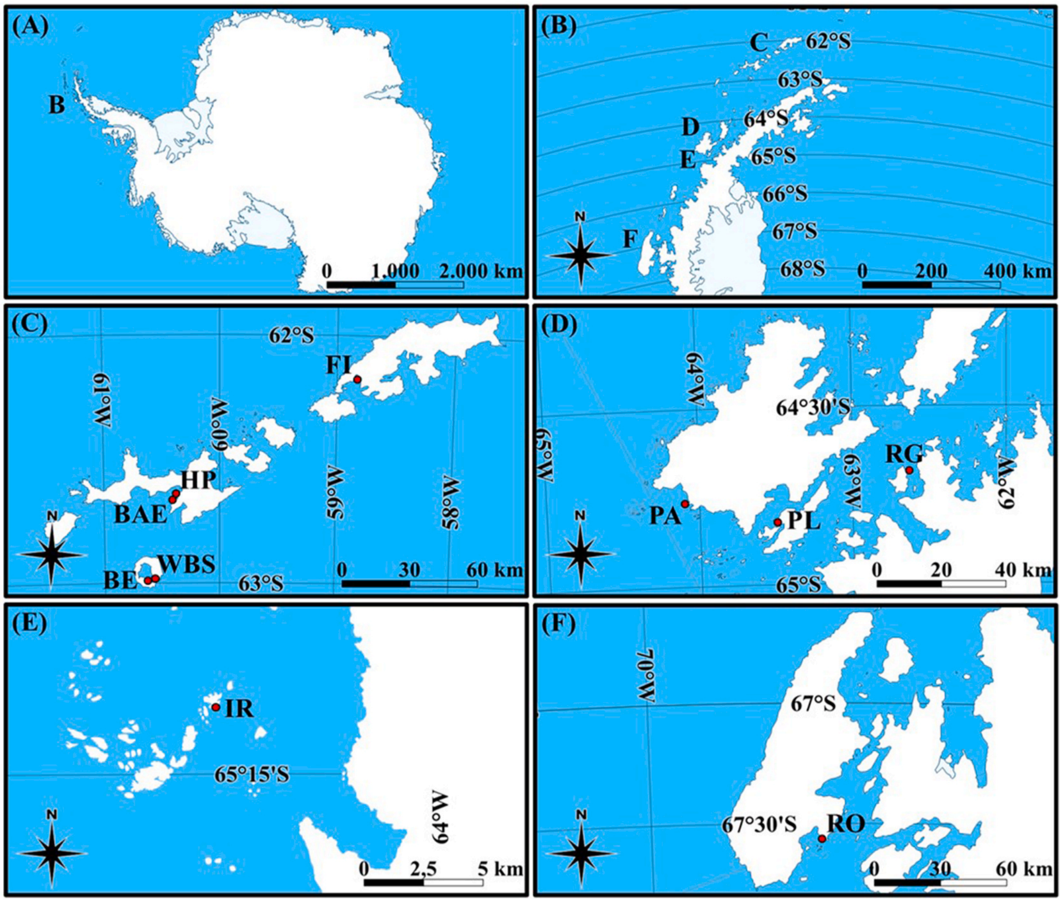

Fig. 1. (A) Map of Antarctica showing the Antarctic Peninsula; (B) map of Antarctic Peninsula indicating the sampling stations along the latitudinal gradient; (C) map of South Shetland Islands indicating Fildes Bay (FI) station at King George Island, Hesperides Point (HP) and Antarctic Spanish Base (BAE) stations at Livingston Island and Whaler's Bay South (WBS) and Bidones East (BE) stations at Deception Island; (D) map of Palmer (PA) station at Anvers Island, Port Lockroy (PL) station at Goudier Island and Rongé Island (RG) station; (E) map indicating Irizar Island (IR) station; and (F) map of Adelaide Island indicating Rothera (RO) station. Maps were made using the Quantarctica package of the QGIS software (Matsuoka et al., 2018).

