

Global Climate Change and the Origin of Modern Benthic Communities in Antarctica¹

RICHARD B. ARONSON^{2,*} AND DANIEL B. BLAKE[†]

**Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528; and Department of Marine Sciences, University of South Alabama, Mobile, Alabama 36688*

†Department of Geology, University of Illinois, Urbana, Illinois 61801

SYNOPSIS. Marine benthic communities living in shallow-water habitats (<100 m depth) in Antarctica possess characteristics reminiscent of Paleozoic marine communities and modern deep-sea communities. The absence of crabs and sharks, the limited diversity of teleosts and skates, the dominance of slow-moving invertebrates at higher trophic levels, and the occurrence of dense ophiuroid and crinoid populations indicate that skeleton-breaking predation is limited in Antarctica today, as it was worldwide during the Paleozoic and as it is in the deep sea today. The community structure of the antarctic benthos has its evolutionary roots in the Eocene. Data from fossil assemblages at Seymour Island, Antarctic Peninsula suggest that shallow-water communities were similar to communities at lower latitudes until they were affected by global cooling, which accelerated in the late Eocene to early Oligocene. That long-term cooling trend ultimately resulted in the polar climate and peculiar community structure found in Antarctica today. Declining temperatures beginning late in the Eocene are associated with the disappearance of crabs, sharks, and most teleosts. The sudden drop in predation pressure allowed dense ophiuroid and crinoid populations to appear and flourish. These late Eocene echinoderm populations exhibit low frequencies of sublethal damage (regenerating arms), demonstrating that there was little or no predation from skeleton-breaking fish and decapods. Current scenarios of global climate change include predictions of increased upwelling and consequent cooling in temperate and subtropical upwelling zones. Limited ecological evidence suggests that such cooling could disrupt trophic relationships and favor retrograde community structures in those local areas.

INTRODUCTION

Modern benthic communities of Antarctica, which are semi-isolated by the Antarctic Circumpolar Current, exhibit characteristics that have not been satisfactorily explained (Picken, 1980; White, 1984; Dayton, 1990; Dayton *et al.*, 1994; Pearse and Bosch, 1994; Crame, 2000). A number of taxa are highly derived and specifically adapted to the physical and biological conditions that characterize the polar environment (Clarke, 1983; Brey and Clarke, 1993; Poulin and Féral, 1996; McClintock and Baker, 1997). Even so, neontologists have long appreciated the archaic, deep-sea char-

acter of the benthic faunas currently living in shallow-water habitats in Antarctica (Dell, 1972; Dayton and Oliver, 1977; Picken, 1985; Clarke and Crame, 1992; Arntz *et al.*, 1994; Dayton *et al.*, 1994; Brey *et al.*, 1996).

Certain ecological features, including the occurrence in shallow water (<100 m) of dense populations of ophiuroids and crinoids (*e.g.*, Fell, 1961; Fell *et al.*, 1969; Dayton and Oliver, 1977; Dearborn, 1977; Fratt and Dearborn, 1984; Picken, 1985), suggest a community structure in which skeleton-crushing predation, typical of modern, shallow-water marine communities, is minimal. Because the diversities of teleostean fishes and batoid skates and rays are low, and because sharks and brachyuran crabs are absent, slower-moving invertebrates that do not crush hard-shelled prey, including asteroids, ophiuroids, nemerteans,

¹ From the Symposium *Antarctic Marine Biology* presented at the Annual Meeting of the Society for Comparative and Integrative Biology, January 4–8 2000, at Atlanta, Georgia.

² E-mail: raronson@disl.org

anthozoans, giant pycnogonids, large isopods, and shell-drilling gastropods, are responsible for the preponderance of predatory activity in antarctic communities (Dell, 1972; Dayton *et al.*, 1974; Fratt and Dearborn, 1984; McClintock and Baker, 1997, 1998; Amsler *et al.*, 1999). The reduced level of skeleton-breaking predation in Antarctica and the resulting peculiar ecologies of the shallow bottom faunas have their causative roots in a global cooling trend that began late in the Eocene Epoch, about 35 Ma (million years ago).

We begin this paper with a brief review of the history of skeleton-breaking predation from the Mesozoic Era onward. We then examine the responses of benthic communities in Antarctica to global climate change beginning in the late Eocene. Finally, we use the fossil record to predict some local, community-level responses to the rapid climate change expected in the forthcoming decades to centuries.

