

Antarctic echinoids and climate change: a major impact on the brooding forms

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Abstract

Ocean acidification (OA) and the accompanying changes to carbonate concentrations are predicted to have especially negative impacts in the Southern Ocean where, as a result of colder temperatures, there will be shallowing of both the aragonite (ASH) and calcite saturation horizons (CSH). Echinoids are a dominant group of the Antarctic macrofauna which, because of their high-Mg calcite skeleton, are particularly susceptible to changes in the ASH. Using published information on the bathymetric distributions of Antarctic echinoids, we show that the majority of heavily calcified echinoids have their lower bathymetric limit above a depth of ca. 3000 m, approximately the current depth of the CSH. Echinoids whose depth range extends below 3000 m generally have thin, weakly calcified tests and include species from the Order Holasteroidea, and the Families Cidaridae and Schizasteridae. Examination of the reproductive mode of Antarctic echinoids shows that brooding, where calcification of the young occurs in the same CaCO₃ environment as the mother, is primarily found at a depth above 3000 m. The predicted shallowing of the ASH and CSH under OA conditions is likely to negatively impact growth and reproduction of heavily calcified brooders in the Family Cidaridae, which may result in changes to bathymetric ranges, local population extinction, and associated losses in macrofaunal biodiversity. As with other calcified deep sea invertebrates, echinoids may be particularly vulnerable to the impacts of increased CO₂ and OA in the Southern Ocean.

Keywords: Antarctic, brooding, climate change, echinoid, ocean acidification

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Introduction

Marine ecosystems in all parts of the world will be affected by ocean acidification (OA) and the accompanying changes to carbonate concentrations (reviewed in Raven *et al.*, 2005; Kleypas *et al.*, 2006; Fabry *et al.*, 2008; Doney *et al.*, 2009). These impacts are predicted to be especially negative in the Southern Ocean where, as a result of colder temperatures, there will be shallowing of both the aragonite (ASH) and calcite saturation horizons (CSH; Feely *et al.*, 2002, 2004, 2009; Andersson *et al.*, 2005; Gehlen *et al.*, 2007; Gangsto *et al.*, 2008; Lebrato *et al.*, 2010), which will impact calcifying organisms in both pelagic and benthic environments (Raven *et al.*, 2005; Kleypas *et al.*, 2006; Guinotte *et al.*, 2006; Fabry *et al.*, 2008, 2009; Doney *et al.*, 2009; McClintock *et al.*, 2009; Ries *et al.*, 2009). Distributional and experimental studies have shown that in Antarctic and Southern ocean habitats, pelagic pteropods, deep sea corals and calcifying molluscs and brachiopods will have problems with growth and maintenance of their CaCO₃ skeletons as a result of changes to the CaCO₃ saturation

horizons, and that both vertical and horizontal distributions will be affected (Guinotte *et al.*, 2006; Fabry *et al.*, 2008, 2009; McClintock *et al.*, 2009).

Here we conduct a theoretical analysis of the susceptibility of another dominant group of the Antarctic macrofauna to changing carbonate concentrations in the Southern Oceans, the echinoids or sea urchins. We have chosen this group as echinoids have an endoskeleton constructed from high Mg-calcite (>4% MgCO₃, Andersson *et al.*, 2008), are one of the most calcified of the echinoderm classes, and show a prevalence of an alternative reproductive strategy, brooding, where the young are retained externally on the female (Pearse & Lockhart, 2004; Pearse *et al.*, 2009) often in elaborate brooding structures (David *et al.*, 2005). Although providing some protection under spines or in pouches, brooding embryos are still exposed to ambient seawater of the same chemical environment as the adults. While laboratory experiments have shown that planktonic sea urchin larvae, which have CaCO₃ skeletal rods supporting the larval arms, are susceptible to reduced carbonate levels under OA conditions (e.g. Kurihara & Shirayama, 2004; Kurihara *et al.*, 2004; Clark *et al.*, 2009; O'Donnell *et al.*, 2010) the brooding reproductive strategy, where embryo development and

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calcification of the juveniles occurs in the same CaCO_3 environment as the mother, has not yet been considered in an OA context.

Using published information on the distribution of Antarctic echinoids (David *et al.*, 2005; Chiantore *et al.*, 2006; Linse *et al.*, 2008), we examine the bathymetric distribution of each family and consider the affect that changing carbonate saturation depths in the near-future might have on both the adult and developing sea urchins. Our findings suggest that, as in the cold-water deep sea corals (Guinotte *et al.*, 2006), a shallowing of the carbonate saturation horizons may greatly impact heavily calcified families of Antarctic echinoids and that this may have significant ecological impact on the biodiversity, abundance and population stability of Antarctic shelf and deep-water ecosystems.

Methods

Determination of the depth of high Mg-calcite saturation

Predicting the effects of changing saturation horizons on Antarctic taxa with skeletons composed of high Mg-calcite ($>4\%$ MgCO_3) is complex, primarily as calculation of the carbonate saturation state (Ω) requires a value for the stoichiometric solubility constant in seawater (K_{sp}). While K_{sp} values are available for calcite and aragonite, solubility estimates for Mg-calcites are difficult to predict in natural conditions, primarily as Mg-content is not an accurate predictor of solubility for biogenic forms (for a detailed discussion of this research, see Morse & Mackenzie, 1990; Andersson *et al.*, 2005, 2008; Morse *et al.*, 2006, 2007).