2.4. Mineralogical analyses

Mineralogical analyses were conducted at the Scientific and Technological Centers of the University of Barcelona (CCiT-UB) following the same protocol applied in Azcárate-García et al. (2024). Dry echinoderm's skeletal components were grounded in an agate mortar and transferred with 70% ethanol to 25 x 25 × 2 mm quartz crystal substrates, dried at room temperature, and assembled to a standard sample holder for bulk samples (PW1812/00). The d104 peak of the calcite was obtained using a PANalytical X'Pert PRO MPD Alpha1 powder diffractometer in reflection Bragg-Brentano θ/2θ geometry equipped with a X'Celerator detector and a copper X-ray source operating at 45 kV and 40 mA. Finally, a linear interpolation among $CaCO_3$ and $MgCO_3$ was applied to assess the skeletal Mg content (mol% $MgCO_3$) presented in the body skeletal component of collected echinoderms (Chave, 1952). The analytical error of the measurements was ±0.1 mol% $MgCO_3$.

2.5. Statistical analyses

Prior to statistical analyses, normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) of the data were tested. For data that met the criteria, analyses of variance (ANOVA) and multiple post-hoc comparisons (Tukey's pairwise test) were applied. For data that did not meet the criteria, a non-parametric test (Kruskal-Wallis test) and multiple post-hoc comparisons (Dunn test) were applied. Firstly, to identify differences in the environmental conditions among sampling stations, a one-way ANOVA with station (St) as a single factor was applied for each environmental variable. To visualize these differences, a principal component analysis (PCA) was conducted (Fig. 2). Additionally, to validate the substitution of absent seawater temperature data by SST extracted from ERDAP (corresponding to February 2023), a

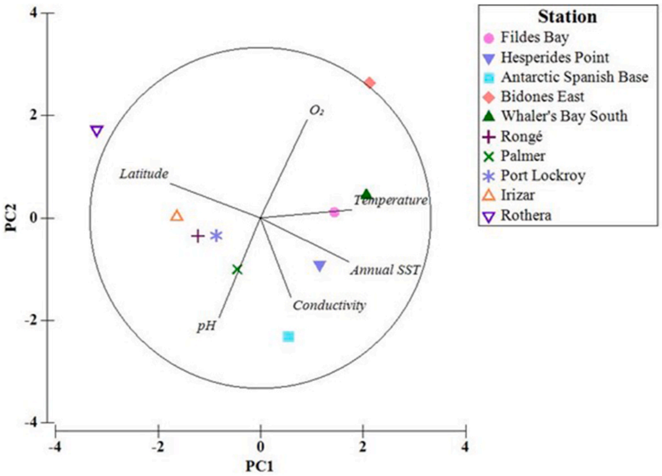

Fig. 2. Principal component analysis (PCA) showing the similarity of the sampling stations where echinoderms were collected based on latitude, seawater temperature (°C), annual sea surface temperature (Annual SST; °C), pH, conductivity (ms cm^{-1}) and oxygen saturation (O_2; %).

one-way ANOVA with data source (Ds) as a single factor was conducted for Bidones East, Whaler's Bay South and Irizar (Supplementary Material Table S3). To study interclass differences in the skeletal Mg content among collected echinoderm classes, a one-way Kruskal-Wallis test with class (Cl) as a single factor was applied (for Ophiuroidea and Echinoidea classes, the skeletal Mg content presented in the arms and test, respectively, was analyzed). To identify interspecific differences in the skeletal Mg content of Asteroidea species, a one-way ANOVA with species (Sp) as a single factor was conducted. To study latitudinal differences in the skeletal Mg content among sampling stations, an ANOVA or Kruskal-Wallis test with station (St) as a single factor was applied for each studied species. To visually compare the potential influence of the environmental variables on the skeletal Mg content between species, another PCA was also conducted (Supplementary Material Fig. S4). Finally, to assess differences in skeletal components in ophiuroid and echinoid species, an ANOVA or Kruskal-Wallis test with skeletal structure (Ss) as a single factor was applied. Statistical analyses were conducted using the statistical software Rstudio 4.1.2 and PRIMER and PERMANOVA 6.

