

DISSOLUTION OF OPHIUROID OSSICLES ON THE SHALLOW ANTARCTIC SHELF: IMPLICATIONS FOR THE FOSSIL RECORD AND OCEAN ACIDIFICATION

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ABSTRACT

The brittlestar, *Ophionotus victoriae*, is abundant in Explorers Cove, offshore Taylor Valley. However its ossicles, composed of high-Mg calcite, have not been reported from Cenozoic cores taken from McMurdo Sound. To identify taphonomic processes we analyzed (1) ossicle dissolution and silhouette area loss during a 2-year *in situ* experiment in which whole dead brittlestars were suspended above or placed on the sediment-water interface at water depths of 7–25 m; (2) ossicle dissolution in a 27-day, *in situ* experiment using ossicles freed of soft tissue; (3) porosities of experimental and pristine ossicles; and (4) abundance of ossicles in short cores taken at shallow depths in Explorers Cove. SEM analysis demonstrates significantly higher levels of dissolution in ossicles submerged for two years than in pristine ossicles. Submerged ossicles also had significant breakage reflected in silhouette area loss. During the 27-day experiment, submerged ossicles lost between 0.07 wt% and 1.31 wt%. At the observed rate of dissolution it would take between 6 and 105 years for vertebral ossicles to dissolve completely. Ossicles submerged for two years had a slightly higher mean porosity than pristine ossicles; porosity is controlled by variability in the porous stereom structure as well as dissolution. Results demonstrate that ossicle dissolution starts soon after death and that the stratigraphic record does not accurately reflect the presence and abundance of ophiuroids, thus complicating their use in paleoenvironmental, paleoclimatic, and paleoecologic reconstructions. These results also provide baseline information about CaCO₃ skeletal dissolution needed to monitor the ocean acidification that is predicted to affect high-latitude benthic ecosystems within decades.

INTRODUCTION

The benthic faunas of the Antarctic continental shelf are distinctive relative to lower-latitude faunas in their abundance of epifaunal suspension feeders, elevated species richness within some taxa (e.g., pycnogonids), depressed species richness in others (e.g., bivalves), and absence of fast, durophagous predators including crabs, lobsters, stomatopods, sharks, and most teleosts and skates (e.g., White, 1984; Clarke and Crame, 1989; Dayton et al., 1994; Aronson and Blake, 2001; Clarke and Johnson, 2003; Gutt, 2007). These unusual faunas have been compared to those both of the modern deep sea and of Paleozoic epicontinental seas (e.g., Dayton and Oliver, 1977; Aronson and Blake, 2001). In spite of persistently frigid water and seasonal food supply, controlled by the polar light regime, diversity, the abundance and biomass of Antarctic shelf benthic faunas, although variable, are generally similar to, or higher than, those at equivalent depths in temperate and tropical settings (Arntz et al., 1994; Brey and Gerdes, 1997; Gili et al., 2001; Pabis et al., 2011).

The abundance of benthic animals on the modern Antarctic seafloor (Fig. 1) also contrasts with the paucity of body fossils recovered from cores drilled on the continental shelf to reconstruct Cenozoic paleoclimate and ice-sheet advance and retreat (Fig. 2). In a few horizons, most notably in Pleistocene deposits of the Cape Roberts Core, well preserved and abundant body fossils yield important paleoecologic and paleoclimate information (e.g., Taviani and Beu, 2003). Typically, however, the cores contain little if any macrofaunal skeletal material (e.g., Scherer et al., 2007).

This study addresses the discrepancy between the abundant and diverse modern benthic fauna of Antarctica and the paucity of hard parts of the benthic fauna recovered from cores of Cenozoic sediments by documenting the taphonomy of ophiuroid ossicles that were exposed for two years or less on the shallow ocean floor at 77° S in McMurdo Sound, and by assessing abundance of ossicles in shallow sediment cores retrieved from the same area. We found only a single report of ophiuroid ossicles (Wrenn and Webb, 1976) in descriptions of hundreds of meters of cored sediments recovered from the Antarctic continental shelf during major coring initiatives (Fig. 2; McKelvey, 1981 [DVDP 10–11]; Barrett and Treves, 1981 [DVDP 15]; Pyne et al., 1985 [CIROS 2]; Barrett, 1986 [MSSTS]; Robinson et al., 1987 [CIROS 1]; Cape Roberts Science Team, 1998 [CRP1]; Taviani and Beu, 2003 [CRP]; Woolfe, 2003 [CRP-3]; Scherer et al., 2007 [ANDRILL 1B, MIS]). The absence of reported ossicles of ophiuroids, one of the most abundant benthic groups on the shelf of Antarctica and in the Southern Ocean, in these core descriptions suggests that a taphonomic filter removes the high-Mg calcite ossicles and thus the record of significant components of fossil assemblages from the preserved sediment record. Although collector or observer bias is always a danger when relying on an absence of reports of a diminutive fossil such as those discussed herein, during the course of this study we analyzed 7775 cm³ of cored sediment, supporting the paucity of ophiuroid ossicles in Explorer Cove seafloor sediment.

The significance of the study is threefold. First, it addresses the question of whether the paucity of shell material in cores of Cenozoic sediments of the Antarctic continental shelf accurately records abundance and distribution of benthic animals at the time of deposition and thus should be accounted for in paleoclimate and paleoenvironmental reconstructions, or whether this paucity reflects destructive taphonomic processes. Second, constraining the fidelity of the post-Cretaceous fossil record, incomplete as it is (e.g., Crame, 1992), allows evaluation of its potential contribution to unraveling the origin and paleoclimatic significance of the unique Antarctic fauna that developed after the opening of the Drake Passage ~35 Ma (Aronson et al., 1997; Clarke et al., 2004). Third, by assessing *in situ* dissolution over a short time period, this study provides a baseline for evaluating the ocean acidification that is increasingly recognized as a threat to the southern ocean and its calcium carbonate-secreting fauna (Andersson et al., 2008; McNeil and Matear, 2008; Moy et al., 2009; McClintock et al., 2009, 2011).

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FIGURE 1—Profusion of ophiuroids (*Ophionotus victoriae*), filter-feeding scallops (*Adamussium colbecki*), and sea urchins (*Sterechinus neunayeri*) on and among plates of anchor ice extending upward from the sediment surface. Eight km south of Explorers Cove. Scallop shells are ~8 cm across.

Study Site

Taphonomic experiments on the brittle star *Ophionotus victoriae* were conducted *in situ* at a depth of 7 to 25 m in Explorers Cove at the mouth of the Taylor Valley (Fig. 2; 77° 34.51'S, 163° 31.79'E). Taphonomic and sedimentary processes, as well as benthic community composition and structure, life history strategies, ecological interactions, and nutrient cycling all are strongly affected by the three following characteristics of Explorers Cove:

1. Because it is contiguous with the ice-free Taylor Valley, in particular the eastern sector that is covered by Ross Sea Drift deposited during expansion of the Ross Sea Ice sheet into the lower Taylor Valley ~22 ka (e.g., Hall and Denton, 2000), Explorers Cove has received significant sediment input over the last few thousand years, averaging 3–4 mm yr⁻¹ (Stuvier et al., 1976). Extensive cover of poorly sorted sand on the sea ice in Explorers Cove attests to the importance of wind transport (e.g., Barrett et al., 1983). Sediment is also delivered to Explorers Cove in the summer by the ephemeral glacier-fed streams that have built deltas since ice retreat 6 to 7 ka (Murray et al., 2012). The modern sedimentation rate is low, estimated as 0.2 mm yr⁻¹ (Bentley, 1979), which is consistent with observations of very little sediment accumulation on experimental apparatuses deployed on the seafloor (Gooday et al., 1996).

2. Explorers Cove typically is covered by multiyear sea ice that is 3–4 m thick. In the winter and spring the sea ice is grounded along the shore, but some years this grounded ice melts in the summer to form a moat between the shore and the floating sea ice. From the 1970s to early 1990s the sea ice in Explorers Cove melted completely every 5 to 7 years (Gooday et al., 1996) but the last ice breakout was in 1999–2000. Dark, windblown sediment on the sea-ice surface causes differential melting which produces irregular topography with increasing relief each year that the ice does not melt completely; in 2010 after 11 years, relief was up to 2 m.

The multiyear sea ice greatly influences the physical and chemical environment of Explorers Cove. It inhibits wave activity year round and tidal flow during the winter and spring. Reported currents in late October to early November, 2001 were low, averaging 2.6 cm s⁻¹ (Cummings et al., 2006), and divers describe currents as being imperceptible or barely perceptible (S.S. Bowser and S. Clabuesch, personal communication, 2010); water temperature is -1.9 °C. The sea ice blocks penetration of sunlight; only two years after the last meltout, light under the sea was 0.2% incident irradiance (Cummings et al.,

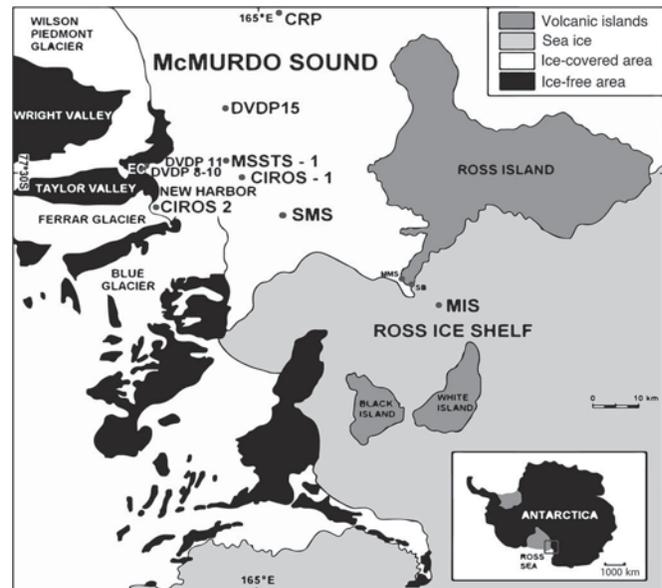


FIGURE 2—Location of study area in Explorers Cove, New Harbor, at the mouth of the Taylor Valley. Locations of cores drilled through Cenozoic sediments are indicated by dots with letters; Dry Valley Drilling Project (DVDP) cores 8–10 were drilled at the Explorers Cove (EC) shoreline. Antarctic Drilling (ANDRILL) cores include Southern McMurdo Sound (SMS) and McMurdo Ice Shelf (MIS) (ANDRILL 1B). McMurdo Station (USA; MMS) and Scott Base (New Zealand; SB) are at the south end of Ross Island.