Additionally, it is well known that Mg-content of echinoid skeletal elements varies at individual, species and population levels. Mg-content can vary between different parts of an individual's skeleton (e.g. Mg-content for test $>$ spine, Vinogradov, 1953; Chave, 1954; Weber, 1969; Ries, 2004), in different species at the same location, and between different populations of the same species (Chave, 1954; Weber, 1969, 1973), suggesting a role for organismal genetics and physiology (Weber, 1969, 1973). Further, there is a well-established relationship between Mg-content and latitude or temperature (Vinogradov, 1953; Chave, 1954; Dickson, 2004; Andersson *et al.*, 2005, 2008) with, in general, lower Mg contents at high latitude/lower mean temperature. Recent research has also suggested that there is an interaction between temperature and salinity with reduced Mg/Ca ratios when both temperature and salinity are low (Borremans *et al.*, 2009). Typically, therefore, a range of high-Mg carbonate saturation curves are calculated varying % Mg content, to consider different species, and using both the 'minimally prepared' and 'cleaned' biogenic solubility curves (e.g., fig. 14 of Andersson *et al.*, 2005; fig. 2 of Andersson *et al.*, 2008).

We have made three assumptions in this study. Firstly, although there has been considerable study on the Mg content of echinoid skeletons there is little information on Antarctic species. Weber (1969) in his comprehensive review reports Mg-

content, based on powder X-ray diffraction (XRD), in *Sterechninus neumayeri* with test 7.8 wt% MgCO_3 and spine 5.9 wt% MgCO_3 . More recent XRD studies on *S. neumayeri* report 5.7 wt% in the test and 4.1 wt% MgCO_3 in the primary spines (Grzeta *et al.*, 2004), and 2.4 mol% MgCO_3 (2.0 wt%) in small spines (ca. 3 mm) of the congener *Sterechninus antarcticus* (Magdals & Gies, 2004). Although the Mg-content of Antarctic echinoids are in the lower part of the range for echinoids as a whole (test: mean 11.55 wt%, range 5.5–17.1 wt% MgCO_3 ; spine: mean 7.25 wt%, range 3.2–12.2 wt% MgCO_3 , Weber, 1969, $N = 292$), we have assumed, in the absence of further data, that the slightly lower Mg-content of the test and spines is representative of values found more generally in Antarctic echinoids, and that the majority of the CaCO_3 making up the skeleton is high-Mg calcite ($>4\%$ Mg).

Secondly, we follow Andersson *et al.* (2008) that biogenic Mg-calcite with 8–12 mol% MgCO_3 (ca. 6.8–10.3 wt% MgCO_3) has approximately the same solubility as aragonite and assume, based on our first assumption, that the tests of Antarctic echinoids have the same solubility as aragonite skeletons. As noted above, there is considerable debate regarding the appropriate saturation horizon for organisms with calcite skeletons containing a high % MgCO_3 . In this paper, we have used the ASH, which is predicted to shallow from the current level of 800–1200 m to reach the surface by 2100 (Feely *et al.*, 2002, 2004, 2009), as a 'worst-case scenario' for Antarctic echinoids, and as the most appropriate for echinoderm skeleton (P. Dubois, personal communication). The CSH, currently at a depth of ca. 3000 m, is also predicted to shallow, although Antarctic surface waters will still be saturated in 2095 (Feely *et al.*, 2009) and therefore offers a 'conservative' scenario for Antarctic echinoids. It is also worth noting that increasing atmospheric CO_2 will lead to shoaling of the carbonate compensation depth (CCD, currently at a depth of ca 4 km, Broecker, 2008) as a result of increasing dissolution of deep sea carbonates and decreasing flux of biogenic carbonates from surface waters (Andersson *et al.*, 2005).

Thirdly, although there will be local changes to the depths of the carbonate saturation horizons in different parts of Antarctica as a result of upwelling and changes between seasons (McNeil & Matear, 2008) for the sake of this theoretical exercise we have assumed a 'worst-case scenario', with the ASH and CSH both shallowing in all parts of Antarctica by 2100.

Bathymetric distribution of Antarctic echinoids

Information on the bathymetric distribution of the 81 species of echinoids found south of the Antarctic convergence was obtained from David *et al.* (2005). Two species of the genus *Ctenocidaris* (*C. nutrix* and *C. speciosa*) are reported with two morphological forms; these forms were retained as if they were separate species in this analysis. We also followed David *et al.* (2005) in considering *Delatopagus brucei* and *Genicopatagus affinis* as separate species, although there is some uncertainty about the taxonomic status of the rarer *D. brucei* [see detailed discussion in David *et al.* (2005) and Smith (2005)]. Additional information on the depth distribution of Antarctic echinoids was obtained from Chiantore *et al.* (2006) and Linse *et al.*

(2008), but only resulted in an upper limit change for *G. affinis* to 199 m from that in David *et al.* (2005).

Upper and lower bathymetric distributions were examined for each family using a box-and-whisker plot in SIGMAPLOT v. 10 with the graphing option set to show all outliers and the Cleveland method (Cleveland, 1985) used to calculate the percentiles (subtraction of 0.5 from the positions before computing percentages, SIGMAPLOT User's Guide). Separate box-and-whisker plots were also produced at the level of genera for the families with the greatest variability, the Cidaridae and Schizasteridae.

