METAPHOR, INFERENCE, AND PREDICTION IN PALEOECOLOGY: CLIMATE CHANGE AND THE ANTARCTIC BOTTOM FAUNA

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ABSTRACT—The fossil record affords us the opportunity to reconstruct the history of communities prior to human intervention, infer the causes underlying that history, and make early, accurate, and mechanistic predictions about their future as human-dominated systems. Paleoecology's unique contribution to conservation lies in providing the rationale, data, and methodological approach to view contemporary biological communities metaphorically in terms of geohistorical time-equivalence. By comparing perturbed communities of the present to paleocommunities that were prevalent in earlier time intervals, we gain insight into the causes and mechanisms of ecological degradation. Such insights are founded on testable hypotheses that ecological processes are scale independent. As an example, nearshore, shallow-benthic communities living in Antarctica today are reminiscent of Paleozoic communities, which were dominated by epifaunal suspension-feeders and lacked the functionally modern, durophagous predators that diversified in the Mesozoic. Establishing a causal link between the absence of durophagy and the retrograde community structure of the Antarctic bottom fauna requires characterizing the relevant predator–prey interactions at multiple scales using a variety of methods. Paleoecological analysis, in corroborating the postulated scale independence of those predator–prey interactions, leads us through a logical sequence of ideas with predictive power: (1) Antarctic marine communities were functionally modern before climatic cooling began 41 Ma; (2) they were forced toward a quasi-Paleozoic composition when the cooling trend reduced and ultimately eliminated durophagous predation; and (3) they will soon be re-modernized as global warming and increased ship traffic in Antarctica permit predators to reinvade. Policy recommendations follow from this paleoecological interpretation of the ecological dynamics of the Antarctic benthos.

INTRODUCTION

THE UTILITY of a scientific discipline turns on the aggregate ability of its practitioners to make predictions that are subsequently corroborated (e.g., Lakatos, 1970). So it is with paleoecology. Excoriated by Williamson (1982, p. 99) as "…a poor-man's applied ecology performed on inadequate data," paleoecology languished in purgatorial semi-legitimacy during an unnecessarily long and annoying controversy over whether there can be such a thing as historical science, in which experimentation is not possible (Cleland, 2001). This *Sturm und Drang* did not deter actual paleoecologists from conducting actual scientific studies. Mercifully, the debate has now been resolved, in large part through our collective recognition that science is about formulating and testing hypotheses, whether through observation, experimentation, or modeling. Paleoecology, like ecology, may not be amenable to strict Popperian falsificationism (Quinn and Dunham, 1983; Cleland, 2001); nevertheless, at the same time Williamson and colleagues were heaping abuse on the field, Gould (1981) and others recognized its potential as *bona fide* science, with hindcasts and forecasts that could be corroborated and had value in both theoretical and practical terms (e.g., Martin, 1998). That potential has now been fully realized.

Paleoecology is an interdisciplinary science that continues to develop rapidly in both theory and methodology. It is a motley but serviceable and ever-improving combination of geology, paleontology, evolutionary biology, paleoceanography, climatology, ecology, and latterly archeology and history. Ecology in turn draws from evolutionary biology, physiology, molecular genetics, morphology, oceanography, atmospheric science, and so on. Big questions in paleoecology are built and tackled with jury-rigged research programs, in which concepts and approaches from different fields are introduced as needed.

This paper offers a case study of interdisciplinary inference and practical application in paleoecology. It focuses on the past, present, and future implications of skeleton-breaking, or durophagous, predation for the structure of marine shallow-water, soft-bottom

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FIGURE *1*.—A notothenioid antifreeze fish, *Pagetopsis macropterus*, at rest in a dense population of ophiuroids, *Ophionotus victoriae* and *Ophiosparte gigas* (the two larger brittlestars to the right of the fish). Notothenioids are not durophagous, and they pose no threat to the ophiuroids. The photograph is from the Weddell Sea at Dundee Island, off the tip of the Antarctic Peninsula, at a depth of 289 m. Scenes such as this are common in nearshore habitats in Antarctica. Photo credit: Julian Gutt, copyright © AWI/Marum, University of Bremen. Used with permission.

communities. I trace the development of the idea that the geohistorical time-equivalence, or metaphorical 'flavor' of a benthic community derives from the intensity of durophagous predation: low-predation communities are structurally reminiscent of the Paleozoic, whereas high-predation communities are more Modern, in the sense of Sepkoski's (1981, 1991a) three evolutionary faunas. I then show how this framework can be used to conceptualize the history of the Antarctic benthos and predict its near-term future in response to rapid climate change. The paper concludes with a prospectus for applying metaphors of geohistorical time-equivalence in a broader sense to conservation problems that reach well beyond marine benthic communities.

I use the term paleocology to denote the multidisciplinary scientific process of drawing inferences from the fossil record about ecology in times past. Paleobiology is the multidisciplinary study of both evolutionary and ecological pattern and process in the fossil record and, therefore, subsumes paleoecology. Obviously, the demarcation between the ecological and evolutionary aspects of paleobiology is in many cases indistinct.

SCALE INDEPENDENCE

The 1980s and 1990s witnessed an explosion of literature on the issues of scale and hierarchy in ecology and paleobiology. Gould's (1985) influential essay on hierarchical disjunction was taken as marching orders by many paleobiologists, who earnestly set about demonstrating the universality of scale dependence in pattern and process. That scale dependence became the common *a priori* assumption of paleobiology was a collateral overreaction to the perceived failure of optimality models to explain empirical observations.

On the ecological side, models of optimal foraging did not adequately match the behavioral patterns of study animals, leaving investigators to search *a posteriori* for external or internal constraints to explain away departures of observation from theory (e.g., Aronson and Givnish, 1983). The situation was much the same in evolutionary biology. Gould and Lewontin (1979) famously argued that phyletic, biomechanical, and architectural constraints effectively prevent specific features of organismal design from evolving to optimality. Instead of searching for optimality *per se*, we should inquire whether the organism's complete behavioral repertoire or design package can be considered adaptive given known constraints. In arguing against optimality and for historical contingency, Gould implicitly and explicitly argued against scale independence.