- 2006). Summer melting creates a low-salinity lens several meters deep under the ice, whereas freezing results in hypersaline brine that sinks, killing benthic animals, and leading to local anoxia (e.g., Bernhard, 1987). Spatially and temporally patchy anchor ice (e.g., Dayton et al., 1969, 1970) transports bottom sediment with associated benthic animals upward where it attaches to sea ice and, given sufficient ablation, may eventually be exposed on the sea-ice surface. There are iceberg gouges in Explorers Cove, but the number of observed icebergs, and by inference, the severity of their effects, is less than in areas to the north and south in western McMurdo Sound (Oliver, 1984).

3. Explorers Cove is oligotrophic (sediments with total organic carbon <1% and chlorophyll *a* ~0.5 µg g⁻¹ sediment; Cummings et al., 2006), a fact attributed to low productivity currents emerging from under the Ross Ice Shelf and moving northward slowly along the west side of McMurdo Sound (Dayton and Oliver, 1977; Barry, 1988; Barry and Dayton, 1988). In addition, the persistence of sediment-laden sea ice for years in Explorers Cove and the resulting low light levels must inhibit the development of the diversity, productivity, and complexity of algal and microbial life that has been documented within sea ice elsewhere (Arrigo and Thomas, 2004; Ryan et al., 2006; Massom and Stammerjohn, 2010; McMinn et al., 2010). The unique occurrence of very large agglutinated foraminifera (DeLaca et al., 1989) on the shallow seafloor of Explorers Cove, characteristic of deeper water habitats, has been attributed in part to the forams' ability to survive extended periods of limited resources by reducing metabolic rate and increasing it rapidly when resources become available (Gooday et al., 1996). Presumably in response to the pattern of food availability in Explorers Cove (long famines and short, unpredictable feasts) common large benthic animals in Explorers Cove tend to utilize a diverse food source as opportunistic feeders (e.g., ophiuroids; Fratt and Dearborn, 1984), or suspension feeders (e.g., phytoplankton, ice algae, sediment; Norkko et al., 2007). In Explorers Cove density of the most abundant epifaunal animal, the Antarctic scallop, *Adamussium colbecki*, is greatest near tidal cracks through which sediment and microalgae from the shallow moat are funneled during the summer (e.g., Stockton, 1984; Thrush et al., 2006). Scallops resuspend sediment by valve clapping,



FIGURE 3—*Ophionotus victoriae* in Explorers Cove. Disc of specimen elevated on its legs (foreground) is 2.5 cm across.

thus making sediment food resources available to suspension feeders (e.g., Chiantore et al., 1998; McClintock et al., 2010). Thus, the dominant vagile epifaunal animals in Explorers Cove, the ophiuroid *Ophionotus victoriae* and the scallop *A. colbecki*, both use sediment food sources extensively—food sources which are documented to provide a significant food bank that buffers the highly seasonal productivity (e.g., Smith et al., 2006). In the process, these animals churn the upper ~5 cm of sediment at a rate far outstripping the rate of sedimentation (Broach et al., 2011); this creates a thick taphonomically active zone (TAZ; Davies et al., 1989) that exerts strong influence on taphonomic processes and on the resulting fossil record.

Ophiuroid Distribution and Ossicle Anatomy

Echinoderms dominate the epifauna of some areas of the Antarctic shelf in terms of numbers and weight. Up to 75% of the echinoderms by number are ophiuroids, and the group constitutes a third of the echinoderm biomass (Moya et al., 2003; LeBrato et al., 2010; Rehm et al., 2011).

Ophionotus victoriae is a widespread, eurybathic (5 to >1000 m) ophiuroid that is endemic to Antarctica (Arnaud et al., 1998). It is the dominant ophiuroid in the Antarctic Peninsula–South Shetland Island region (Arnaud et al., 1998; Moya et al., 2003; Lovell and Trego, 2003; Manjon-Cabeza and Ramos, 2003), on the west side of McMurdo Sound (Cummings et al., 2006), and in some areas of the Weddell Shelf (Piepenburg et al., 1997). It also occurs in the Ross Sea (Fell, 1961) and is ubiquitous and locally abundant at bathyal and abyssal depths in the Weddell Sea (Linse et al., 2007). Based on its abundance and widespread distribution, one would predict that its skeletal elements would be present, even common, in the Antarctic marine sedimentary record.

In Explorers Cove, *O. victoriae* (Fig. 3) is common, occurring in densities of 0.3–1.0 m⁻². Only the scallop *Adamussium colbecki* (2–9 m⁻²) and the sponge *Homaxinella balfourensis* (1–4 m⁻²) that attaches to the scallop and to a pencil urchin are more common epifaunal animals (McClintock, 1994; Norkko et al., 2002; Cummings et al., 2006; Mead et al., 2009).

The internal skeleton of *O. victoriae*, like that of all ophiuroids, consists of ossicles (~1500 per individual) of diverse sizes and shapes held together by muscle, mutable connective tissue, and dermis ligamental tissue (Byrne, 1994). These ossicles disarticulate soon after death (Schäfer, 1972; Lewis, 1986, 1987; Allison, 1990; Kidwell and Baumiller, 1990; Donovan, 1991; Brett et al., 1997; Kerr and Twitchett, 2004). They are composed of high-Mg calcite secreted intracellularly in sclerocytes or in syncytia (Märkel and Röser, 1985; Tucker, 1991; Byrne, 1994; Freiwald, 1998).

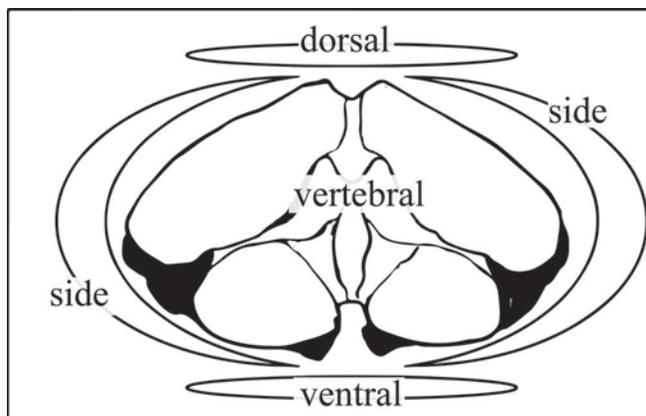


FIGURE 4—Location of ossicles in ophiuroid leg. Vertebral ossicles are most robust and likely to be preserved.

The most abundant robust ossicles are vertebral ossicles (Fig. 4), long stacks of which form the core of each arm. Although the jaw ossicles ($n = \sim 10$ per individual) are thicker and presumably more preservable, the vertebral ossicles are so much more abundant ($n = \sim 400$ per individual and more if the arm is autotomized; Hyman, 1955; Wilkie and Emson, 1987; Clark et al., 2007) that they are the most likely ossicles to be recovered from the sedimentary record, and they have been reported from marine sediments elsewhere (Mallikarjuna et al., 1999; Štorc and Žítt, 2008; Dynowski, 2012).

Each ossicle is composed of meshlike stereom, shown in Figure 5A, that is composed of trabeculae (rods of solid calcite) and intertrabeculae spaces (pore spaces; Hyman, 1955). The distal side of each vertebral ossicle (hereafter ossicle = vertebral ossicle) includes (Fig. 5B): (1) an upper margin where the ossicle is relatively thin; (2) an upper fossa rich in muscle and connective tissue including mutable collagenous tissue (MCT); (3) a lower fossa similar to the upper fossa; (4) a lower margin, similar to the upper margin; and (5) a knob, which is the central hinge point and experiences the most friction during movement (Byrne, 1994; LeClair, 1995). The knob has a higher trabecular to intertrabecular ratio than either the upper or lower fossa or upper or lower margin.

METHODS

Ophiuroid ossicle dissolution and damage in Explorers Cove were assessed by (1) *in situ* experiments in which sacrificed ophiuroids were, for two years, either suspended above the sea floor or embedded in sediment at the sediment-water interface (SWI), and in which ossicles freed of soft tissue were suspended in Explorers Cove for one month; (2) analysis by SEM and X-ray tomography of textural characteristics of experimental ossicles, control ossicles, and ossicles that were purposefully broken by grinding or had had soft tissue removed by bleach (6.15% sodium hypochlorite) or peroxide (3% dihydrogen dioxide); and (3) search for ossicles in sediments from shallow cores taken from the seafloor in Explorers Cove and textural analysis of these ossicles. In addition, ossicles were recovered from a pile of ossicles on the seafloor and examined, and ossicles of *Ophionotus victoriae* recovered from the distended guts of three living specimens of a larger carnivorous brittle star, *Ophiosparte gigas*, were subjected to textural analysis.

In Situ Experiments

In November 2008, specimens of *Ophionotus victoriae* were collected from the seafloor in Explorers Cove at depths of 9–25 m by SCUBA divers and were immediately frozen. Specimens were divided; one half for the raised or Pole experiments and half for the Aquarium

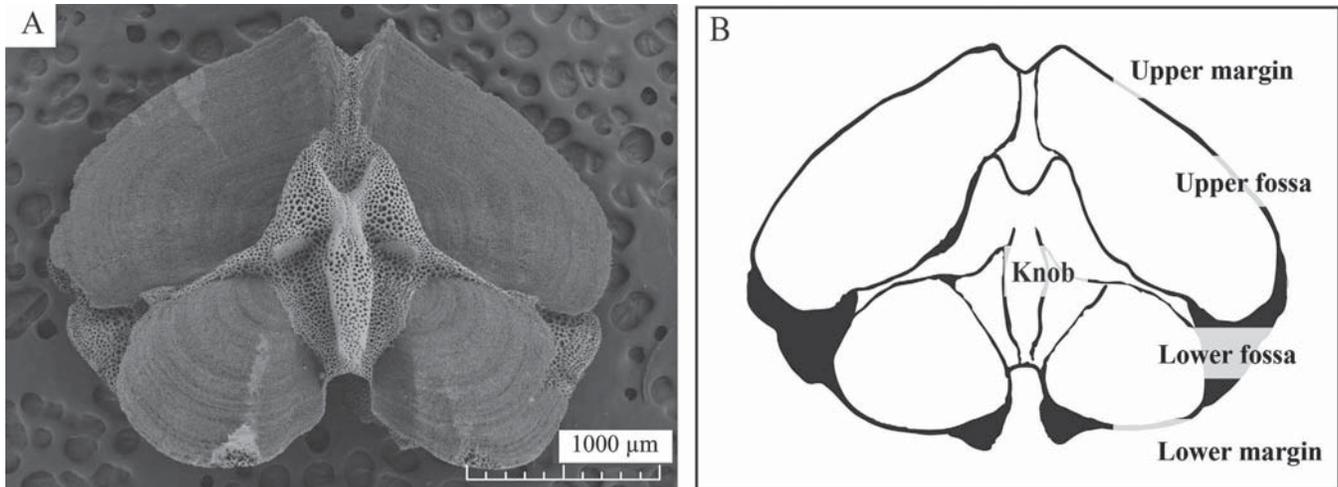


FIGURE 5—Distal side of a vertebral ossicle. A) SEM (Tescan VEGA3) image; complexity in shape of actual ossicle (in comparison to view B, a drawing that indicates the distinctly different areas of the ossicle itself). B) Major features of ossicle.

experiments at the SWI. For the Pole experiments, a frozen brittle star ($n = 42$) or the soft-tissue-free ossicles from a frozen ophiuroid ($n = 12$) were placed in a bag composed of nylon (mesh size ~ 1 mm); the bags were suspended by fishing line from PVC pipe poles 15 to 40 cm above the SWI at locations throughout Explorers Cove; each pole had three bags. For the Aquarium experiments the freeze-killed brittle stars were placed in the sediment at the SWI in 7 aquaria (11 cm \times 3.6 cm \times 15 cm) that were filled with Explorers Cove sediment. Three mesh-covered holes (2.5 cm diameter) on each side of the aquarium allowed movement of water, oxygen, nutrients, and organisms through the sediment within the aquaria. Both the Aquarium and Pole experiments were placed on the seafloor in Explorers Cove (Fig. 2) by divers at 7–25 m water depth in November 2008 and were recovered in October 2010. Controls were (Pristine) *O. victoriae* ossicles that were freed from soft tissue by natural decay. After thawing the frozen *O. victoriae* samples, the soft tissue readily fell away from the ossicles. We considered this unassisted decay natural.