3. Results

3.1. Environmental variables

Significant differences in the seawater temperature (°C), pH, and oxygen saturation (%) were observed among sampling stations (ANOVA, $P < 0.05$; Supplementary Material Table S4). Overall, higher seawater temperatures were measured at the stations located in the South Shetland Islands (2.24 ± 0.31 °C) (i.e., King George, Livingston and Deception Islands; Table 1) compared to southern stations (1.00 ± 0.30 °C) (i.e., Rongé, Palmer, Port Lockroy, Irizar and Rothera). The pH levels measured in seawater at Deception Island stations were also lower than those from other stations. In particular, the most acidic conditions were observed in Bidones East (7.79 ± 0.01). Deception Island also showed higher seawater oxygen saturation compared with Livingston, Rongé, Palmer, Port Lockroy and Rothera stations. By contrast, no significant differences in the seawater conductivity among stations were observed (ANOVA, $P > 0.05$).

The principal component analysis (PCA; Fig. 2) grouped the stations distributed at higher latitudes (i.e., Rongé, Palmer, Port Lockroy, and Irizar). The stations located at the South Shetland Islands (i.e., Antarctic Spanish Base, Hesperides Point, Fildes Bay, and Whaler's Bay South) were also grouped, but they were more disperse, showing larger variability in the environmental parameters. Finally, Rothera and Bidones East were more separated from the other two groups, indicating that their environmental conditions differed more markedly than those of the rest of the stations. The PCA results indicated that the PC1 (51.6% of variation; λ: 3.10) and the PC2 (32.6% of variation; λ: 1.96) were both significant and explained 84.2% of the variance.

3.2. Latitudinal variations in skeletal Mg content

Significant differences in the skeletal Mg content among echinoderm classes were observed (Kruskal-Wallis, $P < 0.05$; Supplementary Material Table S5), with asteroid specimens displaying the highest mean values (17.7 ± 0.3 mol% $MgCO_3$), followed by the ophiuroid specimen (arms and central disk: 16.8 ± 0.3 mol% $MgCO_3$), the holothuroid specimen (15.7 ± 1.8 mol% $MgCO_3$) and the echinoid specimen (test: 10.9 ± 0.6 mol% $MgCO_3$; spines: 3.7 ± 0.3 mol% $MgCO_3$; Aristotle's lantern: 11.2 ± 1.6 mol% $MgCO_3$).

Significant interspecific differences were observed among asteroid species (ANOVA, $P < 0.05$). The two species belonging to the genus *Odontaster* showed the lowest skeletal Mg content among the studied asteroid species. In particular, *O. meridionalis* (17.5 ± 0.2 mol% $MgCO_3$) showed significant lower skeletal Mg content than *Diplasterias brucei* (17.8 ± 0.2 mol% $MgCO_3$), *Perknaster* sp. (17.9 ± 0.2 mol% $MgCO_3$) and *Labidiaster annulatus* (17.9 ± 0.3 mol% $MgCO_3$), while *O. validus* (17.6 ± 0.2 mol% $MgCO_3$) showed significant lower skeletal Mg content than *Perknaster*. No significant differences were observed among the other asteroid species. Furthermore, the asteroid species analyzed did not show any significant differences in their skeletal Mg content among sampling stations (ANOVA, $P > 0.05$) (Fig. 3; Supplementary Material Table S6).

In the case of the ophiuroid *Ophionotus victoriae*, while no significant differences were observed among the arms and the central disk (ANOVA, $P > 0.05$; Fig. 4), there were significant differences among sampling stations in both arms and central disk (ANOVA, $P < 0.05$). In particular, the skeletal Mg content measured in both skeletal body components at BAE (arms: 16.8 ± 0.1 mol% $MgCO_3$; central disk: 16.9 ± 0.1 mol% $MgCO_3$) and Bidones East (arms: 17.0 ± 0.1 mol% $MgCO_3$; central disk: 17.2 ± 0.1 mol% $MgCO_3$) showed significantly higher skeletal Mg content than in Rothera (arms: 16.5 ± 0.1 mol% $MgCO_3$; central disk: 16.4 ± 0.1 mol% $MgCO_3$). Additionally, the Mg content of *O. victoriae* showed positive correlation with seawater temperature (R^2: 0.79; $P < 0.05$; Fig. 5).