Developmental mode of each species was defined as one of three types: brooding (B), where in echinoids the young are retained externally by the female often in pouches or marsupia; larval development (L) where the embryos and larvae have an independent existence from the female, usually in the plankton; and unknown (U) where there is insufficient information about the biology of the species to assign developmental mode. Developmental mode information was obtained primarily from table 1 of Poulin & Feral (1996). Changes to species names and updated information on developmental mode were also incorporated from David *et al.* (2005) where this was available. A conservative approach was adopted in assigning developmental mode. If all other species in a genus were known brooders or with larval development, but there was, as yet, no evidence for developmental mode in Species X

then it was assigned to the unknown category. It should also be noted that for consistency we have used the assignments of developmental mode in Poulin & Feral (1996), even though contradictory assignments were in some cases made in a similar listing by Pearse & Bosch (1994).

Information on the test and spine morphology of the species was obtained from David *et al.* (2005) and the text and photographic images on 'The Echinoid Directory' web-site (Smith, 2005).

Results

Bathymetric distribution

The 81 echinoid species within Antarctica are found within nine families, representing both the regular and irregular echinoids, and covering a depth range from the intertidal (0 m) to a maximum of 6290 m (David *et al.*, 2005). The bathymetric distribution of the majority of Antarctic echinoids is contained above the current CSH at approximately 3000 m (Feely *et al.*, 2002, 2004; Fig. 1).

In general, the lower bathymetric limits fall into three main groupings: (1) families with limits above 3000 m, (2) families with limits that extend below 3000 m, (3)

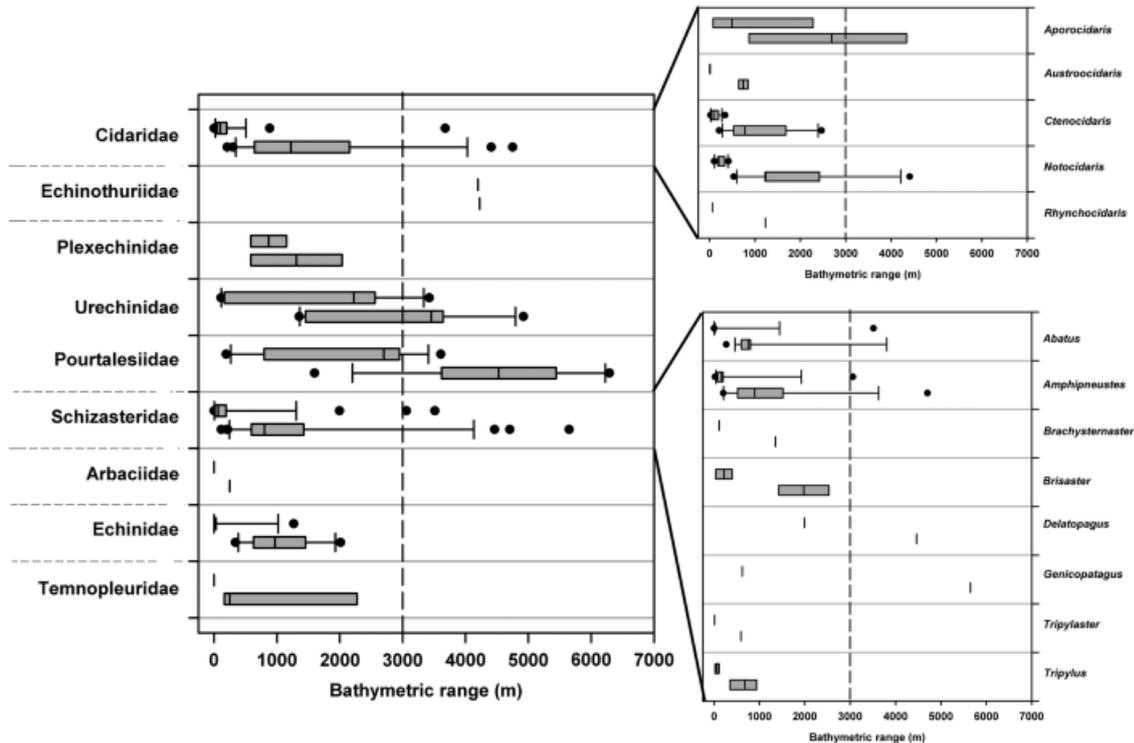


Fig. 1 Upper and lower bathymetric limits of Antarctic echinoids by family or genera (F. Cidaridae, Schizasteridae). Box and whisker plots used Cleveland method in Sigmaplot v. 10. The order of families within the figure is based on the combined morphological and molecular tree of Smith *et al.* (2006), with the basal groups at the top. Dotted lines between families on the y-axis of left panel indicate different orders of echinoids. Dotted line at 3000 m separates bathymetric Groups 1 and 2 and is the current depth of the calcite saturation horizons (CSH, see text for details).

families Cidaridae and Schizasteridae, where the lower limit of the majority of the species is <3000 m, but there are a subset of species found at depths >3000 m (Fig. 1). We briefly describe these groupings below. Except where noted, all information is derived from David *et al.* (2005).

Group 1 – lower bathymetric limit <3000 m (Families Arbaciidae, Echinidae, Temnopleuridae). This grouping consists of 11 species of regular echinoids of the families Arbaciidae ($N=1$), Echinidae ($N=7$) and Temnopleuridae ($N=3$), which are familiar from shallow water temperate environments, and morphologically are characterized by well-formed tests and relatively large spines. This group includes five species of the genus *Sterechinus*, including the abundant and well-studied *S. neumayeri* and the more bathyal *S. antarcticus*; species for which we have information on Mg content of the skeleton. The majority of the species have an upper limit in shallow waters (0–50 m) and lower limits <2000 m, with the exception of *Pseudechinus marionis* (F. Temnopleuridae) for which all records are <600 m except for a single collection at 2950 m.