To constrain rate of dissolution, a Hanging Bag experiment was deployed in Explorers Cove for 27 days in November, 2010. Four sets of 7 pristine, proximal vertebral ossicles isolated from soft tissue of 4 individuals were weighed on a Mettler Toledo UMX2 Ultra-microbalance, placed in mesh bags and hung 1.5 m above the seafloor where they were exposed to normal bottom water conditions. Each bag contained 7 ossicles. The bags were separated by blasting wire and suspended by a rope attached at the surface and dropped through a hole in the ice. The apparatus was weighted down by a canvas bag of rocks.

For comparison to the Hanging Bag experiment, nine sets of six pristine, weighed ossicles were sewn into polyester 300-mesh bags and stored in a refrigerator for 259 days, at an average temperature of 1 °C. Filtered water (NANOpure ultrapure water system; Barnstead) was mixed with Instant Ocean, to create a salinity of 35 ppt, which mimics Explorers Cove.

SEM and X-Ray Tomography Analysis

Scanning Electron Microscope (SEM).—To evaluate and characterize dissolution and microstructural damage on the ossicles, each ossicle was sputter coated with gold in a vacuum and imaged with a Hitachi S-4200 SEM. Five locations (Fig. 5B) on the distal side of each ossicle were examined at a variety of magnifications. At higher magnification (field of view ~ 35 μ m) the microstructural damage was characterized as chemical or physical. Both chemical and physical damage were assessed through an experiment that amplified the destruction caused by

physical crushing and chemical etching by HCl (Forced Damage Experiment explained below). Results from this forced damage experiment provided the basis for distinguishing between chemical versus physical damage to the ossicles recovered from Explorers Cove. Images at lower magnifications (field of view >150 μ m) showed whether or not the damage type was localized, spotty, or widespread.

Initial SEM imaging revealed a variety of microstructural dissolution patterns. To systematically evaluate and record intensity of dissolution at each location on each ossicle, a descriptive scale of dissolution intensity was created and is demonstrated in Figure 6 with 0 for no dissolution to 7 for extensive dissolution (Fig. 6). The scale of dissolution is also visually represented in Figure 7. The SEM images in Figure 7 were created using a Tescan VEGA3 SEM. They are from the same locations on the same ossicles as original images taken with the Hitachi S-4200. Five locations on the distal side of each ossicle were observed (field of view = 35 μ m) and the highest level of dissolution observed on each ossicle was recorded. Levels of dissolution seen on Pristine, Pole, and Aquarium ossicles were compared using the Kuskal-Wallis H-test. Highest levels of dissolution observed on ossicles recovered from the gut of dissected specimens of *Ophioparte gigas* were determined and compared to those of Pristine ossicles using the Mann-Whitney U-test.

SEM images were used in a technique termed Silhouette Area Loss to quantify on a larger scale the effects of physical breakage on each ossicle; the amount of silhouette area that should be present on each ossicle was calculated and compared to the amount of silhouette area that is actually present. The area that should be present was calculated using the equation of a regression line of a plot of the lengths of the vertical central axis on the distal side of the 20 Pristine ossicles versus

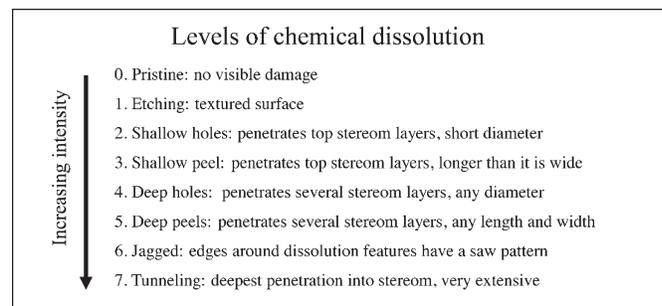


FIGURE 6—Semi-quantitative scale of level of dissolution of ophiuroid ossicles based on SEM analysis.

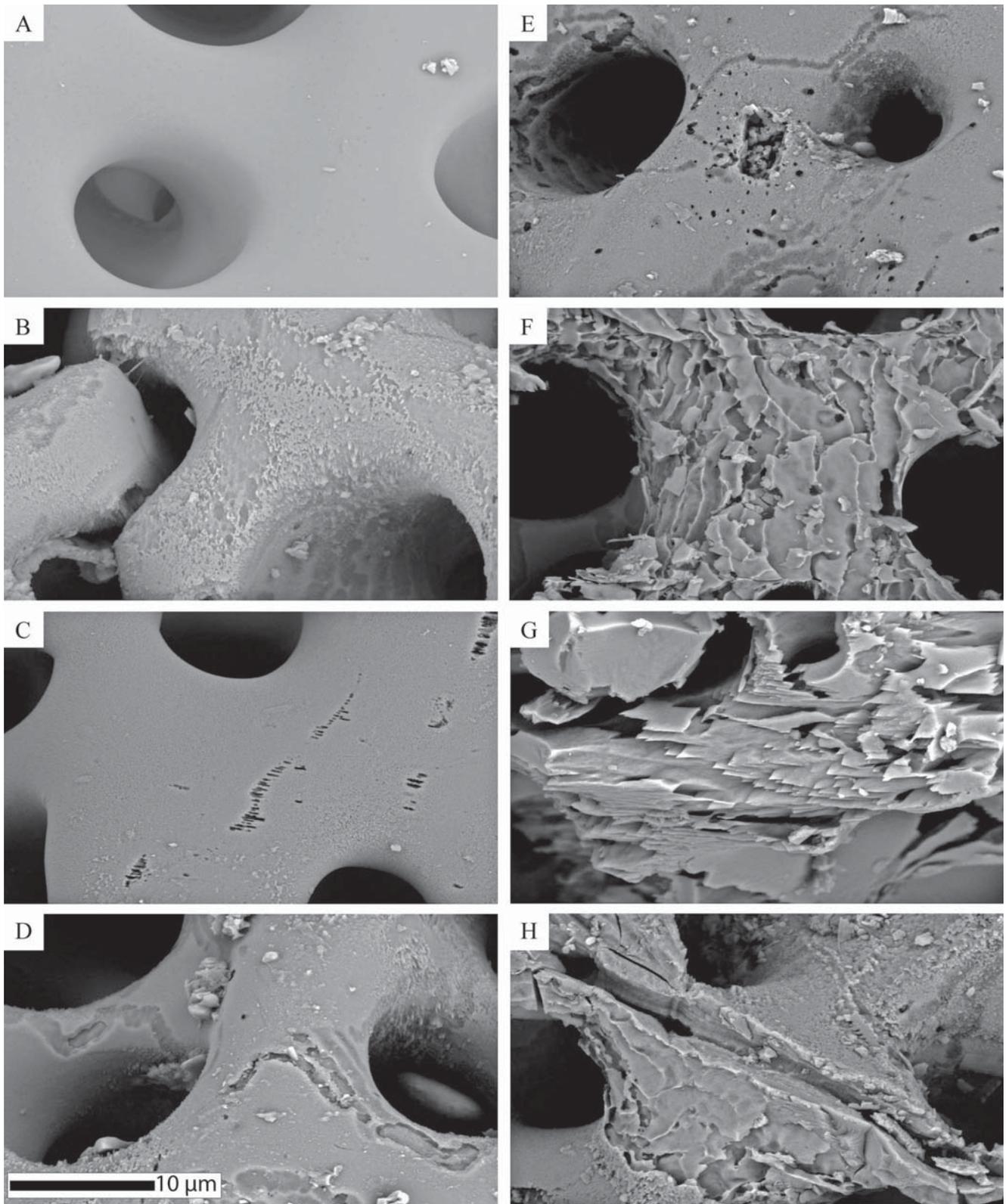


FIGURE 7—SEM (Tescan VEGA3) images of *O. victoriae* ossicles from Explorers Cove illustrating dissolution levels 0–7 in A–H respectively. Each image is of the stereom structure on the knob of an untreated ossicle. The ossicles for A) came from the stomach contents of *Ophioparte gigas*; B), D), and E) came from the Pole experiments; C) came from the Hanging Bag experiment; F) and H) came from the Aquarium experiments; and G) was found in the sediment search. Scale bar in D applies to all images.

their silhouette areas. Even if an ossicle has been damaged, the length of the vertical central axis can be measured on printed copies of SEM images, because this area is least susceptible to breakage. Silhouette area was calculated using a paper proxy, assuming the weight and thickness of the paper is held constant. Using the ratio of known weight and area we could then calculate any area given a known weight. This ratio was then used to calculate the surface area of ossicles, from the weights of the cutout of the ossicles, whose image was cut from a printout of the whole ossicle. The weight and the ratio were then used to determine the final area of the ossicle. Based on inspection of a plot of silhouette area A versus axis length l , we assume a relation between these, of the form

$$A = al^m \quad (1)$$

that is linear in log-log space, so that we use linear regression in $\log(A)$ versus $\log(l)$ space to derive estimates of b and m . Because A has units of $[L^2]$ and l has units of $[L]$ it is desirable if $m = 2$ wherein a is dimensionless. In the calculation $m = 1.63$, which suggests it approximately represents an allometric relationship with appropriate dimensions, although here it is used purely as an empirical curve to relate A and l . This technique was used to obtain the initial area. We used area loss (i.e., initial area minus final area) divided by the initial area to compare ossicles.

Forced Damage Experiments.—To facilitate identification of microstructural features caused by physical breakage or chemical dissolution, ossicles and freshly broken calcite fragments were broken by blunt force or grinding, or subject to chemical treatments. Chemical treatments included submergence in HCl (3.5% for 8 seconds), household bleach (6.15% sodium hypochlorite for 27 hours), or household hydrogen peroxide (3% dihydrogen dioxide for 27 hours). All of these results were then evaluated with the same SEM protocol as used on ossicles used in the *in situ* experiments.

