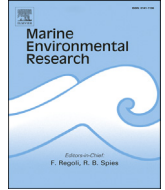




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Variability in magnesium content in Arctic echinoderm skeletons

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ABSTRACT

In this study, 235 measurements of magnesium concentration in echinoderm's skeletons were compiled, including 30 species and 216 specimens collected from northern and western Barents Sea. We aimed to reveal the scale of Mg variation in the skeletons of Arctic echinoderms. Furthermore, we attempted to examine whether the Mg concentration in echinoderm skeletons is determined primarily by biological factors or is a passive result of environmental influences. We found that the Mg concentration in echinoderm skeletons was characteristic for particular echinoderm classes or was even species-specific. The highest Mg contents were observed in asteroids, followed by ophiuroids, crinoids, and holothuroids, with the lowest values in echinoids. These results strongly imply that biological factors play an important role in controlling the incorporation of Mg into the skeletons of the studied individuals.

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1. Introduction

Echinoderms are numerous and widely distributed benthic organisms that are important components of marine ecosystems. In the Arctic seas, Echinodermata are often dominant invertebrates, having a large contribution to the remineralisation and redistribution of organic carbon (Renaud et al., 2007; Blicher and Sejr, 2011; Jørgensen et al., 2015). Moreover, they are involved in global cycles of other major (e.g. sulphur, phosphorus, calcium) and minor (e.g. magnesium, strontium, iron) elements. The endoskeleton of most echinoderms consists of a fenestrate lattice of calcium carbonate, called stereom, which is interpenetrated with organic mesodermal tissue (Towe, 1967). The echinoderm biomineralisation strategy is the initial formation of amorphous calcium carbonate (ACC) precursors, that subsequently transform into crystalline phases. The final mineral phase of the skeleton is made

of magnesium-rich calcite and ~0.1 wt% (percentage by weight) of occluded organic molecules (e.g. Weiner, 1985; Dubois and Chen, 1989). This organic material plays a crucial role in transient stabilization of ACC (e.g. Politi et al., 2004), controlling crystal growth (Berman et al., 1988; Ameyé et al., 2001) and modulation of magnesium content (e.g. Hermans et al., 2011).

In aquatic environments, magnesium (Mg) is a common additive in biogenic carbonate minerals. Among echinoderms, the amount of Mg in skeletons can vary, and calcitic skeletons are subdivided into low-Mg calcite (0–5 mol% MgCO₃), intermediate-Mg calcite (5–8 mol%) and high-Mg calcite (>8 mol%) (Morrison and Brand, 1986). High-Mg calcite, with magnesium concentrations higher than 10 mol%, is known to be a thermodynamically unstable polymorph under ambient conditions (Raz et al., 2000). Synthetic high-Mg calcite can be precipitated only under high temperature and high pressure (Long et al., 2014), although marine invertebrates are often able to produce this unstable phase of calcium carbonate under conditions of modern seawater.

Magnesium is incorporated into carbonate minerals by direct substitution for calcium in the CaCO₃ crystal structure (Morrison and Brand, 1986). For echinoderms, the potential sources of

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magnesium are food (Asnaghi et al., 2014) and ambient seawater. Nakano et al. (1963) and Lewis et al. (1990) showed with radioactive calcium that, in echinoderm skeletal calcite, calcium is derived from seawater, and magnesium has likely the same origin. The Mg/Ca ratio of modern seawater is ≈ 5.2 (Stanley and Hardie, 1998) therefore, the inorganic precipitation of high-Mg calcite should be favoured (Mackenzie et al., 1983). However, aragonite precipitation occurs more readily since Mg ions inhibit calcite precipitation (Morse, 1983: “Mg poisoning effect”). Crystallisation of high-Mg calcite is therefore only possible in the presence of organic additives, such as citric and malic acids, which are known to enhance the secretion of (magnesian) calcite in magnesium-rich calcifying fluid. The addition of Mg to the medium where crystallisation occurs provides new morphological possibilities, although the role of Mg ions in determining the morphology of calcite crystals is less clear (Meldrum and Hyde, 2001).

Pure calcite is extremely brittle as a single crystal (Long et al., 2014). The precipitation of high-Mg calcite, which is a composite of inorganic ions and biomolecules in invertebrate skeletons, greatly enhances the mechanical properties of calcium carbonates. The hardness, stiffness and elastic modulus are demonstrated to be higher for Mg-bearing calcite than for pure synthetic calcite (Ma et al., 2008). Even relatively low concentrations of Mg (≈ 1 mol%) in calcite play a significant role in hardening crystalline calcium carbonate (Kunitake et al., 2012). Additionally, the enhanced mechanical properties of high-Mg calcite are strongly linked to such structural features as the presence of macromolecules, occlusion of Mg ions and crystal orientation (Long et al., 2014).