Mayr (1983) reacted strongly against abandoning optimality theory. Even though natural selection does not require the perfection of design, Mayr advocated optimality as a working hypothesis, an ideal against which to compare empirical observation of the products of evolution. In a similar vein, scale independence seems the logical choice of a simple and falsifiable initial assumption about ecological/evolutionary pattern and process. Many ecological and paleoecological phenomena, including predation, diversification, and extinction are scale independent in at least some respects (Aronson, 1994; Aronson and Plotnick, 1998; Miller, 1998; Bambach et al., 2004).

THE MESOZOIC MARINE REVOLUTION

Our understanding of the scale-independent effects of predation in marine paleocommunities owes its conceptual foundation to the imaginative work of Geerat J. Vermeij. In a classic paper (Vermeij, 1977), two ground-breaking books (Vermeij, 1978, 1987), and many subsequent publications, Vermeij explored the positive correlation between durophagy (his neologism) and the defensive architecture of marine invertebrates—in particular benthic gastropods—along gradients of latitude, longitude, and Phanerozoic time. Beginning in the Mesozoic, the evolutionary diversification of fast-moving, skeleton-breaking predators—teleosts (modern bony fish), neoselachians (modern sharks and rays), and reptant decapods (crabs, lobsters, and other modern, bottom-walking crustaceans)—was accompanied by, and likely drove, the evolution of larger spines, thicker outer lips, narrower apertures, and a host of other defensive adaptations in marine snails living in nearshore, shallow-water habitats. Vermeij (1977) called this macroecological trend of predator–prey escalation the Mesozoic marine revolution. In an analogous fashion, durophagous predation and defensive architecture in gastropods increase from the poles to the tropics, and in the tropics from the Atlantic to the Indo-Pacific (Vermeij, 1978; Alexander and Dietl, 2003).

Another radical change to shallow-water, soft-sediment ecosystems during the late Paleozoic and Mesozoic was an increase in the depth and intensity of bioturbation (Thayer, 1983; Bottjer and Ausich, 1986). The combination of increasing trophic pressure from diversifying predatory taxa and increasing sediment destabilization and resuspension from bioturbation led to, or at least strongly contributed to, a Mesozoic decline of epifaunal suspension-feeders on soft substrata in shallow-water environments and a trend toward infaunalization of the benthos. The effects of escalating predation and bioturbation on shallow-water taxa and the paleocommunities they comprised transcended the end-Cretaceous extinction and continued during the Cenozoic. Alexander and Dietl (2003), Harper (2003), and Aberhan et al. (2006) provide recent reviews of the Mesozoic marine revolution.

Subsequent studies have considered the morphological evolution of prey taxa other than mollusks, shell-drilling *versus* shell-crushing predation, the evolutionary implications of lethal *versus* sublethal predation, refinements to the basic scenario of a Mesozoic marine revolution, and pre-Mesozoic revolutions in predation (e.g., Signor and Brett, 1984; Vermeij, 1995; McRoberts, 2001; Kelley et al., 2003; Aberhan et al., 2006). The salient point for our purposes is that the large-scale spatial and temporal correlations of predation intensity with prey defense are scaled-up versions of phenotypic and genotypic effects in ecological space and time. Predatory introductions to modern, local communities induce the same kinds of defensive attributes in snail shells that we observe biogeographically and geologically (reviewed in Aronson, 1994; Moody and Aronson, 2007). Patterns at large scales and hierarchical levels are thus the summations of individual predator–prey interactions occurring over ecological time in local communities. Likewise, the inferred action of increasing bioturbation in radically restructuring soft-bottom paleocommunities is a scaled-up version of the trophic amensalism hypothesis that Rhoads and Young (1970) formulated for processes operating on ecological scales. The role of increasing productivity as an extrinsic cause of the Mesozoic marine revolution (Bambach, 1993; Vermeij, 1995; Martin, 1998), and the role of mass extinctions in accelerating or decelerating its macroevolutionary and macroecological effects (Dietl et al., 2002, 2004; Harper, 2003; Kelley and Hansen, 2003) remain incompletely understood.

THE ONSHORE–OFFSHORE HYPOTHESIS

Bambach (1985, 1993) viewed the Mesozoic marine revolution as part of a Phanerozoic trend of increasing utilization of ecospace: marine faunas progressively occupied major categories of marine ecosystems and major ecological roles within those ecosystems through time. Mapped onto the bathymetry of the oceans, the Mesozoic changes were part of an onshore-to-offshore trend in evolutionary innovation and community structure. The following summary of the onshore–offshore hypothesis draws from reviews by Sepkoski (1991a), Aronson (1994), and Sheehan (2001).

Sepkoski (1981, 1984) performed a factor analysis of his compilation of the stratigraphic ranges of marine families, partitioning taxa into what he termed Cambrian, Paleozoic and Modern evolutionary faunas. The Cambrian Fauna, which was dominated by trilobites and other surface deposit-feeders as well as inarticulate brachiopods and other low-lying suspension-feeders, diversified during the Cambrian Period and then declined. The brachiopod-rich Paleozoic fauna, which diversified rapidly in the Ordovician, represented the functional expansion of epifaunal suspension-feeders, which operated at multiple canopy and sub-canopy levels above the sediment-water interface (Bottjer and Ausich, 1986). Rhynchonelliform (articulate) brachiopods, stalked crinoids, ophiuroids, stromatoporoids, stenolaemate bryozoans, rugose and tabulate corals, and a variety of other sessile and semi-mobile, epifaunal suspension-feeders characterized soft-substratum communities through much of the Paleozoic Era. Predators included asteroids, polychaete worms, ectocochleate (shelled) cephalopods, placoderms, primitive chondrichthyans, and conodonts. Bioturbation expanded downward into the sediments. The end-Permian extinction severely reduced the diversity of the Paleozoic fauna. The mollusk-rich Modern fauna, which diversified throughout the Phanerozoic, was less affected by the end-Permian extinction. In addition to gastropods, infaunal bivalves, and regular and irregular echinoids, the Modern fauna included radiations of functionally modern, durophagous predators, including teleosts, neoselachians, reptant decapods, marine reptiles, marine mammals, and coleoid cephalopods (cephalopods lacking an external shell; Packard, 1972; Aronson, 1991a).