X-ray Tomography.—To determine the porosity of the ossicles, 24 samples were imaged at the GeoSoilEnvironCARS beamline (sector 13) of the Advanced Proton Source (APS) at Argonne National Laboratory in Chicago, Illinois. X-ray tomography was used because it is a nondestructive way to create a three-dimensional (3-D) map of the linear attenuation coefficient (for details, see Rivers et al., 1999; Landis and Keane, 2010) that can be used to calculate the total volume of the ossicles. For mapping, four ossicles were stacked in a plastic pipette tip, separated by foam and enclosed with transparent adhesive tape. The vials were placed on a rotating stage; a radiograph was taken at every 0.25° step, with a total of 720 radiographs taken for each tomogram. Tomograms were obtained at 19keV with resulting cubic volume elements (voxels) of 6.1 or 8.9 micrometers in each linear dimension. Reconstructions were performed using *tomo_display* (Rivers and Gualda, 2009).

IDL routines implemented in *vol_tools* (Rivers and Gualda, 2009) and *Blob_3D* (Ketchum, 2005) were used for image processing. The routine *vol_detect* of *vol_tools* was used to compute the volume of each ossicle, inclusive of its pores; it uses a morphological close algorithm to select both ossicle and pore voxels and separate from surrounding air voxels, resulting in the total volume of the ossicle. Using the mass of each ossicle as measured with a precision scale, the ossicle density can be calculated by the ossicle mass divided by the total volume. Knowledge of calcite density allows calculations of the pore volume:

$$\begin{aligned} \text{Total Volume}(\text{Voxel}^3 - \text{cm}^3) - \frac{\text{Ossicle Mass}(\text{g})}{\text{Calcite Density}(\frac{\text{g}}{\text{cm}^3})} \\ = \text{Porve Volume}(\text{cm}^3) \end{aligned} \quad (2)$$

Sediment Search

SCUBA divers collected sediment cores by pushing plastic tubes 7.5 cm in diameter and 30 cm in length into the seafloor at Explorers

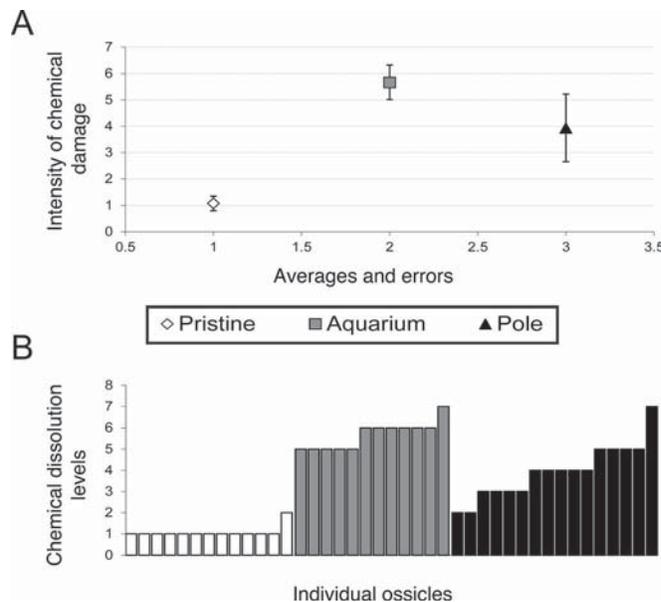


FIGURE 8—Highest levels of ossicle dissolution observed on pristine (control) ossicles, and ossicles submerged for 2 years in Explorers Cove, either suspended a few decimeters above the seafloor (pole), or at the sediment-water interface in small aquaria (aquarium). A) Averages and errors for pristine (mean = 1.08 ± 0.28), aquarium (mean = 5.67 ± 0.65), and pole ossicles (mean = 3.94 ± 1.9). B) Highest level of dissolution observed on each ossicle.

Cove. Each core was frozen and shipped to Vanderbilt University. They were then divided into ~ 30 one cm samples. Each sample was sieved and separated into grains larger than or smaller than $250 \mu\text{m}$. The grains larger than $250 \mu\text{m}$ were examined under a dissecting light microscope (Wild M4A TYP 376788; Heerbrugg, Switzerland). Ossicles were removed from the sediment by a fine paint brush, then transferred and glued to a micropaleontology slide for observation.

RESULTS

In Situ Experiments

Decay and Ossicle Recovery.—After two years on or near the seafloor, no soft tissue remained on any ophiuroids, and ossicles had begun to dissolve. Ossicles were recovered from 35 of the 54 mesh bags in the Pole experiments and from 3 of the 7 Aquarium experiments. Seven mesh bags from the Pole experiment and the mesh lining of one aquarium had holes in the mesh that presumably were produced by scavengers.

Chemical Dissolution.—Both Aquarium and Pole ossicles had higher mean levels of dissolution than the Pristine (control) ossicles (Fig. 8A). The Kruskal-Wallis H-test (Johnson, 2005) shows that ossicles from Aquarium and Pole experiments are all statistically different in levels of chemical dissolution than seen on Pristine ossicles ($H = 30$, $df = 2$, $p > 0.001$). Ossicles from the aquaria consistently showed the highest maximum levels of dissolution (Fig. 8B). Pole ossicles had the highest level of dissolution, but also had the widest range of maximum dissolution levels (Fig. 8B). The knobs consistently had the highest levels of dissolution, although high levels of dissolution could occur at other locations as well (Fig. 5B).

Ossicles from the Hanging Bag experiment had levels of dissolution similar to that of the Pristine ossicles. However, they lost between 0.07 wt% and 1.31 wt% over the course of the 27-day experiment (mean = 0.56 wt%). With this range in rates of dissolution, ossicles would dissolve completely in 6 to 105 years. Ossicles suspended for 259 days in cold filtered water with artificial sea water lost between 0.11 wt% and 4.62 wt%, suggesting total dissolution in 15 to 645 years.

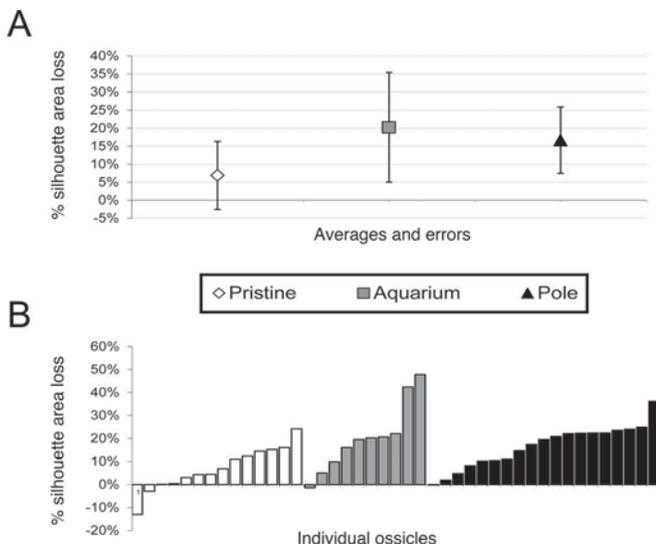


FIGURE 9—Estimated percent of silhouette area loss for pristine, aquarium, and pole ossicles. A) Averages and errors for Pristine (mean = 6.9 ± 9.5%), Aquarium (mean = 20.2% ± 15.2%), and Pole ossicles (mean = 16.7% ± 9.2%). B) Silhouette area loss of each ossicle.

Silhouette Area Loss.—Ossicles from the Pole and Aquarium experiments have means of silhouette area loss that differ significantly from that of Pristine ossicles (Kruskal-Wallis H-test, $H = 7.84$, $df = 2$, $p > 0.05$) (Fig. 9). The percent silhouette area loss for the Pole and Aquarium experiments was 2 to 3 times greater than the Pristine ossicles.

Porosity.—The ossicles from the Pole experiments have the highest mean percent porosity (77.7%) of all the experimental ossicles (Fig. 10), and all experimental ossicles have higher porosities than the Pristine ossicles. The porosities of the ossicles from the Pole and Aquarium experiments differ significantly from that of the Pristine ossicles (Kruskal-Wallis H-test, $H = 34.5$, $df = 2$, $p > 0.01$).

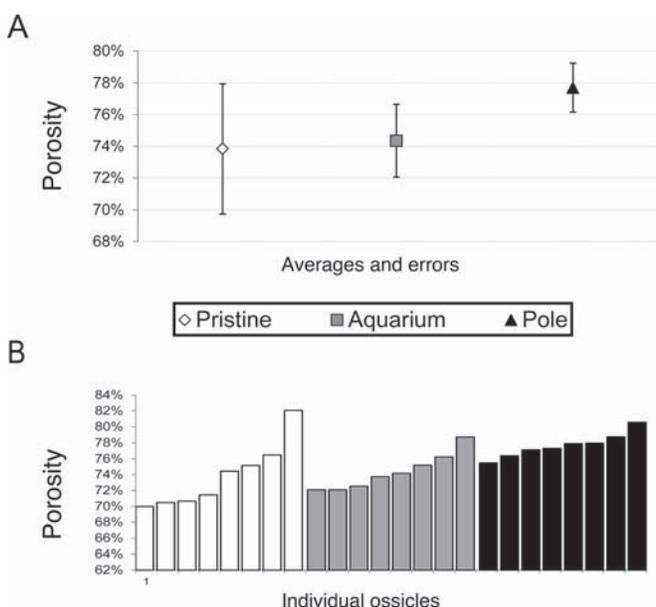


FIGURE 10—Percent porosity for pristine, aquarium, and pole ossicles determined using X-ray tomography and IDL software analysis. A) Averages and errors for pristine (mean = 73.8% ± 0.04%), aquarium (mean = 74.4% ± 0.2%) and pole ossicles (mean = 77.7% ± 0.02%). B) Porosity of each ossicle.



FIGURE 11—Aboral dissection of disc of *Ophioparte gigas* showing ossicles of complete disc of *Ophionotus victoriae* that had been ingested whole by the *O. gigas*. Tweezers at right for scale, space between the tweezers is approximately 1 cm.

Other Ossicles: Forced Damage and Retrieved from Ophiuroid Gut

Forced Damage.—Effects of the physical breakage were observed at both the macroscopic and microscopic levels. On the macroscopic level, ossicles lost stereom area from both the upper and lower fossae (Fig. 5B); under SEM the trabeculae were clearly fractured.

Macroscopically, ossicles from the peroxide and bleach treatments looked unaltered, yet microscopically they showed pitting or shallow holes. Ossicles in the HCl treatment exhibited a greatly reduced silhouette area macroscopically and commonly showed thinning of stereom struts on the microscopic scale.