THE ORIGIN OF MODERN PREDATOR-PREY RELATIONSHIPS

Predation, prey morphology, and sublethal damage

Many of the architectural features displayed by skeletonized invertebrates are interpreted as evolutionary consequences of durophagy, the ability of predators to consume those hard-shelled prey. The fossil record suggests that durophagous predation increased several times during the Paleozoic (Hutchinson, 1961; Signor and Brett, 1984; Vermeij, 1989b), but the most dramatic changes occurred as part of the "Mesozoic marine revolution" (Vermeij, 1977). Modern, skeleton-breaking predators, particularly teleosts, neoselachian sharks and rays, and decapod crustaceans, began to diversify in nearshore environments during the Jurassic Period (Fig. 1; Thies and Reif, 1985; Vermeij, 1987). Radiations of these durophagous taxa were accompanied by, and are thought to have stimulated, the evolution of architectural defenses in gastropods, bivalves, cephalopods, crinoids, and other marine invertebrates during the Mesozoic and Cenozoic (Vermeij, 1977, 1987; Meyer and Macurda, 1977; Aronson,

1991a; Harper, 1991). The macroevolutionary adaptations of gastropod shells to increasing predation pressure included increased spination, ribbing, and other defensive sculpture, decreased width and increased dentition of the aperture, and tighter coiling (Vermeij, 1977, 1987). Similar changes in the morphology of gastropod shells have occurred with increasing predation on smaller temporal scales (Seeley, 1986; West *et al.*, 1991). Increased expressions of antipredatory morphology in gastropods are also associated with spatial gradients in shell-breaking predation on a variety of scales (*e.g.*, Kitching *et al.*, 1966; Vermeij, 1978).

Vermeij (1982) argued that the frequency of sublethal shell damage (repaired cracks) in a gastropod population should be positively related to the survival value of that population's morphological defenses: increased sublethal damage should imply decreased lethal predation. In agreement with this prediction, shell repair in gastropods generally increased in frequency beginning in the Jurassic (Vermeij *et al.*, 1981; but see Allmon *et al.*, 1990). Nevertheless, interpreting the frequency of shell repair can be problematic. If only a few shells in a population display sublethal damage, then either the attack rate is high and most attacks are lethal, or both the lethal and sublethal attack rates are extremely low (Schoener, 1979). Furthermore, the frequency of shell repair can vary among habitats and over short distances, potentially obscuring putative temporal trends (Cadée *et al.*, 1997). A second assertion about sublethal damage is that by recording the frequency of sublethal encounters, such injuries provide an index of the selection pressure for antipredatory features (Vermeij, 1982). Sih (1985) contested this claim, arguing that frequent encounters between predators and prey are not necessary to select strongly for the evolution of antipredatory traits in prey. Thus, the significance of sublethal damage to gastropods is not entirely clear.

Unlike the situation with gastropods, sublethal damage is relatively easy to interpret in ophiuroids and crinoids. This is because predators generally attack the arms of these echinoderms before attacking the cen-