In the calcitic skeletons of echinoderms, magnesium is the most abundant minor element and may vary from 3.0 to 43.5 mol % MgCO₃ (Schroeder et al., 1969). The variation in Mg concentration may occur on different levels, such as the variation among particular ossicles within a single specimen or differences among species or higher taxonomic levels. Most marine invertebrates can exert biological control on the magnesium uptake into hard skeletal parts, and this process can lead to enrichment or depletion of the element in skeletal carbonate (Morrison and Brand, 1986). Echinodermata demonstrate strong physiological control on skeletal Mg content (e.g. Chave, 1954; Weber and Raup, 1966; Weber, 1969, 1973; Ebert, 2007), although several studies report that the skeletal Mg/Ca ratio may be shaped, to some extent, by the water temperature (e.g. Clarke and Wheeler, 1917; Chave, 1954; Weber, 1969; Hermans et al., 2010), salinity (e.g. Pilkey and Hower, 1960; Borremans et al., 2009) and the Mg/Ca ratio of ambient seawater (e.g. Dickson, 2002, 2004; Ries, 2004; Hasiuk and Lohmann, 2010). Thus, the final chemical composition of the skeleton is a result of biological control, organism–environment interactions and physiochemical properties of the surrounding seawater.

The knowledge of the factors controlling Mg incorporation into biogenic minerals is widely used to infer the mineral growth conditions and thus has important applications in palaeoecological and geochemical studies. Species bearing magnesium-rich skeletons are on the list of the most vulnerable to the effects of climate change and ocean acidification because higher magnesium levels in calcite are strongly correlated to higher solubility under modern seawater conditions. The calcitic skeletons of echinoderms are sometimes well preserved in fossil records; therefore, the Mg content in fossil echinoderms can be used as a proxy for ancient seawater Mg concentrations or temperatures (Dickson, 2002, 2004; Ries, 2004).

Recently, the Arctic Ocean ecosystem has been changing rapidly as a result of climate warming, increased emissions of atmospheric CO₂ and anthropogenic activities. The reduction in sea ice coverage causes a substantial increase in CO₂ air-sea flux and light availability, thus making the growing season longer and more intense. In addition, the increased Arctic river input and coastal erosion (e.g. Peterson et al., 2002; Mars and Houseknecht, 2007) contribute to an increased nutrient supply, influencing primary productivity, particularly in the shelf area (Jutterström and Anderson, 2010). In the Arctic, the bottom salinity and water temperatures seem to be relatively stable, although changes in primary productivity may significantly change the seawater CO₂ concentration and carbonate saturation state, which can potentially affect skeletal precipitation in Arctic calcifiers. Arctic, cold-water and less calcium carbonate-saturated seawater conditions are generally more unfavourable for calcifying organisms, especially for those producing high-Mg calcite, and progressing ocean acidification makes the process of calcification more difficult (e.g. Andersson et al., 2008). Although the Arctic Ocean is changing on an unprecedented scale, our understanding of the effects of these changes on the living part of this unique system is far from satisfactory. To date, there have been only a few studies dealing with biomineralisation problems in the Arctic, which are based on the larger database (e.g. Andersson et al., 2008; Lebrato et al., 2013; Iglirkowska et al., 2017). Arctic ecosystem changes are progressing quickly; therefore, there is an urgent need to expand and complete our knowledge regarding the precipitation and properties of calcified skeletons in Arctic invertebrates.

The objective of this paper is to reveal the scale of Mg variation in the calcitic skeletons of Arctic echinoderms. In addition to building comprehensive knowledge about Mg concentrations within these skeletons, we test whether the levels of Mg in the skeletons of particular species are species or group specific. The investigated species were often from the same location and were under the influence of the same environmental conditions. We assume that species having different Mg concentrations and therefore having species-specific Mg content in the skeleton would indicate the biological control of Mg incorporation. Based on samples collected across a large spatial scale, where stations differed in environmental conditions, we also test whether the concentrations of Mg in the skeleton of particular species are related to environmental variables (e.g. depth). In this case, we assumed that skeletal Mg concentrations following the same pattern as environmental variables are indicative of environmental control of skeletal Mg content. Additionally, this study aimed to build a solid database of Mg concentrations in the skeletons of Arctic echinoderms, which will act as a baseline for future investigations.

2. Study area

The Barents Sea is a shallow continental shelf sea that covers ≈ 1.6 million km² (Jakobsson et al., 2004). The sea is bounded by the Arctic Ocean to the north and by Norway and Russia to the south. The maximum depth of approximately 500 m is located at the western boundary (Bjørnøyrenna), although the average depth is 230 m, and several basins are between 50 and 200 m. The hydrographic conditions are the result of interactions between the bottom topography and currents. The bottom sediments are variable, with a dominance of finer mud and silt in deeper areas and stony and sandy substrates with mollusc shell fragments on shallower banks (Vinogradova and Litvin, 1960).

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