Functional innovations (i.e., higher taxa) that are emblematic of the three faunas initially appeared in coastal and inner-shelf environments (Jablonski et al., 1983; Sepkoski and Miller, 1985; Jablonski and Bottjer, 1991; Sepkoski, 1991b). Taxa possessing key adaptations then expanded offshore to outer-shelf and deep-sea environments. The abilities of predators to break and crush heavily skeletonized prey by various means are nearshore innovations of the Modern fauna. The clade-by-clade expansion of durophagous elements of the Modern fauna progressively further offshore summed to produce an overall expansion of Modern communities offshore, and an overall displacement of the Paleozoic fauna into deeper-water environments. This is why the deep sea is popularly viewed as the biotically relaxed redoubt of living fossils and the anachronistic, Paleozoic-type communities they comprise. Aronson (1990) extended the onshore–offshore model to include human fishing activity, a trophic innovation that was recently introduced to nearshore marine ecosystems and then expanded to offshore and deep-sea environments.

Although Sepkoski's analyses, as well as subsequent family- and genus-level analyses (Benton, 1995; Foote, 2000), indicated rapid diversification of the Modern fauna during the Mesozoic and Cenozoic, reanalysis with a more complete, genus-level database did not show such a pattern (Alroy et al., 2008). Whether global marine diversity expanded dramatically after the end-Permian extinction or reached a plateau during the Mesozoic, the onshore–offshore dynamics of the predatory innovations of the Mesozoic appear robust (e.g., Jablonski and Sepkoski, 1996; Erwin, 2008).

CRINOIDS AND OPHIUROIDS

The history of stalked crinoids is perhaps the best-documented example of the onshore–offshore trend in predation and community structure. Members of the Paleozoic evolutionary fauna and abundant constituents of shallow-benthic communities in the Paleozoic and early Mesozoic, stalked crinoids persisted in nearshore shallow-water habitats through a mid-Paleozoic escalation in the diversity and function of durophagous taxa by evolving enhanced defensive architectures (Signor and Brett, 1984; Aronson, 1991b; Baumiller and Gahn, 2004). These sedentary, epifaunal suspension-feeders were then eliminated from nearshore habitats of less than ~100 m water depth during the Cretaceous and replaced by the unstalked (comatulid) crinoids (Meyer and Macurda, 1977; Oji, 1985; Bottjer and Jablonski, 1988). The comatulids, being mobile, are better able to avoid their predators in shallow water, whereas the stalked crinoids are now confined to the low-predation environments of the deep sea (Meyer, 1985; Oji, 1996).

Building on these ideas about crinoids, over the last quarter-century I have explored the hypothesis of a scale-independent trophic relationship between epifaunal, suspension-feeding ophiuroids and their durophagous predators. The overall argument fell into a logical sequence, at least in retrospect, although many of the points were addressed simultaneously.

(1) Dense populations of epifaunal, suspension-feeding ophiuroids (‘brittlestar beds’) are found in bathyal environments (Blaber et al., 1987; Fujita and Ohta, 1990). Dense populations also live in restricted coastal, shallow-water habitats in a number of locations, including the British Isles, California, and the northern Adriatic Sea (Warner, 1971; Morris et al., 1980; McKinney and Hageman, 2006). Population densities range in the hundreds to thousands of individuals per square meter. Observations of brittlestar beds living on soft substrata in a marine lake on Eleuthera Island, Bahamas and around the British Isles showed that these populations are restricted to habitats in which durophagous predators are uncommon or rare. Meters to kilometers away, reef habitats contained high densities of durophagous predators and far fewer ophiuroids (Aronson and Harms, 1985; Aronson, 1989a).

(2) I conducted tethering experiments in the Bahamas, Scotland, and the Irish Sea to measure predation potential, which I defined as the activity and propensity of predators to consume the focal prey (Aronson, 1989a; Aronson and Heck, 1995). These experiments, in which ophiuroids were restrained and set out as ‘bait,’ showed that predation potential was far lower in brittlestar beds than in nearby reef habitats (Aronson and Harms, 1985; Aronson, 1989a).

(3) Observations during tethering experiments, ecological surveys, and gut-content analyses showed that the primary predators of ophiuroids in reef habitats were fish and crabs, which are fast-moving, durophagous predators of a Modern functional grade. In contrast, the primary predators of ophiuroids in brittlestar beds on nearby or adjacent soft substrata were asteroids, polychaete worms, and carnivorous ophiuroids, all of which are slow-moving, non-durophagous predators of a Paleozoic functional grade (Aronson and Harms, 1985; Aronson, 1989a; Aronson and Blake, 2001; see Blake and Guensberg [1990] on asteroids as functionally Paleozoic predators).

(4) Tethering experiments in shallow, back-reef habitats at geographically dispersed sites in the Caribbean showed that predation potential, again measured with tethering experiments, was consistently different among sites, both seasonally and on a decadal time scale. Among-site differences in predation potential correlated with differences in the abundance of predatory fish (Aronson 1992b, 1998).

(5) Predation pressure, the time-integrated encounter rate of prey with their predators, was measured as the proportion of ophiuroids in a population bearing sublethal damage in the form of one or more regenerating arms (Aronson, 1989a). Levels of sublethal arm damage were lower in brittlestar beds than in reef habitats, correlating with predation potential as measured by tethering experiments (Aronson, 1987, 1989a). Physical disturbance from storms did not appear to be a significant source of arm damage (Aronson, 1991c).