The skeletal Mg content of the echinoid *Sterechinus neumayeri* showed significant differences among skeletal body components (Kruskal-Wallis, $P < 0.05$), exhibiting higher skeletal Mg content in the test and Aristotle's lantern than in the spines. Significant differences in the skeletal Mg content of the Aristotle's lantern among sampling stations were also observed (ANOVA, $P < 0.05$), displaying significantly higher skeletal Mg content in Bidones East (12.5 ± 1.0 mol% $MgCO_3$) than in Rothera (10.0 ± 1.0 mol% $MgCO_3$). By contrast, no significant differences in the skeletal Mg content of the test and spines among Bidones East (test: 11.3 ± 0.5 mol% $MgCO_3$; spines: 3.7 ± 0.3 mol% $MgCO_3$) and Rothera (test: 10.5 ± 0.5 mol% $MgCO_3$; spines 3.6 ± 0.3 mol% $MgCO_3$) were observed.

The skeletal Mg content of the holothuroid *Heterocucumis steineni* showed no significant differences among sampling stations (ANOVA, $P < 0.05$), displaying a mean skeletal Mg content of 15.7 ± 1.8 mol% $MgCO_3$.

4. Discussion

Our study offered valuable insights into how environmental and biological factors influence skeletal Mg content in a range of Antarctic echinoderm species along a latitudinal gradient. Notably, we provided the first data on skeletal Mg content for the species *D. brucei*, *C. involutus* and *H. steineni*. All the echinoderms examined here exhibited HMC in their skeletal structures, except for the sea urchin spines, which showed LMC, consistent with previous findings in the literature data (Catarino et al., 2013; McClintock et al., 2017; Iglikowska et al., 2018; Azcárate-García et al., 2024).

4.1. Interclass and interspecific variations of skeletal Mg content

Our results revealed significant interclass variations in skeletal Mg content, with asteroid species having the highest values of skeletal Mg content, followed by ophiuroids, holothuroids, and echinoids. This pattern aligns with previous mineralogical studies on echinoderms (e.g., McClintock et al., 2011; Iglikowska et al., 2017; Duquette et al., 2018b; Azcárate-García et al., 2024). The skeletal Mg content ranges observed in our study are consistent with previous research on Antarctic echinoderms (11.7–18.7 mol% $MgCO_3$ in asteroids; 14.2–17.3 mol% $MgCO_3$ $MgCO_3$ in ophiuroids (central disk and arms); 11.8–12.9 mol% $MgCO_3$ in holothuroids; 9.5–16.1 mol% $MgCO_3$ in echinoids (test)), except for holothuroids, which exhibited higher values here (12.2–18.0 mol% $MgCO_3$) (McClintock et al., 2011; Azcárate-García et al., 2024). Interspecific differences in the skeletal Mg content were also detected among sea star species. Specifically, *Perknaster* sp., *L. annulatus, D. brucei* and *C. involutus* showed higher skeletal Mg content compared to *O. meridionalis* and *O. validus*. These results are consistent with previous