Two species of the irregular echinoid Family Plexechinidae (Order Holasteroidea) are also included in this group. *Plexechinus planus* has been collected in the outer Weddell Sea from depths of 1153–2037 m and *P. sulcatus* has been collected from a single locality near the Kerguelen Islands at 585 m. Both species have the thin test and short spines characteristic of the holasteroids (Smith, 2005).

Group 2 – lower bathymetric limit extends >3000 m (Families Urechinidae, Pourtalesiidae, Echinothuriidae). This grouping consists of two families of irregular echinoids within the Order Holasteroidea (Families Urechinidae, Pourtalesiidae), and a single record of a regular echinoid from the Family Echinothuriidae (*Kamptosoma asterias*). The Urechinidae and Pourtalesiidae, in common with other living holasteroids are typically deep-water inhabitants with exceedingly thin and fragile tests with short spines (Smith, 2005). Similarly the test in Echinothuriidae is soft, deformable, and extremely fragile (Mooi *et al.*, 2004).

Within the Holasteroids in Group 2, four out of six species in the Urechinidae have a lower bathymetric limit >3000 m, with *Pilematechinus vesica* found to a depth of 4923 m (Fig. 1). In the Pourtalesiidae, seven of the eight species have a lower bathymetric limit >3000 m, with the maximum depth recorded in *Pourtalesia debilis* of 6290 m (Fig. 1).

The single echinothuriid, *K. asterias*, is reported at a single location (4220–4225 m) within the Antarctic–Subantarctic region (Fig. 1).

Group 3 – variable lower bathymetric limit (Families Cidaridae and Schizasteridae). The Family Cidaridae are regular sea urchins with a hard, rigid symmetrical test, and very large primary spines, that may be up to $3 \times$ the test diameter in length (Thomson, 1874). The majority of the 23 species have a lower bathymetric limit <3000 m, with two species in the genus *Aporocidaris* and *Notocidaris hastata* being found at greater depths (Fig. 1). Interestingly, these two genera are noted for having relatively thin and fragile tests (Smith, 2005).

The Family Schizasteridae, within the Order Spatangoida, are irregular sea urchins commonly known as heart urchins and are the most diverse Antarctic echinoid group ($N=30$ species). Tests of schizasterids are generally very fragile with long, slender and fine spines (Smith, 2005). Schizasterid species with lower bathymetric limits >3000 m include two species of the genus *Abatus* (*A. beatriceae*, *A. cavernosus*), *Amphineustes mironovi*, *D. brucei* and *G. affinis*. The last two species are considered synonyms by Smith (2005), with *Delatopagus* noted to have a thin shelled test.

In summary, the data from the three groups show a trend for species that have a greater degree of calcification (test and/or spines) to have a lower bathymetric limit above 3000 m, and the species that extend below this depth to be from families or genera that are characterized by thinner, less calcified tests.

Developmental mode with depth

The lower bathymetric limit was used to sort species into 250 m wide depth classes that covered the range of all 81 species (0–6290 m), and this is plotted with developmental mode in Fig. 2. About half of the Antarctic echinoid species are brooders (42/81 = 52%), and are concentrated in two families, the Cidaridae (70%

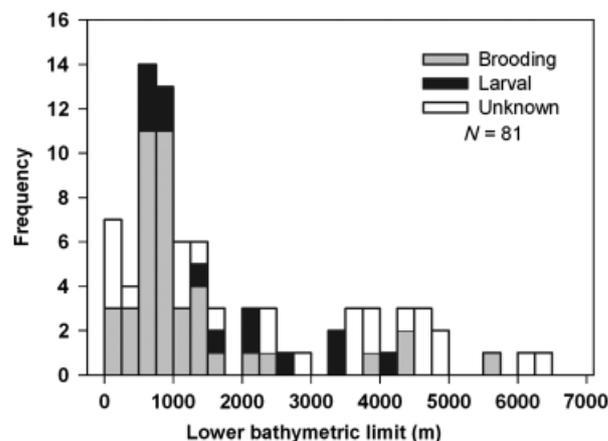


Fig. 2 Distribution of developmental mode in Antarctic echinoids using 250 m size classes of the lower bathymetric limits ($N=81$).

brooders, $N = 23$) and Schizasteridae (80% brooders, $N = 30$). Thirteen species have larval development (16%) and for the remainder the developmental mode is unknown ($26/81 = 32\%$).

The distribution of lower bathymetric limits in Fig. 2 shows, in a different form, the separation of species into two groups at a depth of ~ 3000 m. Thirty-eight of the 42 brooders are found at depths < 3000 m, with reproductive mode known for only seven of the 20 species with lower bathymetric limits > 3000 m. The brooders found below this depth include *A. cavernosus*, for which there is only one record at a depth > 1000 m, *N. hastata*, *D. brucei* and *G. affinis*.

Larval development is rare overall, but is more common in the shallower water Families Echinidae and Plexechinidae. However, larval development is also found at depths in species of the Families Urechinidae (*Antrechinus drygalskii*, *Cystechinus wyvillii*) and Echinothuridae (*K. asterias*). Its rarity may also be a sampling artifact because of limited sampling in the Antarctic deep sea (Brandt *et al.*, 2007), and the fact that brooding as a developmental mode can be determined by observation of a single female with a brood, while confirmation of larval development requires more extensive seasonal sampling.