(6) Dense populations of infaunal, suspension-feeding ophiuroids (hundreds to thousands of individuals per square meter) persist in areas of high predation pressure in northern Europe, the northern Gulf of Mexico, and elsewhere. Durophagous predators, primarily teleosts, crop the brittlestar arms protruding from the

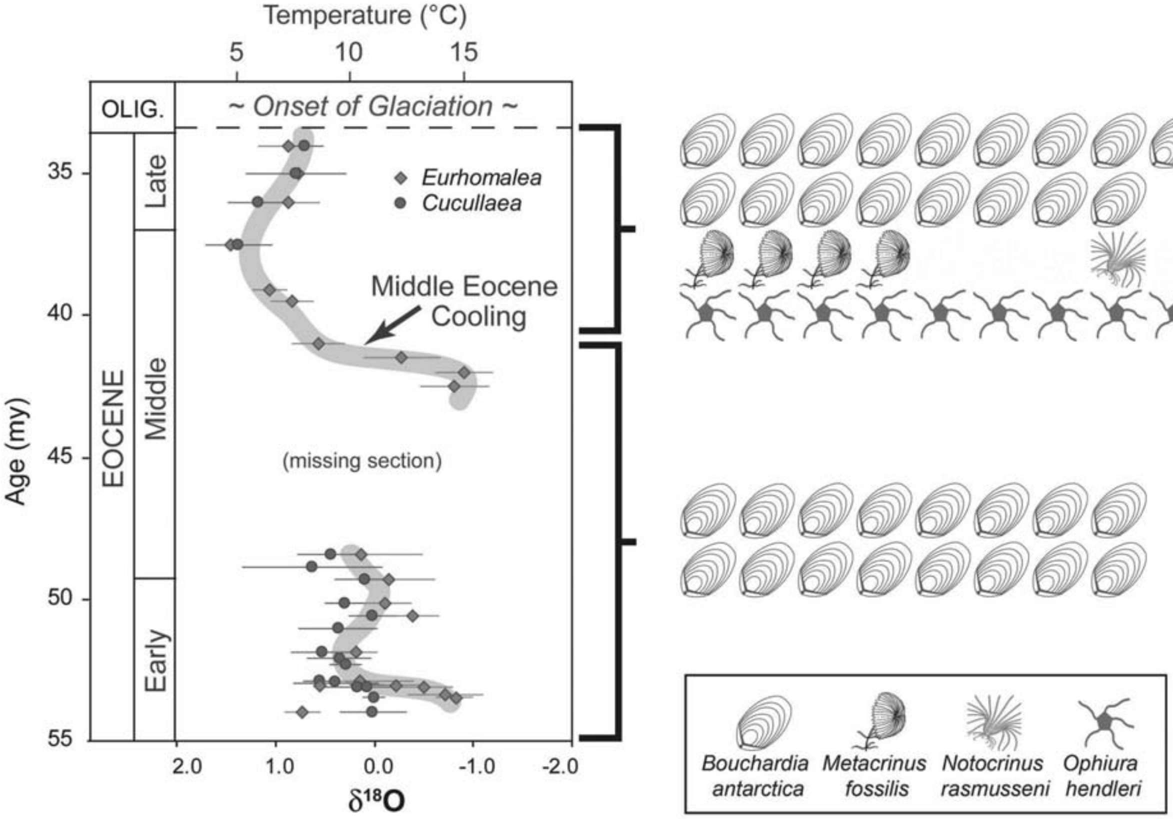

FIGURE 2.—Comparison of occurrences of dense assemblages of echinoderms and brachiopods in the La Meseta Formation at Seymour Island in response to the 41-Ma cooling step. The temperature–δ^{18}O curve for Seymour Island, left, is redrawn from Ivany et al. (2008); *Eurhomalea* and *Cucullea* were the two bivalve genera used in the isotopic analysis. The frequency distributions of dense brachiopod and echinoderm concentrations across the 41-Ma event, right, are significantly different ($\chi^2 = 10.291$, $df = 1$, $P = 0.001$). Credit: Aronson et al. (2009), an open-access article distributed under the terms of the Creative Commons Attribution License.

sediment (Duineveld and van Noort, 1986; Munday, 1993; Sköld et al., 1994). Pilot tethering experiments with infaunal ophiuroids in the Gullmar Fjord off the west coast of Sweden indicated that predation potential was high in dense infaunal populations (R. B. Aronson, unpublished data).

(7) Historical records from the Isle of Man, corroborated through interviews with Manx fishermen, showed that an epifaunal brittlestar bed in the Irish Sea persisted continuously for more than a century (Aronson, 1989a). In contrast, data from scientific trawling surveys in the western English Channel suggested an oceanographically driven, negative relationship between epifaunal brittlestar beds and the abundance of predatory asteroids and bottom-feeding fishes (Holme, 1984). On a spatial scale of tens to hundreds of kilometers and a temporal scale of decades to centuries, brittlestar beds were widespread in the western Channel when their predators were rare, and *vice versa* (see also Aronson, 1992a).

(8) On a global spatial scale and a temporal scale of tens to hundreds of millions of years, dense, autochthonous (or parautochthonous) fossil accumulations of ophiuroids from nearshore, shallow-water facies occur worldwide in Paleozoic, Mesozoic, and Cenozoic deposits (Aronson, 1989b, 1992a). Most of these dense, fossil ophiuroid assemblages are interpreted as event beds resulting from rapid burial of dense living populations, judging from the lithology of the matrix and the abundance within single bedding planes of articulated ophiuroids in life position (Aronson and Sues, 1987; Aronson, 1989b). Based on morphology, phylogenetic

relationships, and preserved bodily attitude, the ophiuroids that formed these dense paleopopulations lived epifaunally.

(9) Sublethal arm damage is a valid measure of predation pressure in fossil ophiuroid populations, as it is in living populations (Aronson, 1987, 1991c). The proportion of ophiuroids with sublethal arm damage is very low in these dense fossil accumulations, indicating that predation pressure was low (Aronson, 1992a).

(10) How are these dense, low-predation, and epifaunal brittlestar beds in shallow-water environments distributed through geological time? Brittlestar beds are uncommon in the fossil record, but sample sizes are sufficient for statistical analysis. Binomial testing of the frequencies of occurrence of brittlestar beds in adjacent stratigraphic intervals revealed that they declined precipitously after the Jurassic, around the time durophagous predators were beginning to diversity, strongly suggesting a causal connection (Aronson, 1989b, 1992a).

These results support the hypothesis of a scale-independent relationship between ophiuroids and their predators. The paleontological data suggest that dense populations of epifaunal ophiuroids in nearshore environments responded to increasing predation in the Mesozoic in a similar fashion to populations of stalked crinoids, declining in response to the radiations of Modern durophagous predators. Brittlestar beds living in nearshore, shallow-water habitats are ecological anachronisms. Low predation pressure from durophagous predators has produced a retrograde structure and function strongly reminiscent of Paleozoic shallow-water communities.