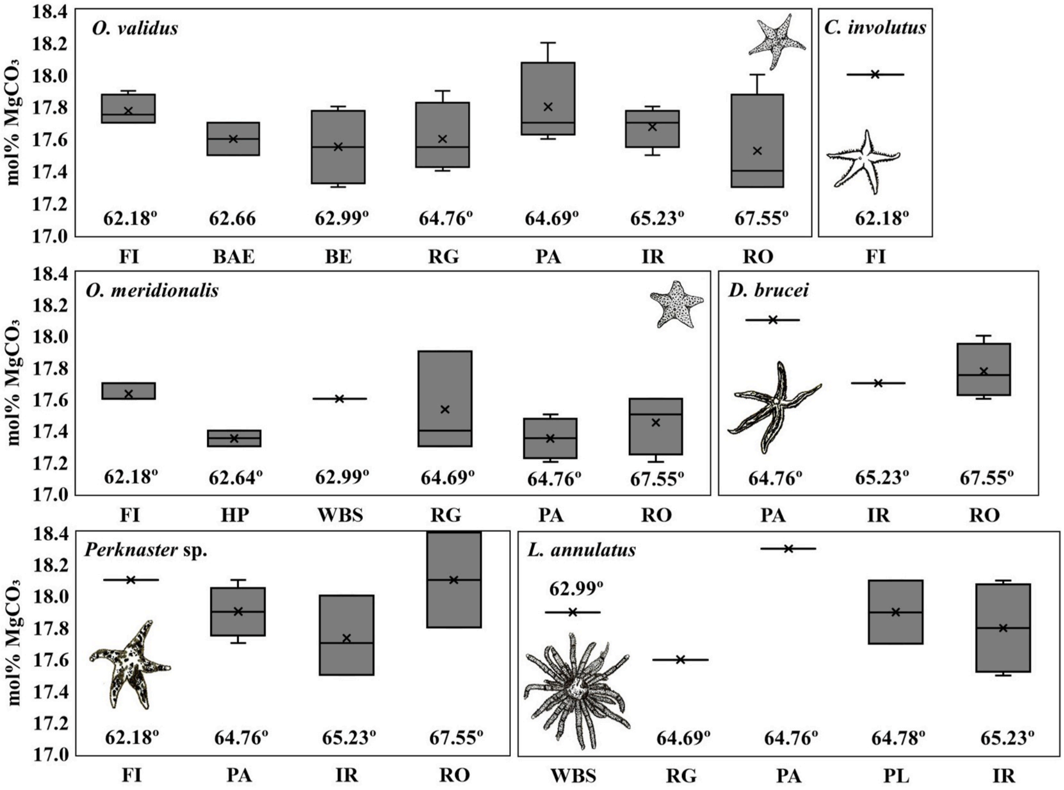

Fig. 3. Mean skeletal Mg content (mol% $MgCO_3$ ± SD) in the asteroids *Odontaster validus*, *Cuenotaster involutus*, *O. meridionalis*, *Diplasterias brucei*, *Perknaster* sp. and *Labidiaster annulatus*. The latitude of the sampling stations is indicated. Sampling stations: Fildes Bay (FI), Antarctic Spanish Base (BAE), Hesperides Point (HP), Bidones East (BE), Whaler's Bay South (WBS), Rongé (RG), Palmer (PA), Port Lockroy (PL), Irizar (IR) and Rothera (RO).

analyses by our research team on species collected at Deception and Livingston Islands (Azcárate-García et al., 2024). Notably, the two species of the genus *Odontaster* (17.7 ± 0.2 mol% $MgCO_3$) had lower skeletal Mg content than those from the genera *Perknaster* (18.3 ± 0.4 mol% $MgCO_3$) and *Diplasterias* (17.9 ± 0.3 mol% $MgCO_3$) (Azcárate-García et al., 2024).

The observed interclass and interspecific variations could be linked to specific biological traits, such as growth rates or feeding behaviours, unique to each class or species. For instance, experimental studies have shown that individuals of *Paracentrotus lividus* (Lamarck, 1816) exhibited a higher content of Mg when consuming Mg-rich diets, such as calcareous algae with HMC (Asnaghi et al., 2014; Kołbuk et al., 2019). Notably, some asteroid and ophiuroids species in this study are active predators or scavengers that feed on other echinoderms (e.g., Fratt and Dearborn, 1984; Dearborn et al., 1991; McClintock, 1994; Zenteno-Devaud et al., 2022), which may also contribute to the differences in skeletal Mg levels observed in these species.