Brooding echinoids in Antarctica are found in three families: the Cidaridae, Schizasteridae and Urechinidae (David *et al.*, 2005). While all brood large yolky eggs in depressed and isolated pouches on the test of the females, there are differences in the morphology of the brooding structures between the families (Schinner & McClintock, 1993; David *et al.*, 2005). The test morphology of brooding cidaroids shows the least modification, with the brood held around the peristome by the primary spines, or on the aboral surface shielded by the aboral spines (David *et al.*, 2005). Although some cidaroids show a slight depression on the peristomal membrane (David *et al.*, 2005) the developing young are completely exposed to the seawater in which the mother resides.

The irregular echinoids, in contrast, brood the young in strongly modified parts of the test known as pouches or marsupia, with different and non-homologous forms in the Schizasteridae and Urechinidae (Schinner & McClintock, 1993; David *et al.*, 2005). In the spatangoids, within the family Schizasteridae, the brooded young develop in pouches in the sunken petaloid ambulacra (David *et al.*, 2005). The degree to which the young are exposed to the surrounding seawater can vary with age. In *Amphineustes lorioli*, for example, the embryos and early juvenile stages are in the deep recesses of the marsupia, with the oldest juveniles clustered amongst the spines covering the pouch (Galley *et al.*, 2005). Calcification of the juveniles begins, therefore, at the base of the marsupia (Galley *et al.*,

2005) but only the spines separate the pouch from the surrounding seawater.

The most extreme form of brooding in Antarctic echinoids is found in two species of the holasteroids, *Antrechinus mortenseni* and *Antrechinus nordenskjoldi* (David *et al.*, 2005). Here invaginated extensions of the body wall form pouches that are functionally inside the female's test, communicating with the outside environment through a short birth canal (David & Mooi, 1990). The pouches show young of different developmental stages, with 'rarely more than three large juveniles, four or five smaller juveniles, and approximately six ova in a single female' (David & Mooi, 1990, p. 83). Although the juveniles of these species show the greatest degree of separation from the surrounding seawater, the pouches are in constant communication with the external environment (David & Mooi, 1990).

In summary, Antarctic echinoids have brooding as the most common developmental mode and, although there are slight differences in the mechanisms of brooding, in all cases the calcification of the developing young takes place in seawater of the same carbonate concentration as that in which the mother resides.

Discussion

Potential impacts of shallower saturation horizons on Antarctic echinoids

Calcification and growth. Our simple analysis of the bathymetric distributions of Antarctic echinoids has shown there is a general trend, though with some exceptions (e.g. the burrowing schizasterids), for the more calcified species of Antarctic echinoids to be found in shallower waters than the less calcified, thinner test, sea urchins. One hypothesis for this pattern could be that there is a relationship between the depth of CaCO_3 saturation horizons and echinoid distributions, as has been proposed for Southern Ocean foraminifera assemblages (Saidova, 1998). However, as the bathymetric distribution data used here comes from different locations within Antarctica, to test this hypothesis we need to use location-specific information on echinoid distributions (e.g. Linse *et al.*, 2008) in relation to local CaCO_3 saturation horizons, or alternatively conduct focused studies on areas such as the Crary Trough in the Weddell Sea where the CCD, and saturation horizons, are very shallow (Brandt *et al.*, 2007). Such an approach might highlight species with a strong linkage to saturation horizon depth that could be used as an early-warning for changing ocean conditions.

Echinoderms are particularly vulnerable to altered saturation horizons as, although they have an

endoskeleton, the CaCO_3 is covered by only a layer of epithelial tissue, which is permeable to salts, dissolved organic matter, oxygen and Ca^{2+} (Lawrence, 1987; Dubois & Chen, 1989). Studies testing the impacts of OA on sea urchins have shown that the epithelium is not a barrier to endoskeletal dissolution, with thinner tests and reduced growth rates at high levels of CO_2 (Shirayama & Thornton, 2005; Miles *et al.*, 2007) and 80% mortality of deep-sea urchins in conditions simulating CO_2 sequestration (Barry *et al.*, 2002).

For Antarctic echinoids, we predict that the maintenance of a calcium carbonate exoskeleton and positive growth rates will depend on a number of factors, including the degree of calcification of the skeleton, and their depth relative to the ASH. As, in general, calcification decreases with decreasing saturation state (reviewed in Kleypas *et al.*, 2006) sea urchins that live at or near the current boundary of the ASH are the most likely to be impacted by shallowing of carbonate saturation horizons; particularly as many species have limited mobility or are burrowing forms. Local changes in the carbonate saturation environment, from external seawater or through pH declines in sediment containing burrowing urchins (Dashfield *et al.*, 2008), might also result in greater costs to producing skeletons (Porter, 2007), changes to growth rates, thinner and weaker skeletons that reduce their competitiveness and affect future population abundance (Tyrrell, 2008), or make the urchins more vulnerable to predation or susceptible to disease (Raven *et al.*, 2005).

A significant barrier to our understanding of how climate change might affect Antarctic echinoids is the limited information available on the Mg-content of the CaCO_3 in Antarctic species and the process of calcification and/or dissolution in what is a carbonate-poor environment (Feely *et al.*, 2004). As noted earlier, the Mg-content of the only Antarctic echinoids for which information is available, *S. neumayeri* and *S. antarcticus* are lower than in temperate and tropical echinoids in both the adult (Weber, 1969; Magdans & Gies, 2004) and, for *S. neumayeri*, the larval phase (Clark *et al.*, 2009). More information on the level and variability in Mg-content in Antarctic echinoids is therefore essential to make species-specific predictions on the affects of changing carbonate conditions. Here, based on depth distribution and test morphology, we can highlight particular families which might be highly impacted by shallowing of the ASH.