PRIMARY PRODUCTIVITY

Top-down controls clearly determine where and when brittlestar beds will persist on multiple spatiotemporal scales. Bottom-up controls are important as well. Epifaunal and infaunal brittlestar beds persist only in areas where fluxes of phytoplankton or particulate organic matter are sufficient to support the energetic requirements of the millions of suspension-feeders in the populations (Warner, 1971; Rosenberg et al., 1987; Aronson, 1989a; Zuschin and Stachowitsch, 2009).

On macroevolutionary scales, Bambach (1993) and Vermeij (1995) argued persuasively that increasing energetic inputs drove escalating predation and infaunalization, as discussed above. Scaling down the productivity argument, McKinney and Hageman (2006) suggested that high-nutrient conditions in the western portion of the northern Adriatic Sea have driven shallow-benthic communities away from dominance by epifaunal suspension-feeders, including foliose bryozoans and ophiuroids, and toward energetically demanding bioturbation and infaunalization. In contrast to the eutrophic northwestern Adriatic, the oligotrophic northeastern Adriatic was characterized by the Paleozoic-like dominance of epifaunal suspension-feeders. Low predation pressure was viewed as a background condition in the northern Adriatic, making possible the contrast in benthic community structure. The authors compared their results to the difference in benthic community structure on opposite sides of McMurdo Sound, Antarctica. Dayton and Oliver (1977) showed that the nutrient-rich eastern side had high infaunal densities, whereas the oligotrophic western side had "patterns of mobile epifauna and low infauna density similar to bathyal and deep-sea communities." The hypothesis of McKinney and Hageman (2006) conflicted with the idea of high energetic requirements for the establishment and persistence of dense brittlestar beds.

Zuschin and Stachowitsch (2009) argued that the greater density of epifaunal suspension-feeders observed in northwestern Adriatic reflected the greater availability of shelly and other hard substrata, rather than a difference in food availability. They concluded that nutrient concentrations were sufficient to support communities dominated by epifaunal suspension-feeders on both sides of the northern Adriatic. They also pointed out that McMurdo Sound is not comparable to the northern Adriatic: although densities of infauna are higher on the nutrient-rich eastern side of McMurdo, so too are the densities of epifaunal suspension-feeders. Finally, they suggested that levels of durophagous predation are not in general low in the northern Adriatic. This latter assertion, however, was not based on predation potential or predation pressure measured for the focal prey in the focal communities.

Sufficient nutrient concentrations and suspended-matter (i.e., energetic) flux are critical to the establishment and persistence of living, dense suspension-feeder communities on ecological scales. Increasing productivity on a macroevolutionary time scale provided the energetic driver of increased bioturbation and the resultant emphasis on infauna in Modern soft-substratum communities. There is no paradox here: unlike predation, the qualitative effects of nutrient input and resultant primary productivity are scale-dependent. Low predation pressure from modern, durophagous taxa remains an essential background requirement for epifaunal ophiuroids, crinoids, and presumably other Paleozoic-type suspension-feeders, regardless of scale.

BRACHIOPODS

Brachiopods are the most abundant marine macrofossils from the Paleozoic. They were numerically important components of Paleozoic suspension-feeding communities in shallow, nearshore environments on soft substrata as well as unconsolidated, mixed substrata (i.e., substrata containing small rocks and bioclasts, to which they attached). Brachiopods declined precipitously in the end-Permian extinction and were replaced by bivalves (Gould and Calloway, 1980).

Rhynchonelliform, or articulate, brachiopods were/are sessile, epifaunal to semi-infaunal suspension-feeders. Today they live on hard bottoms and unconsolidated, mixed substrata. They are common components of some modern, hard- and mixed-bottom communities in nearshore and outer-shelf environments in the Southern Hemisphere, in all latitudinal zones and under both high- and low-productivity conditions (Dell, 1972; Foster, 1974; Smith and Witman, 1999; Kowalewski et al., 2002). In Antarctica they can occur in dense aggregations on the continental shelf on both hard and mixed substrata (Brey et al., 1995; Peck, 1996). Dense aggregations of epifaunal brachiopods occur rarely in nearshore environments in the Northern Hemisphere (e.g., Noble et al., 1976).

Brachiopods are considered poor competitors in Modern-type benthic communities because of their low metabolism and slow growth rates (Jackson et al., 1971; Thayer, 1981; Rhodes and Thompson, 1993; Peck, 1996). Whether and how aggregations of epifaunal brachiopods fit along the metaphorical continuum from low-predation, Paleozoic-type assemblages to high-predation, Modern-type assemblages is incompletely understood (James et al., 1992). Morphological evidence points to an evolutionary response to increasing predation in the Devonian, particularly in the paleotropics (Dietl and Kelley, 2001). In contrast, brachiopods were not affected, or only weakly affected, by the Mesozoic increase in durophagous predation, possibly due to their low energy content and postulated deployment of unpalatable secondary metabolites (Leighton, 2003).

THE MODERN BENTHOS IN ANTARCTICA

The endemic, shallow-benthic fauna of Antarctica is functionally different from the nearshore benthos in tropical, temperate, and Arctic latitudes (Dell, 1972; Arntz et al., 1994; Clarke et al., 2004; Aronson et al., 2007). Dense, quasi-Paleozoic assemblages of epifaunal suspension-feeders, including ophiuroids (Fig. 1) as well as sessile forms, are found in Antarctic shallow-water habitats where productivity is sufficiently high (Dayton and Oliver, 1977; Gili et al., 2006). A second retrograde feature is the extremely low level of durophagous predation in Antarctica (Aronson and Blake, 2001; Aronson et al., 2007). The top predators of shallow-water benthos are slow-moving, non-durophagous invertebrates of a Paleozoic functional grade, including asteroids, giant nemerteans, and giant pycnogonids.