Retrieved from Ophiuroid Gut.—Divers collected six specimens of the large carnivorous ophiuroid *O. gigas* with distended guts. Three of these specimens contained parts (leg fragments to a complete disc; Fig. 11) of *Ophionotus victoriae*. All ossicles removed from the dissections had 0 through 3 levels of chemical dissolution (Figs. 6, 7) and minimal physical breakage. Comparing the ossicles retrieved from gut dissection to pristine ossicles, there was no significant difference using the Mann-Whitney U-test between the groups in either silhouette area loss ($Z = -0.15$, $p < 0.05$) nor the chemical dissolution levels ($Z = 0$, $p < 0.05$) (Fig. 12).

Sediment Search

A total of 12 ophiuroid ossicles were recovered from 7775 cm³ of sediment from cores in Explorers Cove that were examined. Two highly degraded vertebral ossicles were found (Fig. 13C), but only one was analyzed using X-ray tomography; which has a porosity of 78.3%. The degraded vertebral ossicles and 5 other ossicles were retrieved at a core depth of 6 cm (below SWI) whereas the others were retrieved from the top three cm. No ossicles were found at core depths greater than 6 cm.

DISCUSSION

Dissolution and Degradation of *Ophionotus victoriae* Ossicles

This study demonstrates that ophiuroid ossicles dissolve significantly in two years at water depths of 25 m or less on the shallow seafloor covered by multiyear sea ice in Explorers Cove. Significantly higher levels of dissolution were found on ossicles that were submerged *in situ* than on pristine ossicles recovered from sacrificed ophiuroids (Fig. 8). Dissolution was greater on ossicles placed at the SWI (sediment-water interface) than those suspended in seawater above the seafloor. This is consistent with studies demonstrating enhanced dissolution of calcareous foraminifera at the SWI due to oxidation of organic matter and

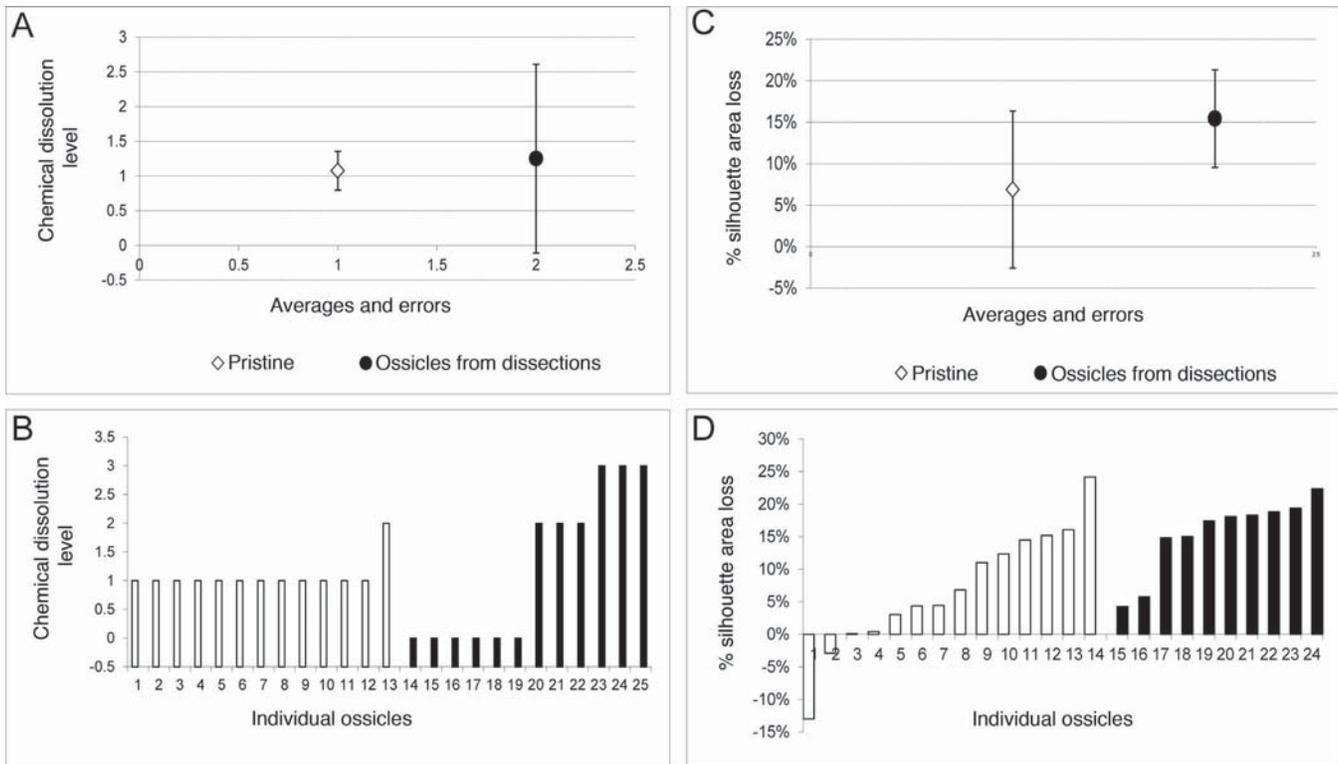


FIGURE 12—Comparison between Pristine ossicles and those recovered from gut dissections of *Ophiopartia gigas*. A) Maximum levels of dissolution observed on pristine ossicles and those recovered from dissection of *O. gigas*. B) Averages and errors of maximum dissolution levels on pristine ossicles and those recovered from dissection of *O. gigas*. C) Silhouette area loss on pristine ossicles and ossicles from dissection. D) Averages and errors of silhouette area loss on pristine ossicles and ossicles from dissections.

other materials, which lowers pH (e.g., Green et al., 1993; Steinsund and Hald, 1994).

On a short time scale, the experiment in which preweighed ossicles were suspended *in situ* in Explorers Cove for 27 days resulting in ossicles losing a mean of 0.56% of their initial weight (range = 0.07% to 1.31%). Ossicles kept at 4 °C in artificial seawater in a laboratory lost on average of 0.96% of their initial weight after 259 days (range = 0.11% to 4.62%). Assuming a constant rate of dissolution and normalizing the mean ossicle weight loss of the 259 day experiment to the short duration of the *in situ* experiment, the estimated weight loss of laboratory ossicles in 27 days is 0.10%, somewhat less than that of the ossicles suspended in seawater in Explorers Cove. The lower rate of dissolution in the laboratory treatment may reflect reduced microbial activity; although the ossicles were not sterilized prior to immersion in the artificial seawater, they had been air dried, which may have been deleterious to microbes. As discussed below, microbial activity has been implicated in initiation of dissolution of biogenic carbonates (e.g., Glover and Kidwell, 1993; Freiwald, 1995, 1998).

Although ossicles did not develop dissolution features during these short-term experiments, the weight loss suggests that dissolution starts soon after submergence. We predict that the weight loss would have been greater and the dissolution features better developed, had the ossicles been at the SWI in Explorers Cove rather than suspended 1.5 m above the substrate.

Dissolution-degradation is also shown by changes in silhouette area (Fig. 9) and porosity as determined by X-ray tomography (Fig. 10). Evaluation of silhouette area loss demonstrated breakage and loss at the margin of the ossicle where it is thinnest and most likely to break, especially after dissolution has started (Green et al., 1993). The negative values for two pristine ossicles and the large variances in silhouette area within the Pristine, Aquarium, and Pole groups of ossicles reflect limitations of the method (Fig. 9). However, the differences in means of silhouette area loss between the Pole and Pristine ossicles and between

the Aquarium and Pristine ossicles indicate significant differences in breakage. Increased breakage in submerged ossicles is consistent with the observed effects of dissolution on the submerged ossicles. Unfortunately because the key feature for calculating the silhouette area was not preserved on degraded vertebral ossicles recovered from the core, the differences in silhouette area between these severely degraded ossicles and submerged experimental ossicles could not be determined.

Assessing differences in porosity between pristine and experimental ossicles using X-ray tomography would seem to be a means of evaluating dissolution; those subject to greater dissolution should be more porous, but the results did not prove this to be the best method for assessment. Ossicles that had been submerged in Explorers Cove for two years had higher porosity than the pristine ossicles (Fig. 10). However, the differences are small and only a limited number of ossicles in each category were analyzed ($n = 5-8$). Based on porosity, ossicles suspended above the SWI in the Pole experiments lost the greatest volume of calcite (Fig. 10; mean porosities: Pristine = 73.8%; Aquarium = 74.4%; Pole = 77.7%). This conflicts with the analysis of dissolution textures that suggests that the greatest degradation occurred to ossicles at the SWI in the Aquarium experiments (Fig. 8). The porosity of the highly degraded ossicle recovered from the sediment was only slightly higher (78.3%) than that of ossicles submerged for two years. Significant natural variation in stereom structure and porosity within and between ossicles reduces the fidelity of porosity as a proxy for dissolution. However, the fact that ossicles submerged in seawater for two years had higher porosity than pristine ossicles is consistent with evidence from dissolution features and silhouette area analysis that submerged experimental ossicles underwent significant degradation.

A challenge in setting up experimental arrays in the field at Explorers Cove was isolating ossicles from sacrificed ophiuroids; limited time and facilities precluded separation of hard and soft tissue by natural decay. To speed the process, some ophiuroids were submerged in solutions of