The Family Cidaridae, as the most heavily calcified of the Antarctic sea urchins, are likely to be the most susceptible to changes in the depth of the carbonate saturation horizons. In addition, uniquely among the echinoderms, the shaft of the spines is not protected by an epithelial layer (David *et al.*, 2005) making the skeleton

of the spines in direct contact with seawater. Along with the regular sea urchins that have a lower bathymetric limit <3000 m, we predict that any shallowing of the ASH might push these urchins into shallower waters where the costs of calcification might be reduced and positive growth could occur. Only the species of cidaroids with lower levels of calcification (*Aporocidaris* and *Notocidaris*), that currently live below 3000 m, might be able to fulfill the energetic demands of calcification in a less favourable carbonate environment.

In contrast, the Orders Holasteroidea and the Echinothurioidea, whose lower bathymetric limits currently occur below 3000 m, might be predicted to be less affected by shallowing of the ASH as a result of climate change. These orders are found globally in deep-sea habitats (Mooi & David, 1996) and have small thin, poorly calcified tests (Mooi & David, 1996; Mooi *et al.*, 2004). Data from tropical deep-sea echinothurids shows that they have a lower degree of skeletal material in the body wall and spines compared with cidaroids [ash content = 69.8–76.01% DW ($N = 3$ echinothurids) compared with 90.0–90.2% ($N = 2$ cidaroids), McClintock *et al.*, 1990]. Changes to the ASH might therefore alter the relative abundances of Antarctic echinoids to favour those groups with reduced costs of calcification.

In addition to changes in the costs of calcification, the growth rate of Antarctic echinoids is likely to be impacted by changes to the phytoplankton and zooplankton community at the ocean's surface. The Western Antarctic Peninsula, which is one of the most rapidly changing ecosystems on the planet (Barnes & Peck, 2008), has already seen significant changes in surface chl *a* concentrations (decreases <63°S; increases >63°S) with a predicted shift in phytoplankton community composition (Montes-Hugo *et al.*, 2009). Reduced or altered phytoplankton composition in surface waters may result in altered phytodetrital pulses to the deep sea, which will impact the majority of the Antarctic irregular echinoids which are deposit-feeders (Smith *et al.*, 2008). Furthermore, changes to the ASH are predicted to severely impact herbivorous pteropods and result in altered organic carbon and CaCO_3 flux to the deep sea (reviewed in Fabry *et al.*, 2008, 2009), which might indirectly affect omnivorous regular sea urchins (echinids and cidaroids) that consume animals such as sponges and hydroids (Jacob *et al.*, 2003) that depend on this flux. As previously noted for deep-sea corals (Guinotte *et al.*, 2006), any changes to salinity and the direction or velocity of currents that provide sources of food could also have important impacts on many Antarctic echinoids.

Reproduction, local persistence and potential extinctions. To be reproductively successful, brooding echinoids must

live in an environment where the developing young can form a calcium carbonate skeleton. In many Antarctic species, the brooded young are grown to a large size (>2 mm), with a complex system of skeletal plates and spines; see for example the juvenile of *A. mortenseni* in David & Mooi (1990). As echinoid calcite passes through a highly soluble amorphous calcium carbonate (ACC) phase during larval and test/spine growth (Beniash *et al.*, 1997; Politi *et al.*, 2004), we predict that unless a female echinoid is living at depths above the ASH then there may be constraints, both in terms of energetic costs and chemical dissolution, to producing calcified young.

Is the investment in the calcium carbonate skeleton of brooded young greater than that of indirectly developing larval forms? There are two components that we need to consider when we answer this question – the first is where in the water column the calcification occurs, and secondly the amount of CaCO₃ that is deposited. For both components, information on shelf and deep sea echinoids is limited.

Experimental data from two Bahamian deep sea echinoids, the cidaroid *Stylocidaris lineata* and the spatangoid *Archaeopneustes histrix*, has suggested that the lower depth limits of both species and the upper bathymetric limit of *A. histrix* corresponds to the thermal tolerances of embryos and early stage echinoplutei (Young *et al.*, 1998). In Antarctica, in contrast to the Bahamas (Young *et al.*, 1998), there is not a strong thermal gradient between the deep sea and shallow water (Aronson *et al.*, 2007), so all 13 species with larval development are likely to have thermotolerances that allow survival in the water column above the ASH. Planktotrophic larvae of *S. neumayeri* are regularly collected in the top 50 m of the water column (M. A. Sewell, unpublished results), and thus, in contrast to the brooded species, calcification of a large proportion of Antarctic echinoid larvae is likely to be occurring in the more favourable carbonate conditions above the ASH.

The relative investment in calcium carbonate skeleton in larval vs. brooded forms is more difficult to ascertain, as there are two points in echinoid larval development when calcium carbonate structures are formed – during the growth of the skeletal rods supporting the body and arms, and during rudiment formation. For larval sea urchins the only published information, we could find was the calcification index [CI = % inorganic content (ash) of total dry weight] of early stage echinoplutei of four species of sea urchins (Clark *et al.*, 2009). *S. neumayeri* larvae have a lower CI (17.05%) than temperate (54.91, 67.42%) and tropical forms (45.68%, Clark *et al.*, 2009). No information could be found of a similar measurement in rudiment stage larvae or newly metamorphosed settlers, where pub-

lished information provides only the linear dimensions and not the ash content. As many of the Antarctic echinoids with a larval phase are planktotrophic (Poulin & Feral, 1996; Pearse *et al.*, 2009) it is predicted that the major periods of calcification will occur in shallower surface waters above the ASH with available phytoplankton food. However, if the ASH reaches the surface as predicted (Feely *et al.*, 2004, 2009) even planktotrophic echinoid larvae might be undergoing calcification in a less-than favourable environment in the near future.