Cold sea temperatures and a generally narrow, steeply sloping continental shelf with a deep shelf-break have maintained strong ecological and evolutionary connections between the region's shallow-nearshore and deep-sea faunas (see reviews cited above, and Barnes and Peck [2008] on brachiopods). Glaciations forced the bottom fauna down the continental shelf and slope, simultaneously limiting elements of the fauna to ice-free refugia in shallow areas (Clarke et al., 2004; Thatje et al., 2008a). These strictures were then relaxed during subsequent interglacials. The continuity of deep-sea and shallow-water environments is one reason for the archaic character of the benthic fauna.

The other important reason, of course, is that durophagous predation is severely limited (Dell, 1972; Dayton et al., 1974; Arntz et al., 1994; Aronson and Blake, 2001; Aronson et al., 2007). Functionally modern, skeleton-crushing taxa, which structure nearshore benthic communities elsewhere, are absent from Antarctica. There are no crabs or lobsters; sharks and rays are entirely absent as well, and skates are rare; and the limited higher-level diversity of bony fish does not include durophagous taxa.

The only teleosts in Antarctica at present are the notothenioids (Fig. 1) and liparids, which have evolved antifreeze glycoproteins (AFGPs) to survive cold sea temperatures. Like antifreeze in a car, AFGPs prevent the fatal nucleation of ice crystals inside the fishes' bodies. Notothenioids and liparids are not durophagous, but there is nothing about producing AFGPs that inherently excludes durophagy in teleosts. In fact, durophagous Arctic gadids (cod) have convergently evolved AFGPs. Other durophagous taxa in the Arctic include pleuronectids (flatfish), cottids (sculpins), zoarcids (eelpout) and a squalid (dogfish, or horned shark). These fishes have a variety of physiological and behavioral adaptations to survive freezing temperatures. The Arctic also has walruses and gray whales, but there are no durophagous marine mammals in Antarctica. In summary, evolution of the Antarctic bottom fauna has been driven by the physical extremity of the polar environment and by historical contingency.

HISTORY OF THE ANTARCTIC BOTTOM FAUNA

The historical roots of the living bottom fauna date to a long-term cooling trend that began in the Eocene. By the time of the Eocene, Antarctica was close to its present position. The climate of the early Eocene was what we would describe as cool-temperate today, and the marine fauna was typical of Tertiary faunas elsewhere. Sea temperatures began to decline in the middle Eocene, eventually leading to today's extremely cold, polar environment. The first major drop in temperature, a decline of as much as 10 °C, occurred over a period of several million years beginning ~41 Ma (million years ago). The thermal step-down coincided with the initial opening of Drake Passage and establishment of the Antarctic Circumpolar Current, or ACC (Scher and Martin, 2006; Ivany et al., 2008). Permanent ice sheets were established in Antarctica at the Eocene–Oligocene boundary, ~33.5 Ma (Zachos et al., 2001; Ivany et al., 2006).

The Eocene La Meseta Formation at Seymour Island contains the best record of marine macrofossils in Antarctica, and it spans this critical time in the history of the bottom fauna. Seymour Island is located in the Weddell Sea, close to the northern tip of the Antarctic Peninsula. Geological evidence shows that the La Meseta Formation was deposited in a nearshore, shallow-water, soft-substratum setting under fully marine conditions (Ivany et al., 2008). Sometime after the 41-Ma cooling event, durophagous teleosts, reptant decapods, and neoselachians (with the exception of a few skates) became extinct, drastically lowering predation pressure and, by their absence, restructuring the Antarctic bottom fauna. The ACC is thought to have created an oceanographic barrier that helped isolate marine life in Antarctica.

Evidence from the La Meseta Formation strongly suggests that predation on epifaunal, suspension-feeding echinoderms declined across the 41-Ma cooling event. Dense, autochthonous or parautochthonous fossil aggregations, representing dense paleopopulations of epifaunal ophiuroids (*Ophiura hendleri*) and stalked isocrinid crinoids (*Metacrinus fossilis*), as well as one dense paleopopulation of comatulid crinoids (*Notocrinus rasmusseni*), have been documented within the formation (Aronson et al., 1997, 2009). (Note that the stalk of *M. fossilis* was reduced to a short dart, making it essentially a stalkless stalked crinoid that planted itself in the soft sediment [Meyer and Oji, 1993].) Assessments of sublethal arm damage in *Ophiura* and *Metacrinus* indicated very low levels of predation pressure (Aronson et al., 1997). These low-predation paleopopulations flourished after 41 Ma but did not occur before, suggesting a decline in durophagous predation pressure associated with the cooling event (Aronson et al., 1997; Aronson and Blake, 2001).

In contrast, dense paleopopulations of epifaunal or semi-infaunal, rhynchonelliform brachiopods (*Bouchardia antarctica*) occurred commonly both before and after the 41-Ma cooling event and its associated decline in predation (Fig. 2). Of the hundreds of *Bouchardia* examined from paleopopulations that lived before and after the cooling event, none displayed signs of sublethal damage in the form of repaired shell breaks. Furthermore, none of the *Bouchardia* showed signs of predation by shell-drilling naticid gastropods. The naticids did, however, drill infaunal bivalves both before and after 41 Ma, with roughly the same frequency in both intervals (Aronson et al., 2009).

The contrasting patterns of occurrence of dense paleopopulations of epifaunal, suspension-feeding echinoderms and rhynchonelliform brachiopods are consistent with the differential responses of the two groups to escalating predation on larger scales in the Mesozoic. Supporting the hypothesis of a decline in durophagous predation in Antarctica during the Eocene, the epifaunal, suspension-feeding hiatellid bivalve *Hiatella tenuis* also formed dense populations at what is now

Seymour Island after, but not before, 41 Ma.

Conditions favorable to dense ophiuroid, crinoid, and hiatellid populations may have been enhanced after 41 Ma by upwelling events that increased productivity (references in Ivany et al., 2008). There were, however, dense populations of infaunal, suspension-feeding bivalves both before and after the cooling event (Stilwell and Zinsmeister, 1992; Aronson et al., 2009), so presumably productivity was sufficient to support dense echinoderm populations before 41 Ma, at least at certain times and places. This line of reasoning might be supported by the even distribution of dense aggregations of *B. antarctica* across the 41-Ma event, because its living congener, *B. rosea*, forms dense aggregations in upwelling zones on the outer shelf of Brazil (Kowalewski et al., 2002). Declining predation remains the best candidate for the essential condition that permitted dense ophiuroid and crinoid populations to become established and thrive after 41 Ma.