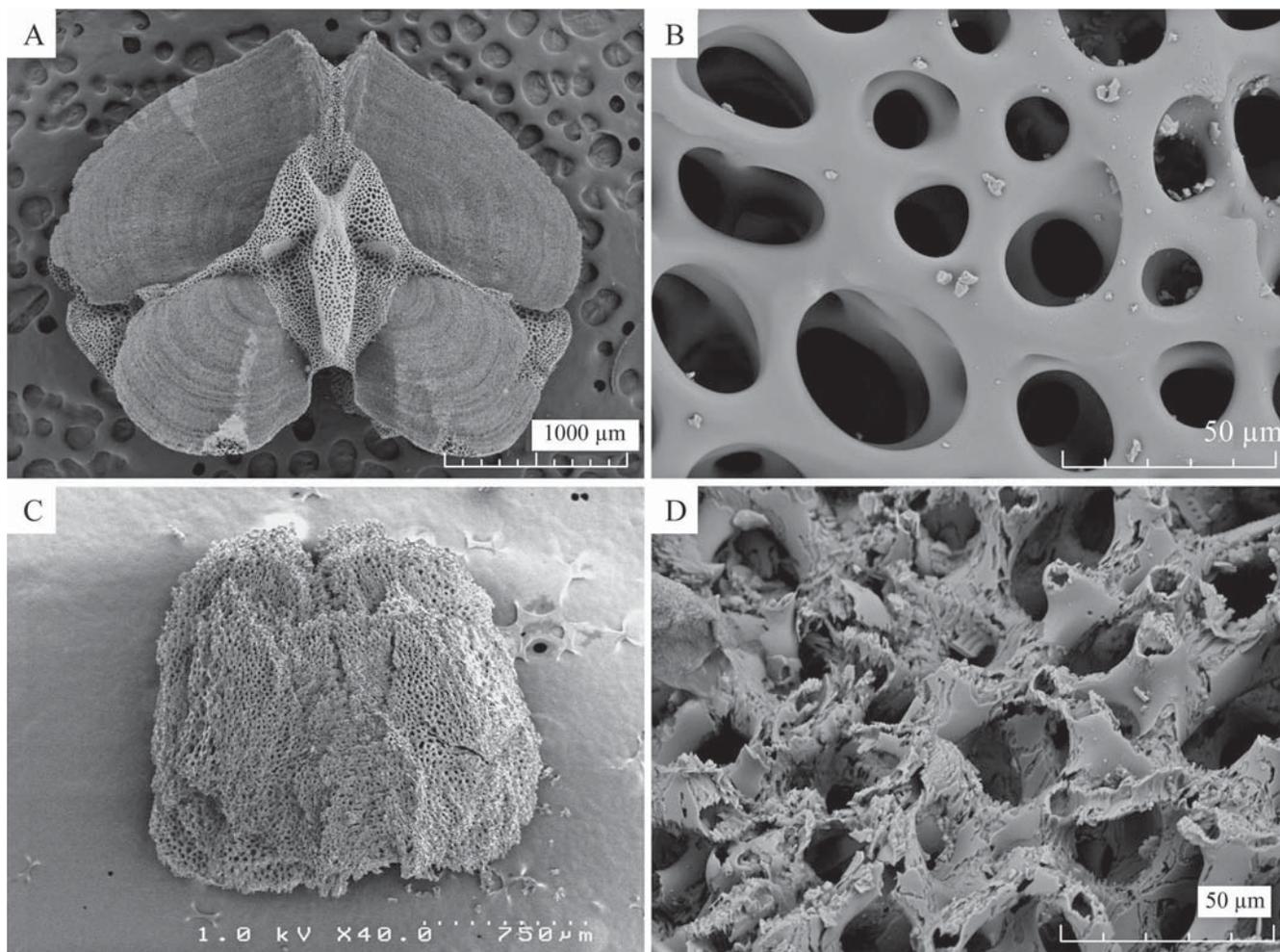


FIGURE 13—SEM (Tescan VEGA3) images of vertebral ossicles. A) Entire ossicle that is considered pristine when you look closely at the stereom structure as seen in view B. B) Stereom structure of the same pristine ossicle at knob location (Fig. 5). C) Highly degraded ossicle from sediment core. D) Stereom of ossicle in C at knob location (Fig. 5) showing dissolution.

hydrogen peroxide or bleach. The effect of these solutions on ossicles was later tested in the laboratory. Comparison using SEM images of surface textures of ossicles treated with peroxide or bleach with those of ossicles allowed to decay naturally showed that ossicles exposed to chemicals had pitting that was absent on ossicles isolated from soft tissue by natural decay. For this reason, only ossicles from ophiuroids that had decayed naturally *in situ* while submerged in Explorers Cove were used in this study.

Factors Contributing to Ossicle Dissolution and Degradation

Ossicle dissolution-degradation in Explorers Cove is controlled by characteristics of the ossicles themselves, by abiotic environmental conditions in Explorers Cove, and by bioturbation that is pervasive on the Explorers Cove seafloor.

Ophiuroid ossicles, like all echinoderm skeletal components, are composed of high-Mg calcite that is metastable at surface conditions. The amount of Mg in Mg calcite varies because Mg calcite with significant mole percent (mol%) Mg is more soluble than calcite or aragonite; and because high-latitude seawater is less saturated with respect to carbonate than lower-latitude seawater, skeletal material with high mol% Mg produced in high-latitude seawater is particularly prone to dissolution (Andersson et al., 2008). *Ophionotus victoriae* ossicles from the Antarctic Peninsula are composed of 14.31 mol% MgCO₃ (wt.% = 9.25; McClintock et al., 2011). Using the minimally prepared

solubility curve, average high-latitude surface seawater is undersaturated with respect to 12, 15, and 18 mol% Mg calcite; it is not undersaturated if a different (biogenic cleaned) solubility curve is used (Andersson et al., 2008). Given the low water temperature in Explorers Cove (−1.9 °C), which increases carbonate solubility, and the high mol% MgCO₃ of the ophiuroid ossicles, the ossicles clearly are close to a dissolution threshold. With addition of atmospheric CO₂, seawater will become increasingly undersaturated with respect to >12 mol% MgCO₃ as well as to aragonite, with potentially significant effects on the Antarctica fauna (Andersson et al., 2008; Fabry et al., 2009; McClintock et al., 2011).

The structure and small size of the ossicles increases their vulnerability to dissolution and degradation. The stereom structure is very porous (>70% porosity) providing a large surface area for interaction with seawater or pore water and for colonization by microbes; increasing surface area increases rates of dissolution. Because of the ossicles' small size (approximately that of coarse to very coarse sand) they can be resuspended and remain near the SWI in contact with cold, oxygenated seawater and available for microbial colonization. As dissolution proceeds, the increasingly fragile ossicles are likely to break as they are suspended and moved near the SWI (Green et al., 1993).

Organic matter associated with ossicles may both impede and enhance dissolution and degradation of the ossicles. Taphonomic studies focused on mollusk shells have demonstrated that dissolution is initiated by microbial breakdown of organic matter within the shell

(e.g., Glover and Kidwell, 1993; Freiwald, 1995, 1998). Ophiuroid ossicles differ fundamentally from mollusk shells in that they are secreted by encompassing syncytia and during life they are surrounded by organic matter (Byrne, 1994). Muscle fibers and ligaments hold the ossicles together so effectively that freshly killed ophiuroids do not disarticulate even after 72 hours in a tumbler (Kerr and Twitchett, 2004). Disarticulation occurs faster with greater decay time prior to tumbling (Lewis, 1980; Kerr and Twitchett, 2004); the same is true of echinoids (Kidwell and Baumiller, 1990). In addition to being bound together and embedded in organic matter, in living echinoderms the pores in the stereom structure of the ossicles are filled with amorphous mesodermal tissue (Lewis, 1980) or collagenous fibers (Freiwald, 1998).

While the ophiuroid is living, the ossicles are protected from dissolution-degradation by cold seawater (in Explorers Cove, $T = -1.9$ °C) and bacteria and fungi by the surrounding and embedded organic matter. However, after death and decay of the organic matter, the ossicle is no longer buffered from microbially mediated and/or cold-water-facilitated dissolution. At or just below the SWI, dissolution may be increased if pore water is undersaturated with respect to carbonate as a result of microbial respiration or products of oxidation (Aller, 1982; Green et al., 1993). Patches of anoxic sediments have been documented in Explorers Cove (Bernhard, 1987). In oligotrophic Explorers Cove, the organic matter in an ophiuroid carcass provides a "bonanza" for microbes. It is quickly and densely colonized by bacteria and fungi, creating a favorable microbial environment to accelerate hard tissue (ossicle) degradational processes soon after soft-tissue decay. In this scenario, the organic matter buffers against dissolution-degradation during life and for some period after death as well. However, it later enhances dissolution-degradation via decay-mediated alteration of pore-water chemistry and stimulation of microbial activity.

Major abiotic environmental factors in Explorers Cove affecting the rate of dissolution of ossicles include the extremely low water temperature and inferred low carbonate saturation state, the low rate of sedimentation, and the presence of patches of anoxic sediment.

The persistent below-freezing water temperature (-1.9 °C) in Explorers Cove and elsewhere near the Antarctic coast promotes dissolution of carbonates, especially the high-Mg calcite (14 mol% MgCO_3) that comprises *O. victoriae* ossicles (Andersson et al., 2008; McClintock et al., 2011). Fabry et al. (2009) showed that the current aragonite saturation depth in the Southern Ocean is 730 m. Recent analysis of the distribution of carbonate sediments and calcareous macrofauna on circum-Antarctic shelves indicates that the Ross Sea generally has low sedimentary carbonate content (<2%; Hauck et al., 2012). This is attributed to high primary productivity, yielding high respiration rates that alters seawater chemistry on the seafloor, resulting in carbonate dissolution. Seafloor sediment samples from the Ross Sea were collected in deep water in areas with only seasonal ice cover, and thus high productivity, that differs significantly from the persistent multiyear sea ice and oligotrophic conditions in shallow Explorers Cove. Interestingly, in Antarctic shelf areas with surface sediment carbonate content >2%, the predominant carbonate mineral is low-Mg calcite; aragonite was absent from samples, and high-Mg calcite (9.9–13.9 mol% $(\text{Mg,Ca})\text{CO}_3$) was detected in only 8% of the samples (Hauck et al., 2012). Given the abundance of high-Mg calcite-secreting echinoderms in Antarctic benthic faunas (e.g., Piepenburg et al., 1997; Manjon-Cabeza and Ramos, 2003; Moya et al., 2003; Rehm et al., 2011) and their importance as carbonate producers (Lebrato et al., 2010), one would predict high-Mg calcite to be much more common than it actually is in carbonate sediments of the Antarctic shelf.

Recent investigation of temporal variation in aragonite saturation state of Antarctic coastal seawater, including that in the western Ross Sea (~50 km from Explorers Cove), documented large shifts in aragonite solubility from the summer (4.5) to autumn (1.1) with the low solubility state lasting for ~8 months (McNeil et al., 2011, fig. 1). Modeling of the future aragonite solubility suggests that

undersaturation of the Ross Sea with respect to aragonite would occur in 2015 if the ocean and atmosphere were in CO_2 equilibrium, but will be delayed for a few decades because of the effects of CO_2 disequilibrium caused by sea ice and deep-water currents (McNeil et al., 2010). Given the seasonal variability, the persistence of the low-aragonite saturation state for much of the year, the greater solubility of high-Mg calcite than aragonite (Andersson et al., 2008), and the paucity of information about saturation under multiyear sea ice, it is possible that carbonate saturation states in some shallow-water Ross Sea areas, including in Explorers Cove, permit dissolution of ophiuroid ossicles composed of 14 mol% MgCO_3 .

Low sedimentation rates in Explorers Cove, estimated to be a few mm yr^{-1} (Stuvier et al., 1976; Bentley, 1979), mean that ossicles remain near the SWI where they are in contact both with oxygenated Explorers Cove seawater and with sediment pore water that may be less well oxygenated. Patches of anoxic sediment form where dense hypersaline brines associated with sea-ice formation impinge on the seafloor, killing the benthic fauna. Subsequent decay causes locally anoxic conditions (Bernhard, 1987), with altered and corrosive pore-water chemistry (e.g., Green et al., 1993).