4.2. Intraspecific variations in skeletal Mg content

In our study, no significant intraspecific differences were observed among sampling stations for any of the studied asteroid (i.e., *O. validus*, *O. meridionalis*, *Perknaster* sp., *D. brucei* and *L. annulatus*) and holothuroid (i.e., *H. steineni*) species, suggesting that the ranges of variation on the environmental variables analyzed (i.e., seawater temperature (0.50–2.60 °C); mean annual SST (−0.63–0.26 °C); pH (7.77–8.10); O_2 saturation (90.50–117.30%)) among the sampling stations did not influence their Mg content. No significant differences in the skeletal Mg content between populations were detected, consistent with previous findings for certain asteroid species from Antarctica (i.e., *Bathybiaster loripes* Sladen, 1889, *Glabraster antarctica* (E.A. Smith, 1876), *Cheiraster* sp., *Lysasterias* sp. and *Diplasterias* sp.) and the Arctic (i.e., *Ctenodiscus crispatus* (Bruzelius, 1805)) (Iglikowska et al., 2017; Duquette et al., 2018b; Azcárate-García et al., 2024). Similarly, previous studies did not report any effect of environmental factors on the skeletal mechanical properties of other species either, such as asteroids (i.e., *O. validus*) and echinoids (i.e., *S. neumayeri*, *Eucidaris tribuloides* (Lamarck, 1816) and *P. lividus*) (Collard et al., 2016; Dery et al., 2017; Di Giglio et al., 2021). We thus suggest that these species may exert a strong regulatory capacity over their skeletal Mg content. Supporting this, several studies have shown that echinoderms can regulate their internal fluid pH under more acidic conditions, thereby mitigating potential stress (e.g., Catarino et al., 2012; Calosi et al., 2013; Collard et al., 2013; Holtmann et al., 2013). In asteroid and holothuroid species, buffering occurs mainly through the diffusion of internal CO_2 through tissues to the external medium and the function of specialized organs for gas exchange (Collard et al., 2013). Echinoids may also use compensatory mechanisms, such as buffering compounds, due to their lower buffer capacity (Miles et al., 2007; Catarino et al., 2012; Collard et al., 2013; Holtmann et al., 2013).

However, some authors have reported local variations in other Antarctic and Arctic asteroid species (i.e., McClintock et al., 2011; Iglikowska et al., 2017; Azcárate-García et al., 2024). For example, McClintock et al. (2011) observed that *L. annulatus* specimens from Lamaire Channel (65°04.66′S, 63°58.21′W; 5–40 m depth) had significantly lower skeletal Mg content (~0.3–0.4 mol% $MgCO_3$) compared to those from Elephant Island (61°12.81′S, 56°01.11′W; 145–175 m depth) and Renaud Island (65°40.48′S; 67°24.49′W; 145–175 m depth). Similarly, Iglikowska et al. (2017) found a notable reduction (~1.0–4.6 mol % $MgCO_3$) at 128 m depth (77°34.01′N, 25°14.18′E; Temperature: −1.37 °C; Salinity: 34.34) compared to a deeper region (309 m depth; 78°15.64′N, 30°10.36′E; Temperature: 0.30 °C; Salinity: 34.91) in the Arctic sea star *Pontaster tenuispinus* (Düben and Koren, 1846). However, these authors did not find a clear correlation between environmental changes and local variations in skeletal Mg content. Additionally,