PHYSIOLOGICAL CONSTRAINTS ON DUROPHAGOUS PREDATORS

Limitations to durophagy at cold temperatures in modern Antarctic environments include: (1) thermal constraints on muscular performance; and possibly (2) the high energetic cost of depositing calcium carbonate at the cold temperatures and low saturation states of polar seas (Aronson et al., 2007). The high cost of biodeposition of calcium carbonate is inferred from the thin shells of mollusks observed in polar regions (Vermeij, 1978). If calcification is costly—and there is some doubt about that (Aronson et al., 2007)—then both the feeding apparatus of durophagous predators and the calcified defenses of their prey should be limited in polar environments.

The teleostean fauna in Antarctica is at present confined to taxa possessing AFGPs, and they happen not to be durophagous. Why there are no bottom-feeding sharks in Antarctica is more of a mystery, although some preliminary hypotheses have been offered (Aronson et al., 2007). Durophagous crustaceans are phylogenetically constrained from surviving in polar seas, and they are found in neither the Antarctic nor the high Arctic.

Reptant decapod crustaceans, including durophagous crabs and lobsters, are incapable of reducing the concentration of magnesium ions in their hemolymph, which as a result equilibrates with the surrounding seawater (Frederich et al., 2001). Magnesium is a narcotic, as anyone who has used Epsom salts—magnesium sulfate—to anesthetize marine invertebrates or ease constipation will know. At temperatures below 1 °C, corresponding to the sea temperatures in Antarctic shelf environments, magnesium narcosis amplifies the extreme torpor induced by low temperature, to the point crabs and lobsters simply stop functioning and die. Of the reptant decapods, the lithodids (anomuran king crabs) are the most cold-tolerant, being able to survive in a torpid, hypometabolic state at temperatures of 1–2 °C (Anger et al., 2003; Thatje et al., 2005). The problem of magnesium regulation does not vanish for reptant decapods at lower latitudes, but temperatures are high enough that magnesium narcosis is not debilitating. Unlike crabs and lobsters, amphipods and isopods are capable of down-regulating magnesium, and they are abundant and ecologically important in the benthic communities of Antarctica.

CLIMATE CHANGE AND THE ANTARCTIC BOTTOM FAUNA

The shallow seas off the Western Antarctic Peninsula (WAP) are among the fastest-warming in the world. Sea-surface temperatures have risen more than 1 °C in the last 50 years (Meredith and King, 2005; Clarke et al., 2007). The observations, data, and conceptual models reviewed above, taken from a variety of disciplines and from multiple scales and hierarchical levels, can be melded into a predictive scenario: durophagous predators will reinvade the nearshore-benthic communities of Antarctica within the next 50–100 years, with potentially dire consequences for the endemic bottom fauna. This unsettling prediction is already coming true, as crabs have begun to reinvade Antarctica by several routes.

First, the Antarctic Circumpolar Current is more permeable to oceanographic exchange than it was once thought to be. Like other current systems, the ACC produces eddies at a range of scales, with cold-core rings traveling north and warm-core rings traveling south (Olbers et al., 2004; Glorioso et al., 2005). Warm-core rings transport the larvae of subantarctic anomuran and brachyuran crabs into Antarctic waters (Thatje and Fuentes, 2003). Rafting on natural and anthropogenic flotsam provides a second avenue for biological invasion

(Barnes, 2002). Increasing ship traffic in Antarctica is a third mechanism for introducing alien species, which are transported in the ships' ballast tanks and on their hulls (Barnes et al., 2006). Two adult subarctic crabs, one male and one female, were recorded off the WAP in 1986, demonstrating the potential for ships to serve as vectors of predatory invasion (Tavares and De Melo, 2004).

The survival and successful recruitment of decapod larvae invading via warm-core rings, flotsam, and ballast water will require shallow-sea temperatures to rise above the critical level for magnesium narcosis. As the Antarctic seas warm, longer growing seasons for phytoplankton will combine with accelerated larval development to promote the decapod invasion (Aronson et al., 2007). On the other hand, climatically driven changes in the composition of the phytoplankton and ocean acidification could be detrimental to incoming decapod larvae (McClintock et al., 2008).

Recent explorations in deep water off the WAP have turned up large populations of adult lithodids on the continental slope (Thatje and Arntz, 2004; García Raso et al., 2005; Thatje and Lörz, 2005; McClintock et al., 2008; Thatje et al., 2008b). The oceanography of the Southern Ocean renders slope waters off the WAP slightly warmer than the shelf waters directly above, allowing the lithodids to tolerate magnesium narcosis and live, albeit at a slow pace. The origin of the lithodid populations is unknown, but it is likely their demersal larvae island-hopped along the topographic highs of the Scotia Arc, a chain of submerged peaks that connects the Andes of South America to the mountains of the Peninsula (Thatje et al., 2005).

King crabs are durophagous predators that eat echinoderms, mollusks, bryozoans, and other benthic invertebrates. At current rates of climate change, another 50–100 years of surface warming along the WAP should render nearshore waters sufficiently warm for king crabs on the slope to walk or send larvae into shallow-benthic habitats. Brachyuran crabs and durophagous fish from the subantarctic might also be able to establish viable populations within a centennial time frame.

The ecological consequences could be devastating. If we run the Eocene record of climatic cooling from Seymour Island in rapid-reverse, we can make specific predictions about particular faunal components (Aronson et al., 2009). Dense populations of ophiuroids should be decimated, whereas shell-drilling predation on bivalves should not change significantly. According to the paleontological data, aggregations of rhynchonellid brachiopods should not be especially vulnerable to increasing predation.

Newly published ecological data potentially contradict the prediction of no strong effect on brachiopods. Harper et al. (2009) showed that unsucccessful predatory attacks occurred much less frequently in living populations of Antarctic brachiopods than in living subantarctic and South American populations. This geographical pattern might mean that generally increasing durophagous predation in Antarctica will affect brachiopods, although issues of relative palatability (Mahon et al., 2003) and the impact of predation on population densities have yet to be resolved.