The final contributing factor to ossicle degradation in Explorers Cove is the high rate of bioturbation relative to sedimentation. Because the multiyear sea ice limits primary productivity, biogenic sedimentation as well as influx of clastic sediments is low. The most abundant and active bioturbators are the epifaunal *Ophionotus victoriae* and Antarctic scallop (*Adamussium colbecki*). The deposit-feeding and scavenging *O. victoriae* disrupts the surficial sediment as it ingests sediment, scavenges, and buries itself shallowly (Broach et al., 2011). The scallop swims via jet propulsion and also emits non-locomotory water jets that disrupt the sediment and form divots a few cm deep. The seafloor of Explorers Cove is covered with these scallop-constructed divots (McClintock et al., 2010; Broach et al., 2011; Murray et al., 2012). During swimming thrusts, the scallop swims at a velocity of 19–43 cm s^{-1} (Ansell et al., 1998). Water moving at the velocity the scallop moves is sufficient to erode particles from silt size up to 1 mm in diameter (based on Hjulstrom diagram, e.g., Boggs, 2006). In fact, the velocity of the water jets must be greater than the velocity of the scallop, implying that even larger grains would be eroded. Small ossicles could be resuspended, and the winnowing of small grains during clapping insures that both larger and smaller ossicles remain near the SWI. It is in this TAZ (Taphonomically Active Zone) that degradational processes are most active and effective (Davies et al., 1989). Whether or not skeletal material is destroyed or preserved in the sedimentary record depends on how long it is exposed to the erosive characteristics of the TAZ prior to deeper burial (e.g., Meldahl et al., 1997; Kosnik et al., 2009). The activities in Explorers Cove of *O. victoriae* itself and of the Antarctic scallop prolong the residence time of *O. victoriae* ossicles in the TAZ, and thus promote their dissolution-degradation.

We predicted that ingestion and digestion of *Ophionotus victoriae* by the predatory ophiuroid *Ophiosparte gigas* would dissolve and degrade *O. victoriae* ossicles. Divers recovered several specimens of *O. gigas* with distended discs, suggesting that they had recently ingested prey, possibly *O. victoriae*. Several specimens did contain parts of *O. victoriae*, and an entire disc of *O. victoriae* was found in one *O. gigas* (Fig. 11). Comparison of the dissolution features of the ingested ossicles with those of pristine ossicles showed no significant difference (Fig. 12), suggesting that rapid dissolution of ossicles within predator ophiuroid gut is not a limiting factor controlling ossicle abundance.

Rate of Ossicle Dissolution-Degradation

In this study the long-term (2-year) experiments were conducted on freshly sacrificed ophiuroids with undecayed soft tissues, whereas in the short-term experiments, soft-tissue-free ossicles that had been weighed

were submerged in seawater for 27 days and then dried and weighed again. Thus, ossicles in the long-term experiment were exposed to seawater for two years minus the soft tissue decay time. Although the rate of soft tissue decay could not be observed, the decay time can be constrained by previous studies on echinoderm and ophiuroid decay and disarticulation.

Ranges of published echinoderm decay times range from fifteen hours (Schäfer, 1972) to 48 days (Allison, 1990). Investigation of ophiuroid disarticulation under different conditions in a tumbler showed that ophiuroid carcasses disarticulate more quickly during tumbling if they previously have been given time to decay than if they are tumbled right after death (Kerr and Twitchett, 2004). Fresh ophiuroid carcasses showed minimal disarticulation after 72 hours of tumbling, whereas those that had decayed at 25 °C for 6 days disarticulated completely immediately after tumbling commenced. On a scale of decay from 0 (fresh) to 5 (loss of structural integrity), those submerged in 25 °C water reached level 5 after 6 days of decay, whereas those at 4 °C reached only decay stage 2 after 14 days of decay. Decay and disarticulation of echinoids follows a similar pattern; low temperature inhibits decay and disarticulation of echinoids more than anoxic conditions (Kidwell and Baumiller, 1990). These authors note that complete disarticulation occurs quickly after some threshold level of decay is reached, probably when cartilaginous tissue has decayed so that it no longer holds the ossicles or plates together (Kidwell and Baumiller, 1990). For ophiuroids, at 4 °C this threshold would be reached after 30–31 days (Kerr and Twitchett, 2004). If it took twice as long at –1.9 °C in Explorers Cove, the decay threshold would be reached in ~60 days. Because microbial communities naturally occur in Explorers Cove, the decay rate of the ophiuroids submerged there might have been greater than those of the laboratory experiments. These laboratory experiments indicate that in spite of the cold temperatures, the decay and disarticulation of the ophiuroids would occur sufficiently rapidly that the ossicles were exposed to cold seawater and microbes for >20 months.

The rate of dissolution that is indicated by the weight loss of ossicles in the short term Hanging Bag and laboratory experiments suggest that complete dissolution would occur in 6 to 105 years and 15 to 645 years, respectively. This is a high rate of dissolution for a shallow-water setting. Combined with Explorers Cove's low rate of sedimentation and a high rate of bioturbation that insures that particles will be exposed at the SWI or remain in the TAZ for many years, it is predictable that ossicles would typically dissolve and not be incorporated into the sedimentary record. This is consistent with the results of the search of >7700 cm³ of sediment retrieved from shallow cores in Explorers Cove that yielded only 2 vertebral ossicles and 10 other ossicles. Calcareous benthic foraminifera are more abundant in the shallow sediment cores than ophiuroid ossicles, and are widespread throughout Explorers Cove (Bernhard, 1987), implying that they are less susceptible to dissolution.

Echinoderm skeletal elements are abundant in nearshore carbonate deposits of San Salvador, Bahamas, with ophiuroid vertebral ossicles consistently comprising 8%–10% of the echinoderm fragments in the sand-sized fraction of the sediments from the shoreline to the fringing reef (Dynowski, 2012). The robust vertebral ossicles are particularly widespread with low levels of bioerosion and fragmentation (Dynowski, 2012). Preservation of molluscan shell fragments has been demonstrated to be better in tropical siliciclastic settings than carbonate settings (Best and Kidwell 2000a, 2000b; Kidwell et al., 2005; Best et al., 2007). This raises the possibility that ophiuroid ossicles might be even more abundant in shallow tropical seafloors receiving clastic input than they are in the carbonate deposits of San Salvador. Contrast between the abundance of ophiuroid ossicles in San Salvador, where ophiuroids are rarely seen, and the paucity of ossicles in Explorers Cove, where ophiuroids are dominant members of the epifaunal community, is consistent with high rates of dissolution of ossicles in Explorers Cove.

There are very few published records of rates of dissolution of echinoderm ossicles, especially at shallow depths at high latitudes. Echinoid fragments composed of high-Mg calcite moored at a depth of 3625 m in the Drake Passage lost ~20% of its initial weight after 52 days, but fragments of a high-Mg calcite red alga lost ~75% of its initial weight at the same depth and location (Henrich and Wefer, 1986). Variation in weight loss during this study among aragonite and high-Mg calcite fragments demonstrates the importance of skeletal structure on rate of dissolution (Henrich and Wefer, 1986). The high rate of echinoderm dissolution at a depth of ~3600 m relative to that in Explorers Cove is not surprising given the proximity of the fragments at that depth to the carbonate compensation depth. Studies have documented dissolution occurring in temperate and northern polar latitudes at shallow depth, but provide no rates (e.g., Alexandersson, 1978; Steinsund and Hald, 1994; Freiwald, 1995, 1998).

The taphonomic histories of mollusk shells and shell fragments, especially those in tropical and temperate settings, are much better documented than those of echinoderm fragments (e.g., Kidwell and Bosence, 1991; Meldahl et al., 1997; Best and Kidwell, 2000a; Callender et al., 2002; Kidwell et al., 2005; Kosnik et al., 2009; Powell et al., 2011). Shells >10,000 years old persist on some outer shelves and ages of several thousand years are not uncommon, although the majority of shells may be only hundreds of years old. These studies, and others, have shown that the survivability of shell material is a function of diverse characteristics of the shell itself (e.g., size, shape, mineral composition, thickness, shell structures, organic content), the organism's way of life (e.g., surface dwelling, depth of burrowing), and environmental conditions (e.g., light, current and wave energy, rates and pattern of sedimentation and erosion, rate and style of bioturbation, oxygen availability, and pore-water chemistry). Shell half-life is the half-life of a shell in the TAZ. Shells leave the TAZ when they are totally destroyed (by dissolution-degradation-fragmentation) or when they are buried beneath the TAZ. Although variable, many molluscan shells commonly have half-lives of 300–500 years (Kosnik et al., 2009), with shorter half-lives in tropical carbonate settings (Kidwell et al., 2005), and longer half-lives (commonly >10,000 years) in temperate siliciclastic intertidal to offshore sediments. These half-lives are much longer than the calculated time needed for total ossicle dissolution-degradation in Explorers Cove based on the Hanging Bag experiment. Although not directly comparable to ossicle dissolution, the shell half-lives and ranges of oldest molluscan shells provide corroborating evidence that the rate of destruction of ophiuroid ossicles in Explorers Cove is greater than typical for molluscan shells worldwide. However, thin-shelled Antarctic mollusk shells lost >3% of their weight when submerged for 9 weeks in cold (4 °C) artificial ocean water with pH 7.4 (McClintock et al., 2009). Current estimates suggest that ocean water will attain this pH by 2300 at current rates of acidification (Caldeira and Wickett, 2003).

An important exception to the generalization that molluscan shells persist longer than ophiuroid ossicles in Explorers Cove is the rapid dissolution of oysters in estuarine waters. In laboratory experiments in which oysters were submerged for two weeks in tanks with water spanning the large pH range of mesohaline estuarine water (7.2–8.0) and weighed every 2–3 days, fresh oyster shells lost as much as 0.2% of their weight per day (Waldbusser et al., 2011). The range of weight loss due to dissolution was ~2%–70% per year, and calculated half-lives range from 1 year (for fresh shells at 7.2–7.4 pH) to ~40 years (dredged shell at pH 7.9); (Waldbusser et al., 2011). These laboratory-derived dissolution rates are consistent with half-lives of Delaware Bay estuarine oyster shells of 1–20 yr, with the shortest half-lives in the mesohaline water (Powell et al., 2006). These rates are much higher than rates of ossicle dissolution in Explorers Cove and are attributed to low and fluctuating salinity and carbonate chemistry conditions (Waldbusser et al., 2011). Salinity in shallow water under multiyear sea ice has been observed to change in response to basal sea ice freezing and thawing (S.S. Bowser, personal communication, 2010; B.J. Walker,

personal observation, 2010). Although these fluctuations and their effects on seawater carbonate chemistry have not been investigated, they may enhance dissolution rate of ossicles in Explorers Cove.

IMPLICATIONS

Documentation of dissolution of ophiuroid ossicles in Explorers Cove has implications both for reconstructing the Cenozoic climate and marine faunal history of Antarctica and for monitoring and evaluating the impact of ocean acidification on Antarctic coastal benthic communities.