In contrast, Antarctic brooding echinoids will undergo calcification at the depth at which the mother resides, which as the ASH shallows will include a greater proportion of the reproductively active population. The ash/CaCO₃ content of brooded juveniles can be high: the cidaroids *Abatus nimrodi* and *Abatus shackletoni*, for example, have an ash content of 33.4% and 25.1% dry weight respectively (McClintock & Pearse, 1986). Additionally, in many echinoids the brood sizes (number of young per brood) under current calcification conditions may be large: e.g. *A. nimrodi* and *A. shackletoni* maximum 97 and 104 juveniles (Schinner & McClintock, 1993); *A. mortenseni* approximately seven large (4.5 mm) juveniles (David & Mooi, 1990); *Ctenocidaris geliberti* maximum 50 juveniles (Lockhart *et al.*, 1994); *A. lorioli* maximum 146 juveniles (Galley *et al.*, 2005). If there are changes to local carbonate conditions, then we predict that there might be a reduction in the sizes of the broods and/or reduced levels of CaCO₃ deposited per juvenile, resulting in thinner test plates or spines. Smaller broods and/or juveniles with thinner tests might be more vulnerable to predation, as recently shown in barnacles (McDonald *et al.*, 2009), and together this might result in decreased recruitment at a local level.

In combination, calcification constraints and changes in food availability might limit the reproductive potential of many brooding echinoids (>50% of Antarctic species), so that successful reproduction may only be able to take place in waters shallower than the ASH. Lower reproductive rates, coupled with low dispersal of brooded young, except for relatively rare drifting or rafting events (Pearse & Lockhart, 2004; Pearse *et al.*, 2009), could reduce the densities of deeper populations to low levels or even to local extinction. Although the fertilization biology of most deep sea echinoids, and especially the brooders, is unknown we would expect that, as in shallow water urchins, fertilization success might be reduced at low population densities due to the Allee effect (Levitan & McGovern, 2005). The Allee effect may also be particularly pronounced in Antarctic species which appear to require higher concentrations of sperm than their temperate counterparts (reviewed in Powell *et al.*, 2001). Reduced reproductive output, as

a result of reduced fertilization or brood size, might thus result in a gradual contraction of the bathymetric ranges of many Antarctic urchins to environments favourable for calcification for their own growth and/or the development of their young.

Synergistic affects of other climate-associated changes on Antarctic echinoids. OA is only one of the environmental changes that Antarctic echinoids will be exposed to under global climate change (GCC). In the next hundred years, Antarctic marine environments >60°S are likely to experience surface seawater temperatures increases of 0.5–1.0 °C, bottom water temperature increases of 0.5–0.75 °C, salinity decreases by 0.1–0.2 units, changes to vertical stratification and the extent of deep mixing which influences currents such as the Antarctic Bottom Water and Antarctic Circumpolar currents, a 33% decrease in annual average sea ice cover, and a sea level rise of 2 m (Convey *et al.*, 2009).

Impacts of GCC on Antarctic echinoids are likely to differ between those species that live on the continental shelves, an average of 450 m deep in Antarctica compared with 100–200 km elsewhere (Aronson *et al.*, 2007), and those in deeper waters. On the continental shelf changes associated with GCC include increased disturbance from ice scour, changes to the duration and extent of sea ice, increased sedimentation and freshening from glacial melt, and thermal events such as El Niño (Barnes & Peck, 2008; Smale & Barnes, 2008). These climate change impacts, which will primarily affect the Antarctic shallow shelf, will likely push the bathymetric ranges of species deeper (Smale & Barnes, 2008), at the same time that impacts predicted to occur with decreased ASH depth are pushing distributions shallower. In addition, warmer sea water temperatures might, via the positive relationship between Mg-content and temperature (Vinogradov, 1953; Chave, 1954; Dickson, 2004; Andersson *et al.*, 2005, 2008), result in calcite skeletal material with a higher Mg-content, making them more vulnerable to dissolution. Thus, Antarctic echinoids on the shelf may get a double-whammy of climate change affects that could severely restrict the bathymetric ranges of many species.

Echinoids in the abyssal environment will be similarly affected by the other GCC impacts. Benthic animals will be subject to reductions in vertical mixing of the water column resulting in a decreased oxygen supply, but with the potential for increased food supply and sedimentation that might increase the frequency of down-slope slumps that can bury communities (Kaiser & Barnes, 2008). As many Antarctic shelf and deep-sea species show high levels of eurybathy (Brey *et al.*, 1996), warmer abyssal temperatures may push species deeper

into cooler water, and therefore into less than favourable carbonate conditions for reproduction and growth. Additionally, as past pH levels in the deep-sea have been constant, deep-sea organisms may be less capable of coping with rapid fluctuations in saturation levels caused by the penetration of surface-acidified seawater (Kaiser & Barnes, 2008).