These alterations in food-web dynamics will overprint the direct, though highly variable, physiological responses to rising temperatures expected of particular taxa (Barnes and Peck, 2008). For ophiuroids and brachiopods, however, native taxa that may be excluded from Antarctica by climate change will likely be replaced by ecological equivalents from the subantarctic, leaving the predictions of altered predator–prey dynamics intact (Aronson et al., 2009). Other expected impacts of climate change include increased ice scour, which will physically disrupt benthic communities, and ocean acidification, which will inhibit calcification and, therefore, possibly de-escalate durophagous predation (Smale and Barnes, 2008).

The implications for conservation policy are clear. Preemptively disrupting the flow of invasive predators will require strengthening the Antarctic Treaty to control ship traffic in general and discharge of ballast water in particular. More difficult will be controlling emissions of greenhouse gases to slow and eventually reverse the effects of climate change (Thatje and Aronson, 2009). Both imperatives will require international cooperation that goes well beyond the usual political posturing.

QUESTIONS AND MORE QUESTIONS

The Paleozoic flavor of the living bottom fauna of Antarctica has been developing since the Eocene, apparently driven by the suppressive effect of declining sea temperatures on durophagous predation. Aronson et al. (2007) noted that the few post-Eocene records of fossil reptant decapods, which are from the early Miocene and Pliocene, correspond to times of relative warmth. Sea temperatures were warmer than at present during the previous interglacial (marine isotope stage 5e, ~125 ka), so what happened to the bottom fauna at that time? Did lithodids colonize during the Pleistocene and move down- and up-slope as the ice advanced and retreated? Did durophagous predation increase during the interglacials? The fossil record of marine life during the Pleistocene interglacials has, unfortunately, been obliterated by the scour of subsequent glacial movements (Barnes and Conlan, 2007). Ongoing genetic work on Antarctic king crabs should help fill the gaps in our understanding, by providing clues to the phylogenetic affinities of lithodids and the timing of their arrival off the WAP (Thatje et al., 2008b; Hall and Thatje, in press).

We do know the situation today is already more extreme than the Pleistocene interglacials. Atmospheric concentrations of carbon dioxide are higher than at any time during the last 2 million years and rising rapidly (IPCC, 2007; Hönisch et al., 2009). Furthermore, humans are injecting durophagous predators into Antarctic waters at a rate far exceeding what would be expected for natural, climatically mediated, latitudinal range shifts (Aronson et al., 2007, 2009).

A second, more general issue in paleobiology is whether the Mesozoic marine revolution went further in Laurasia than in Gondwana. The greater preponderance of rhynchonellid brachiopods in the nearshore and shelf waters of South America and New Zealand, and descriptions of fossil stalked crinoids from Cenozoic shallow-water deposits in South America, Australia, and New Zealand (Oji, 1996; Malumian et al., 2005), hint that living shallow-marine communities of the Southern Hemisphere may be structurally more Paleozoic than the better-studied systems to the north. The possibility of hemispheric-scale asynchrony in Phanerozoic patterns of escalation is a fascinating topic for further study.

CONCLUSION

The fossil record provides far more than a baseline against which to compare living communities threatened by degradation. It is an archive from which we can reconstruct the history of living communities and ascertain the causes of that history. The overarching method of paleoecology, if there is one, consists of conceptual jockeying between paleontology and ecology to test the hypothesis of scale independence. The rest is interdisciplinary common sense. The hypothesis is tested by moving from question to question, with technique dictated by the particulars of the case.

Shallow-benthic communities in Antarctica were functionally modern from the early Eocene until about 41 Ma. The long-term cooling trend that followed reduced durophagous predation and imparted a Paleozoic character to those communities. Ongoing reinvasions of durophagous predators could re-modernize the Antarctic benthos, accelerating the global homogenization of marine biotas. Information content has long been taken as a metaphor and a model for ecological diversity, so, metaphorically speaking, we are dumbing down global marine biodiversity by imperiling the endemic marine fauna of Antarctica.

Metaphors of geohistorical time-equivalence provide a dimension of understanding and predictive power far beyond the reach of real-time ecology. A fascinating terrestrial example is the cascading impact of human arrival and extirpation of the Pleistocene megafauna in the Americas. Adding a trophic level to modern terrestrial communities forced them into a ‘post-modern’ configuration, in which many tropical plants were bereft of dispersal agents (Janzen and Martin, 1982). A purely ecological perspective fails to recognize the ecological legacy of the megafauna, and instead views the plants as poorly adapted to dispersal. But there is more insight to be drawn from the metaphor. Livestock introduced following European colonization and other post-Columbian human activities have to some extent reversed the effects of the loss of megafauna (Janzen and Martin, 1982; Guimarães et al., 2008), although weak and artificial compensation through further perturbation can hardly be construed as a tidy solution of the problem. The radical policy recommendation to ‘rewild’ the American landscape by introducing African megafauna (Donlan et al., 2005) is paleoecology at its most imaginative. To view this proposal as the *reductio ad absurdum* of our science is to miss the essential point of how bad things really are. Environmental destruction is the absurdity, not unconventional thinking.

Assertions that marine communities are back-sliding to a Proterozoic level of organization because of climate change, nutrient loading, overfishing, and other human insults (Hallock, 2001, 2005; Jackson, 2008;

Richardson et al., 2009) are unsettling and controversial. Although the nihilistic vision of a marine biota dominated by jellyfish and cyanobacterial mats may not be correct, it is a paleoecological hypothesis about the future history of marine systems. Like the incipient predatory invasions of Antarctica and the fate of the fruits the gomphotheres ate, the Proterozoic scenario affords us the opportunity to make specific predictions and take preemptive action, a policy option far better than reacting to environmental disaster during or after the fact. Action to save the oceans could render the jellyfish–bacterial slime hypothesis untestable, a scientific irony with which I am sure we all could live. Paleoecology offers us an avenue of prediction from retrospective analysis at a time of rapid global change, when we need to know more than simply to expect nasty surprises.

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