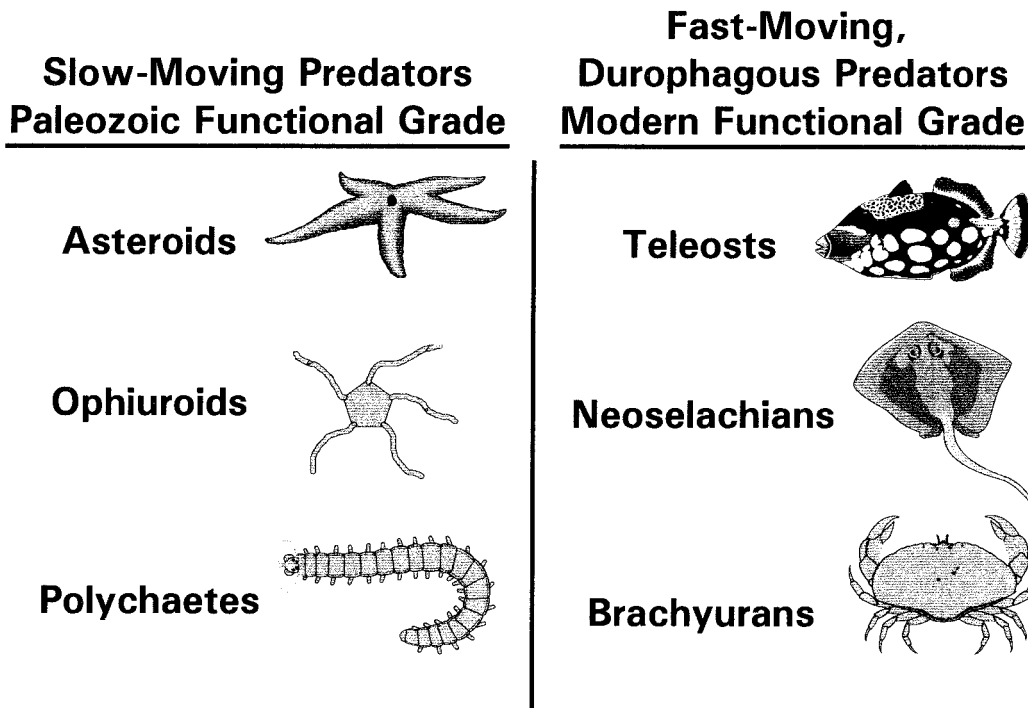


FIG. 1. Functional classification of predators in ancient and modern benthic communities. Slow-moving predators were common consumers in shallow-water benthic communities of the Paleozoic and early Mesozoic. Today they are the dominant predators in the few low-predation, Paleozoic-type communities found in nearshore environments. Fast-moving, skeleton-breaking predators diversified in the Mesozoic and Cenozoic, radically altering the structure of nearshore benthic communities by eliminating most epifaunal suspension-feeders from most soft-substratum habitats.

trally-located viscera (Meyer, 1985; references in Aronson, 1987, 1988; Nichols, 1996). The proportion of individuals regenerating one or more arms in a population is an indicator of the frequency of predator-prey encounters and, hence, the frequency of lethal predation in living and fossil ophiuroids and crinoids (Meyer, 1985; Aronson, 1991b; Oji and Okamoto, 1994). Frequencies of sublethal arm injury were higher in living populations of tropical ophiuroids than in an ecologically comparable fossil population of confamilial ophiuroids from the Jurassic, a result that supports the idea of a Mesozoic increase in skeleton-breaking predation (Aronson, 1991b).

The adaptations of gastropods for drilling molluscan prey also increased during the Mesozoic and Cenozoic (Vermeij, 1977). As a result, the thickness of prey shells, the frequency of drilled prey, the match between predator and prey sizes, and the lo-

calization of drillholes to thin areas of prey shells should have increased through time (Kelley and Hansen, 1993, 1996). Temporal patterns of drilling predation are complex and noisy, however, and they do not always follow these predictions (*e.g.*, Dudley and Vermeij, 1978; Allmon *et al.*, 1990; Hansen and Kelley, 1995). An added complication is that drilling gastropods are themselves subject to changing levels of durophagy, including both shell-breaking predation and cannibalistic drilling (Vermeij *et al.*, 1989; Kelley, 1991).

Population- and community-level responses to predation

Increasing durophagous predation need not result in the increased expression of defensive features in prey. A more direct consequence of increased predation, which we have documented for ophiuroids, is a decline in prey abundance. Dense populations

of epifaunal, suspension-feeding ophiuroids (10^2 – 10^3 ind/m²) thrive in areas where there is a high flux of suspended organic matter (*i.e.* an adequate food supply), but they are excluded from most modern coastal habitats by predatory fish and crabs (Aronson and Harms, 1985; Aronson, 1989*a*). The primary predators of epifaunal ophiuroids living in dense populations are slow-moving invertebrates, including asteroids and polychaetes (Fig. 1), and the low levels of predation are reflected in low frequencies of sublethal arm damage. On a macroecological scale, the diversification of fast-moving, durophagous predators in the Mesozoic caused a global decline in the occurrence of these dense, low-predation ophiuroid populations (Aronson, 1989*b*, 1992).

The Mesozoic-Cenozoic increase in predation was a consequence of the radiations of taxa comprising the “Modern evolutionary fauna” (*sensu* Sepkoski, 1991) in near-shore environments. The Modern fauna replaced the “Paleozoic evolutionary fauna” in coastal environments and subsequently spread to offshore, deeper-water environments. Durophagous predators originated onshore, eliminating epifaunal, suspension-feeding populations from soft-substratum habitats (Bottjer and Jablonski, 1988; Jablonski and Bottjer, 1990, 1991). From the Jurassic onward, epifaunal suspension-feeders on soft substrata were replaced by infaunal and more mobile epifaunal suspension-feeders, giving onshore soft-substratum communities their modern, bivalve-dominated ecology (Stanley, 1977; Vermeij, 1977; Jablonski and Bottjer, 1983; Bottjer and Ausich, 1986). As a broad generalization, predation is lower and community structure is archaic in offshore, deep-water habitats compared to nearshore, shallow-water habitats.

The restriction of dense ophiuroid populations in coastal waters during the Mesozoic is an aspect of the onshore-offshore trend. As another example, stalked crinoids were abundant in shallow water in the Paleozoic and early Mesozoic (Meyer and Macurda, 1977; Oji, 1985; Bottjer and Jablonski, 1988). Living stalked crinoids, most of which belong to the order Isocrinida, occur only offshore, in water deeper

than ~100 m, where predation pressure is lower than onshore, in shallower habitats (Meyer and Macurda, 1977; Oji, 1996). The unstalked crinoids (order Comatulida), which are mobile and thus presumably better able to evade predators, replaced the stalked crinoids in shallow water.