Predicting the effects of OA in combination with other environmental changes in GCC is particularly difficult for any Antarctic species, as we know so little about their physiological tolerances, or the ecophysiological constraints on feeding, locomotion and reproduction (Barnes & Peck, 2008), particularly for those in the abyssal depths (Kaiser & Barnes, 2008). As an example of this complexity, recent research has suggested that early developmental stages of the shallow water sea urchin *S. neumayeri* were found to be less vulnerable to OA in respect to mortality, calcification rate and skeletal rod fine structure than temperate species (Clark *et al.*, 2009). Yet, compared with temperate species, *S. neumayeri* appears overly sensitive to small changes in salinity (4 psu) with a slower development rate and dramatically reduced embryo developmental success (1%) which would have significant impacts on recruitment (Coward *et al.*, 2009). The synergistic effects of OA and variables such as temperature and salinity are at present unknown.

Additional complexity to risk assessment in terms of OA and GCC is provided by the regional responses within the Antarctic itself. The Western Antarctic Peninsula, for example, is particularly vulnerable to exploitation, non-indigenous species invasion and seawater warming (Barnes & Peck, 2008; Smale & Barnes, 2008). Invasions of king crabs have already been reported (Thatje *et al.*, 2005; Aronson *et al.*, 2007) and there are likely to be broad-scale ecosystem changes should invasion of South American macroalgae succeed (Müller *et al.*, 2009). Therefore, echinoids in this region of Antarctica will be influenced by a different suite of environmental changes than elsewhere.

Our best estimates of the combined effects of OA and other GCC environmental factors may, in fact, come from the geological record. During the end Permian mass extinction event, the greatest losses in biodiversity were seen in hypo-metabolic marine invertebrates with a moderate to heavy carbonate skeleton, including articulate brachiopods, corals, bryozoans and echinoderms (crinoids, echinoids; reviewed in Knoll *et al.*, 2007). Knoll and colleagues propose that the 'kill mechanism' for this extinction event was increased $p\text{CO}_2$ (Knoll *et al.*, 2007) and associated low oxygen and high temperatures contributed synergistically to increase the hypercapnic stress on invertebrates with CaCO_3 skeletons in the end-Permian oceans (Pörtner *et al.*, 2005).

Recent physiological analyses of the threats imposed on marine organisms by anthropogenic hypercapnia and synergistic GCC effects have similarly identified echinoids as being particularly vulnerable to OA due to incomplete coelomic fluid buffering and skeletal dissolution at low pH (Miles *et al.*, 2007; Melzner *et al.*, 2009). If we make the assumption that recent echinoids have a similar physiology to genera that were wiped out during the end-Permian mass extinction, then the Antarctic echinoids of today are likely to be particularly vulnerable to increased $p\text{CO}_2/\text{OA}$ and GCC.

Conclusions

In this paper, we have highlighted (1) that High-Mg calcifiers such as echinoids will be particularly vulnerable to changing saturation horizons in the Antarctic and Southern Ocean, and (2) that because many species brood, and brooding occurs in the same environment as the mother, echinoids with this reproductive strategy may be disproportionately affected by OA and changing saturation horizons, with resulting changes to bathymetric ranges and/or local population extinction.

What impact will changing the bathymetric distributions of echinoids have on the Antarctic and Southern Ocean community? Little is known of the ecological relationships between echinoids and other shelf and deep-sea fauna, though recent research has suggested that echinoids contribute 66% of the echinoderm global CaCO_3 production per unit area ($66.72/100.44 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$, Lebrato *et al.*, 2010). As >80% of the global CaCO_3 production from echinoderms is between 0 and 800 m (Lebrato *et al.*, 2010), approximately the mode of lower bathymetric limits in Antarctic echinoids (Fig. 2), any shallowing of saturation horizons in Antarctica that results in population declines or loss is likely to directly impact global CaCO_3 cycling.

One specific impact, however, will be seen on the ectosymbiont fauna of cidaroid spines. In environments where hard substrates are rare, cidaroids are important sources of substrate for sessile organisms such as bivalves, bryozoans, sponges and cnidarians and provide shelter for mobile fauna such as polychaetes, ophiuroids and holothuroids (Brey *et al.*, 1993; Linse *et al.*, 2008; Hétériér *et al.*, 2008). Epibionts of cidaroids are an important source of biodiversity in the Southern Ocean macrofauna (Hétériér *et al.*, 2008; Linse *et al.*, 2008; Cerrano *et al.*, 2009; David *et al.*, 2009), so loss of the urchin host will result in an overall decrease in macrofaunal diversity.

More importantly, perhaps, is that we need to consider the magnitude of the geographic scale of these potential impacts. The Southern Ocean, defined as

being south of the Polar Front, comprises an area of $34.8 \times 10^6 \text{ km}^2$ (Aronson *et al.*, 2007). The distinct biogeographical discontinuity present at the Polar Front results in a Southern Ocean fauna with a high degree of endemism (Aronson *et al.*, 2007). As the ASH is predicted to shallow in the entire Southern Ocean (Feely *et al.*, 2004, 2009) any ecological consequences are likely to have a large geographical impact; it being the exception, rather than the rule, for populations to have sink populations elsewhere.

The combination of climate change forces affecting Antarctic echinoids from both the shallows and, as shown here, from the deep suggests that the High-Mg calcite forming Class Echinoidea are another member of the macrofauna vulnerable to the impacts of increased CO_2 and OA in the Southern Ocean (Andersson *et al.*, 2008). In addition, the predominance of the brooding reproductive strategy means that carbonate conditions that are unfavourable for adult growth, will also impact reproduction, local population persistence, and potentially, in the case of cidaroid spines, lead to an overall loss of biodiversity. It is our hope that in drawing attention to this group that we might encourage more focused research attention on the large gaps in our knowledge with respect to calcification in echinoids and the effects of climate change and OA on a major component of the Antarctic macrofauna.

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