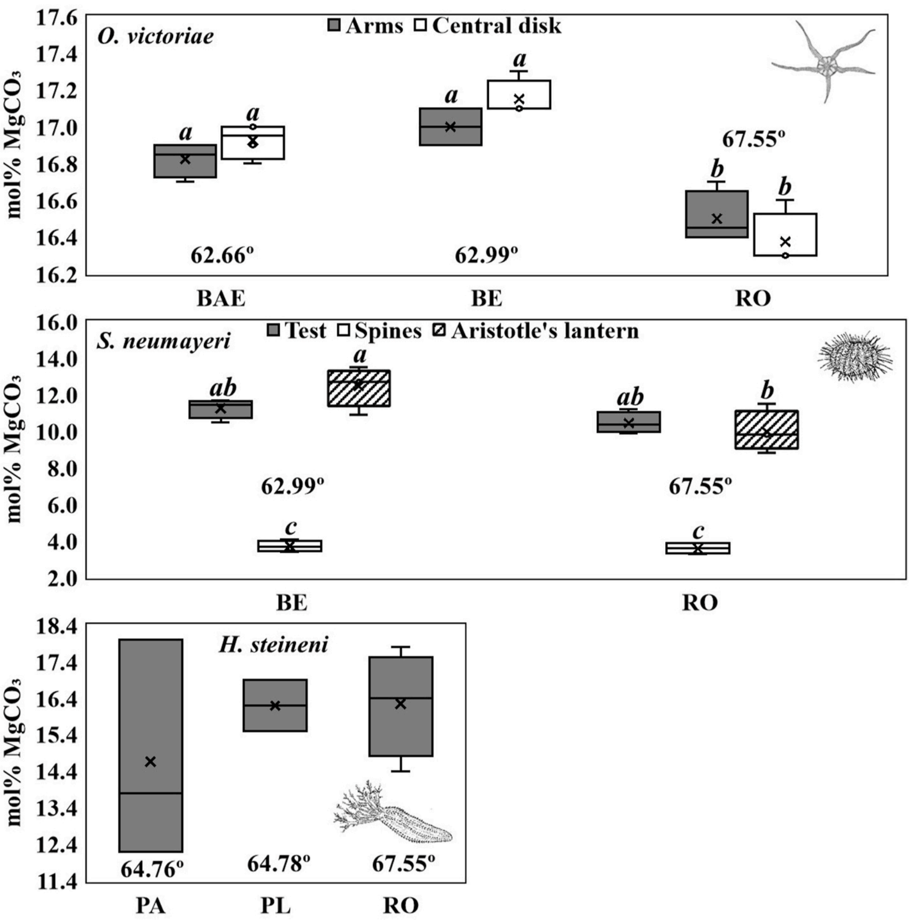

Fig. 4. Mean Mg content (mol% $MgCO_3$ ± SD) in the skeletal structures of the ophiuroid *Ophionotus victoriae* (arms and central disk), the echinoid *Sterechinus neumayeri* (test, spines and Aristotle's lantern) and the holothuroid *Heterocucumis steineni*. The latitude of the sampling stations is indicated. Significative differences between stations and skeletal structures are indicated by using different letters. Sampling stations: Antarctic Spanish Base (BAE), Bidones East (BE), Palmer (PA), Port Lockroy (PL) and Rothera (RO).

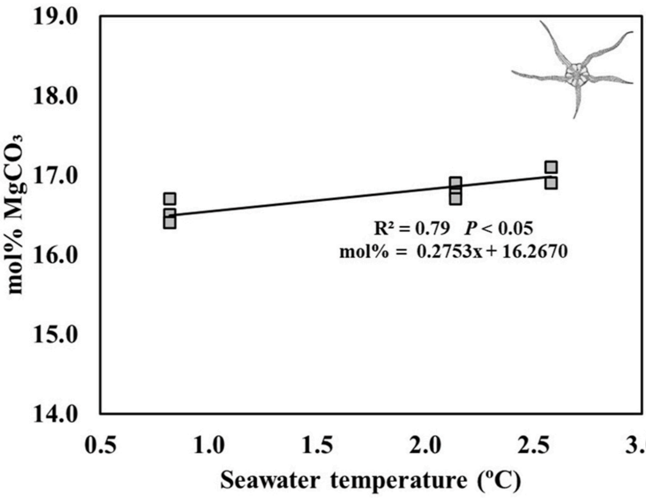

Fig. 5. Correlation among the skeletal Mg content (mol% $MgCO_3$) and seawater temperature (°C) for *O. victoriae* (arms).

fumarolic emissions at Deception Island were shown to influence the skeletal Mg content of *O. validus*, leading to significantly lower Mg levels (from 17.5 ± 0.1 to 18.0 ± 0.1 mol% $MgCO_3$) (Azcárate-García et al., 2024). Therefore, we cannot rule out the possibility that other environmental variables, such as the seawater Mg^{2+}/Ca^{2+} ratio, may have obscured some effects of environmental conditions on the skeletal Mg content in our study, given that echinoderms may incorporate Mg from seawater (Ries, 2010). For instance, previous experiments on the asteroid *Asterias rubens* Linnaeus, 1758, the ophiuroid *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789) and the echinoids *Psammechinus miliaris* (P.L.S. Müller, 1771), *Prionocidaris baculosa* (Lamarck, 1816), *Arbacia lixula* (Linnaeus, 1758) and *P. lividus* showed lower skeletal Mg levels when exposed to reduced seawater Mg^{2+}/Ca^{2+} ratios (Kołbuk et al., 2020, 2021; Gorzelak et al., 2024). The reduction in the skeletal Mg content can also be linked to a decrease in skeletal hardness (Gorzelak et al., 2024), highlighting the relevance of this ratio in echinoderm mineralogy.