Results from *in situ* experiments that demonstrate dissolution-degradation of ophiuroid ossicles combined with the paucity of ossicles in cored sediment from Explorers Cove provide compelling evidence for a taphonomic filter that removes ophiuroid ossicles from the sedimentary record of Antarctic shelf sediments. This is consistent with the lack of reported ophiuroid ossicles from cores of Cenozoic deposits in the western Ross Sea and Dry Valleys (Fig. 2), including the Dry Valley Drilling Project (DVDP; McKelvey, 1981; Barrett and Treves, 1981); McMurdo Sound Sediment and Tectonic Studies (MSSTS; Barrett, 1986); the Cape Roberts Project (Taviani and Beu, 2003; Woolfe, 2003), and Antarctic Drilling (AND-1B; Scherer et al., 2007).

Because ophiuroid ossicles dissolve prior to incorporation into the sedimentary record, the paleoenvironmental and paleoecologic information that could be gleaned from their spatial and temporal distribution is lost. If they were faithfully preserved, their presence-absence would be key in differentiating between sub-ice-shelf deposits and submultiyear sea-ice deposits. The physical environmental conditions under ice shelves and under multiyear sea ice are similar, and both settings lack biogenic sedimentation, leading to similar lithologic and sedimentologic characteristics. However, seafloors under ice shelves are characterized by sparse, low-diversity faunas (e.g., Lipps et al., 1979) unless nutrients are advected in (e.g., Riddle et al., 2007). In contrast, benthic life under multiyear sea ice is diverse and abundant (e.g., Fig. 1; Stockton, 1984; Thrush et al., 2006; Cummings et al., 2006) with many epifaunal ophiuroids and scallops. Because each ophiuroid has >1500 ossicles that disperse after death, ossicles, if preserved, should be widespread and be retrieved in cores of sediment deposited under multiyear sea ice. Cores of sediment deposited under ice shelves would be very unlikely to contain ophiuroid ossicles.

This study demonstrates that rapid postmortem degradation of ossicles removes the ophiuroid ossicles that should be plentiful in sediments accumulating under multiyear sea ice but not originally plentiful in those accumulating under ice shelves. Sub-ice-shelf sediments should be laminated because of the paucity of benthic animals (vertical bioturbation indices of 0–1), whereas sediments deposited under multiyear sea ice are intensely bioturbated by ophiuroids and scallops (Miller et al., 2012; Murray et al., 2012; Broach et al., 2011). This bioturbation by epifaunal scallops and ophiuroids homogenizes the substrate, resulting in massive sediment rather than in discrete biogenic structures. Thus, distinguishing between sub-ice-shelf and submultiyear sea-ice deposits may hinge on the presence of laminated (sub-ice-shelf) versus massive (biologically disrupted under sea ice) sediment as much as on the presence or absence of body fossils. Distinction between deposits recording these two environmental settings is important because ice shelf extent reflects large-scale advance and retreat of ice sheets, whereas extent of multiyear sea ice is controlled by regional temperature, wind, and oceanographic conditions. Unfortunately, bioturbation does not provide discrete biogenic structures that would allow the two settings to be clearly distinguished from one another.

Verification of dissolution-degradation as a taphonomic filter eliminating ophiuroids from the Antarctic fossil record removes the possibility of using their distribution in Cenozoic deposits to elucidate

the origin and history of the Antarctic benthic fauna. Among its unusual characteristics (e.g., White, 1984; Dayton et al., 1994; Aronson et al., 2007, 2009) is a paucity of fast predators, including crabs and other large crustaceans and many types of teleost fish. Ophiuroids have proliferated and constitute a larger percent of the benthic fauna around the Antarctic continent than in temperate and tropical shelf settings. The same is true for other groups including pycnogonids (Clarke and Johnson, 2003; Clarke et al., 2004). The origin of the fauna and the timing of its colonization are poorly constrained (e.g., Clarke and Crame, 1989; Crame, 1992; Brandt, 2005; Thatje et al., 2005); the late Eocene occurrence in Seymour Island (Antarctic Peninsula) of dense ophiuroid assemblages is interpreted to represent an initial appearance or foreshadowing of the Antarctic fauna (Aronson et al., 1997; Aronson and Blake, 2001). The dissolution of ophiuroid ossicles documented in this study implies that the absence of ophiuroids in the Antarctic sediment record to date does not reflect actual ophiuroid abundance and distribution, but is an artifact of taphonomic destruction. The history of ophiuroid diversification in Antarctic waters and, by extension, those of other CaCO₃ secreters, will not be revealed in the sedimentary record.

Ocean Acidification

The dissolution of high-Mg calcite ossicles documented in this study provides needed baseline information for assessing changes that are predicted to occur in the near future as ocean surface water takes up CO₂ from emissions causing decline in the calcium carbonate saturation state and pH of sea water (ocean acidification; e.g., Orr et al., 2005; Andersson et al., 2008). High-Mg calcite producers include echinoderms, bryozoans, benthic foraminifera, and red coralline algae. Echinoderms, especially ophiuroids, are major components of both north and south high-latitude benthic communities, both numerically and in ecosystem functioning (Dearborn, 1977; Moya et al., 2003; Lebrato et al., 2010; Wood et al., 2011). Long-term effects will depend on changes in ocean chemistry and on the responses of calcifying organisms to these changes, both of which involve significant unknowns. Although it is known that high-Mg calcite is less stable than low-Mg calcite, and that the mol% of Mg in MgCO₃ decreases with increasing latitude, the controls of the Mg in calcite are not well understood (Andersson et al., 2008). Although high-Mg calcite is more soluble than low-Mg calcite or aragonite, there is little agreement about which of two solubility curves is more realistic for biogenic carbonates (Andersson et al., 2008), and thus what the current and predicted levels of seawater saturation with respect to high-Mg calcite will be. The mol% MgCO₃ content of ossicles of *Ophionotus victoriae* from the Antarctic Peninsula, as well as that of 25 other species of Antarctic echinoderms, have recently been determined, and vary between 9.58 and 15.27 mol% MgCO₃ (McClintock et al., 2011). *Ophionotus victoriae* ossicles are composed of 14.31 mol% MgCO₃. This places *O. victoriae* in a state of metastability with respect to sea water (Andersson et al., 2008); by 2100 the metastability equilibrium curve will be at lower mol% saturation at all latitudes, and thus the high-Mg calcite of the *O. victoriae* composition will be even less stable. Other research has found that the Ross Sea is slightly oversaturated with respect to aragonite (less soluble than high-Mg calcite), but that there are marked changes in seasonal saturation state relative to aragonite (McNeil et al., 2010, 2011); high-latitude seawater is predicted to be undersaturated with respect to aragonite by 2030 (McNeil and Matear, 2008). The present saturation state with respect to either aragonite or high-Mg calcite of water under multiyear sea ice in the Ross Sea–McMurdo Sound has not been evaluated. The sea ice may reduce atmosphere-ocean exchange such that the CO₂ content of the ocean under multiyear sea ice is not in equilibrium with that of the atmosphere.

Observed effects of changes in pH and temperature on ophiuroid physiology include altered rates of arm regeneration and of food

assimilation (Wood et al., 2011), and lethal and sublethal effects on larval development and growth rate (Dupont et al., 2010). Ocean acidification also is predicted to affect benthic diversity, including keystone species that are crucial to ecosystem functioning and carbon cycling (Widdicombe and Spicer, 2008; Lebrato et al., 2010). These effects are likely to be greatest on high-latitude organisms that secrete high-Mg calcite, including Antarctic echinoderms (Lebrato et al., 2010; McClintock et al., 2011).

Studies of taphonomic processes and the rates of taphonomic destruction have focused on mollusk shells that are in contact with seawater (and potential epibionts) throughout the mollusk's life as well as after death. In contrast, ophiuroid ossicles are buffered from dissolution-degradational processes during life by enclosing organic matter until it decays after death. The effects of ocean acidification on ophiuroids and their preservation is twofold: (1) it will increasingly challenge the ability of ophiuroids to secrete high-Mg calcite ossicles during all stages of their lifecycles and require energy trade-offs (e.g., Wood et al., 2011); (2) disarticulated ophiuroid ossicles will be even more prone to dissolution. The fact that ophiuroid ossicles show signs of initial dissolution after only two years of contact with seawater suggests that they are close to a threshold of dissolution—a threshold not crossed while the ophiuroid is living due to protection by the organic matrix in which it is imbedded. When the organic matter decays after death, the preservable hard parts of the ophiuroids dissolve-degrade at a relatively high rate controlled by the saturation state of the seawater, pore water, and bacterial exposure relative to high-Mg calcite of the ossicles.

CONCLUSIONS

The Antarctic ophiuroid *Ophionotus victoriae* is abundant at shelf to bathyal depths, but it is not present in the Cenozoic fossil record recovered from cores in McMurdo Sound. Its internal skeleton, fossil forming material, is composed of ossicles of high-Mg calcite that are linked and protected by muscles and connective tissue.

During *in situ* experiments in which dead ophiuroids were submerged on or just above the sediment-water interface in water <30 m deep in Explorers Cove, ossicles developed significant dissolution features over two years. Submerged ossicles also had significantly higher levels of silhouette area loss than pristine (nonsubmerged) ossicles. Ossicles weakened by dissolution are prone to breakage. Ossicles at the sediment-water interface had higher levels of dissolution and greater breakage than those suspended just above the sediment-water interface. Ossicles freed of soft tissue showed significant weight loss after being submerged for only 27 days, documenting rapid initiation of dissolution after decay of enclosing soft tissue; assuming a constant rate of dissolution, the ossicles would likely dissolve completely in 6 to 105 years.

Consistent with experimental evidence that ossicles dissolve in the -1.9°C water of Explorers Cove, a search of 7775 cm^3 of sediment retrieved from short cores in Explorers Cove yielded only 12 ossicles, including only two highly degraded vertebral ossicles, all found within the upper 6 cm of the cores. Calculating the porosities did not prove to be the best method for analyzing the state of dissolution because pristine ossicles as well as experimental ossicles have high and variable porosities. The porous steroom of the ossicles increases surface area of the high-Mg calcite, and therefore has the ability to enhance dissolution, as corroborated by the high porosity of ossicles in sediments from Explorers Cove.

The fact that ophiuroid ossicles are dissolving presently in shallow Explorers Cove suggests that high-Mg calcite is close to metastability in cold, high-latitude seawater. It implies that high-Mg calcite secretors in these settings, including the echinoderms that dominate the fauna locally, are vulnerable to the effects of the ocean acidification that is predicted to occur within decades.

Documentation of ophiuroid dissolution indicates that the absence of ossicles from cores of Cenozoic deposits in McMurdo Sound is a

taphonomic artifact rather than an accurate reflection of ophiuroid abundance. This precludes the potential use of ophiuroid ossicles in interpretation of ancient paleoclimate-paleoenvironment (e.g., deposition under ice shelves versus multiyear sea ice) and of the evolutionary history of the Antarctic benthic fauna.

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