In contrast to asteroid and holothuroid species, higher skeletal Mg content was found in the ophiuroid *O. victoriae* (arms and central disk) and the echinoid *S. neumayeri* (Aristotle's lantern) from sampling stations at the South Shetland Islands compared to those from Rothera. Being these regions located at the lowest and highest latitudes of the studied latitudinal gradient, respectively. Our findings suggest that the observed higher skeletal Mg content could be primarily due to higher seawater temperatures, as hypothesized here and in previous studies (e.g., Hermans et al., 2010; McClintock et al., 2011). In agreement with that, *O. victoriae* exhibited a significant positive correlation between skeletal Mg content and the seawater temperature (Fig. 5). Noteworthy, we also observed that the mol% $MgCO_3$ increased at higher seawater temperatures (Supplementary Material Fig. S4). In line with our findings, earlier studies reported local variability in the skeletal Mg content of *O. victoriae* and *S. neumayeri* (Duquette et al., 2018b; Azcárate-García et al., 2024). Our results thus suggest that the ophiuroid and the echinoid species examined here may be more susceptible to future environmental changes compared to the studied asteroid and holothuroid species. Accordingly, it has been previously suggested that ophiuroids may be more vulnerable to environmental changes than other echinoderm species (Kołbuk et al., 2021). However, other studies observed no effect of warming or acidification on the skeletal Mg content of the Arctic and temperate ophiuroids *Ophiocten sericeum* (Forbes, 1852) and *Ophiura ophiura* (Linnaeus, 1758), respectively (Wood et al., 2010, 2011), which may suggest possible biological regulation of their skeletal Mg content. Similarly, the Arctic ophiuroids *Ophiopholis aculeata* (Linnaeus, 1767) and *Ophiura sarsii* Lütken, 1855 did not display any local variability in their skeletal Mg content (Iglikowska et al., 2017). Therefore, species-specific variations in the skeletal Mg content are likely to occur in response to environmental changes.

4.3. *Differing mineralogical responses among skeletal structures*

While both skeletal structures of *O. victoriae* showed similar responses to environmental effects, our results suggest differing responses in the Mg content among skeletal components of *S. neumayeri*. Specifically, the lower skeletal Mg content in the Aristotle's lantern at Rothera suggests a response to cooler seawater temperatures, whereas no differences were observed in the test or spines. A recent study also found mineralogical changes in the test of specimens from Deception Island in response to local environmental conditions, rather than in the Aristotle's lantern (Azcárate-García et al., 2024). These findings suggest different mineralogical responses between skeletal structures to environmental changes. Similarly, the Aristotle's lantern and test of the tropical echinoid *Tripneustes gratilla* (Linnaeus, 1758) exhibited increased skeletal Mg when exposed to experimental elevated seawater temperatures, with no effect on the spines (Byrne et al., 2014). The differences in the Mg levels among skeletal structures may be related to their biological functions. For instance, feeding structures, such as the lantern or teeth in sea urchins, may exhibit higher skeletal Mg levels to enhance hardness (Wang et al., 1997; Ma et al., 2008; Long et al., 2014).

5. Conclusions

This study provides new mineralogical data of the skeletal Mg content of several Antarctic echinoderm species along a latitudinal gradient from the South Shetland Islands to Rothera. It is also the first to examine the skeletal Mg content in three species – the asteroids *Diplasterias brucei* and *Cuenotaster involutus*, and the holothuroid *Heterocucumis steineni*. Our results confirmed that asteroid species have the highest skeletal Mg content, followed by ophiuroid, holothuroid and echinoid species. Additionally, variability in the skeletal Mg content was observed in ophiuroids and echinoids along the latitudinal gradient, likely driven by local environmental factors. In contrast, both asteroid and holothuroid species did not show significant differences along the latitudinal gradient, suggesting they may have a stronger regulatory capacity over their skeletal Mg content and could be more resilient to future environmental scenarios. Furthermore, we found distinct responses among skeletal structures in the echinoid *S. neumayeri*. More research is urgently needed on the mineralogical responses of echinoderms to environmental changes and the role of biological factors, particularly in polar species, which are likely to be among the first affected by global change.

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Data availability

All data are available in supplemental material (Table S7).

CRediT authorship contribution statement

Tomás Azcárate-García: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Conxita Avila:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Blanca Figuerola:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

Data availability

The data have been included in the supplemental material Table S7.

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Appendix A. Supplementary data

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