Smith (1994) suggested that the onshore-offshore pattern is an artifact of geology rather than a biological effect. There are more Mesozoic onshore and more Cenozoic offshore deposits available for study, potentially biasing the fossil record in the direction of the perceived macroevolutionary trend. Regardless of the distribution of rock outcrops, however, all stalked crinoids and most dense ophiuroid populations now live only in deep, offshore habitats. Soft sediments in shallow water are now dominated by bivalves, and the skeletonized invertebrates that have been studied are generally better defended against predators than were their ecological equivalents early in the Mesozoic.

Effects of global change and latitude on predation

Trophic relationships in the Mesozoic evolved within the context of global events. The end-Permian mass extinction opened the way for the diversification of modern predators, perhaps by creating an ecological vacuum of vacant niches (Sepkoski, 1991). Escalation of predator-prey interactions during the Mesozoic also coincided with increased productivity, which apparently supplied the energy required to drive the acquisition of antipredatory features in prey (Rosenzweig and McCord, 1991; Bambach, 1993; Vermeij, 1995; Martin, 1998). Evolutionary innovations of predators and prey transcended the end-Cretaceous mass extinction, and escalation continued in the Cenozoic. Episodes of elevated extinction in the Cenozoic selectively wiped out well-defended prey; this set back escalatory trends, but only temporarily (Vermeij, 1987, 1989*b*; Jablonski, 1989).

Temporal trends in durophagy are mirrored by modern biogeographic patterns in that shell-breaking predation increases with decreasing latitude. Defensive features of gastropod shells, including heavy calcifi-

cation, spines, ribs, tight coiling, narrow apertures, and low spires, increase along the same latitudinal gradient (Vermeij, 1978; Palmer, 1979; see Leighton [1999] for a Paleozoic example). Escalation has occurred to a greater extent in the tropics in part for purely physiological reasons: calcification and enzymatic activity are more rapid and less energetically expensive at higher temperatures (Graus, 1974; Vermeij, 1978). As a result, shells are comparatively thick and ornate in the tropics, and thin and plain at temperate and polar latitudes (Vermeij, 1978). Another reason is that species diversity and the rate of evolution of morphological novelties are greater in the tropics than at higher latitudes (Jablonski, 1993; Rosenzweig, 1995). Well-defended mollusks in the tropics are particularly vulnerable to extinction as temperature and productivity decline (Vermeij, 1987), but there may be no overall bias toward greater extinction vulnerability near the equator (Raup and Jablonski, 1993; see also Clarke, 1993).

Although low temperatures depress shell-drilling activity by lowering metabolic rates (Kabat, 1990), predation by shell-drilling gastropods is thought to increase with increasing latitude as the shell-breaking activity of the predators of those drillers declines (Vermeij *et al.*, 1989; Allmon *et al.*, 1990; Hansen and Kelley, 1995; but see Dudley and Vermeij, 1978). Preliminary observations using scuba in McMurdo Sound suggest that shell-drilling predation is intense in at least some antarctic shallow-water habitats (R.B.A. unpublished data). In this sense the analogy of spatial and temporal gradients in predation is imperfect: shell-drilling increased in the Mesozoic, but apparently it also increases toward the poles.

Herbivory

The consumption of macrophytes is as fundamental a force as predation in structuring living, shallow-water benthic communities in the temperate zone and the tropics (reviewed in Aronson, 1990). Vermeij and Lindberg (2000) recently suggested that herbivory, which has evolved many times in many clades, is a derived condition relative to detritivory, microphagy, and pre-

dation. As an example, sea urchins possessing a robust Aristotle's lantern (the jaw apparatus) are members of the Modern evolutionary fauna (Sepkoski, 1991), and these herbivores may have been important in driving the modernization of algal assemblages during the Cenozoic (Steneck, 1983). Modern macrophyte-herbivore relationships are a product of the Mesozoic marine revolution, and like predator-prey relationships they were probably driven by increased productivity in the Mesozoic. In contrast, herbivory was apparently of minor importance during the Paleozoic (Vermeij and Lindberg, 2000).

GLOBAL COOLING AND PREDATION IN ANTARCTICA

It is clear from isotopic and micropaleontological evidence that global cooling reduced sea temperatures in Antarctica, with a drop of possibly 7–9°C in the late Eocene to early Oligocene, ~37–33 Ma (Kennett, 1977; Clarke and Crame, 1992; Kennett and Warnke, 1992; Mackensen and Ehrmann, 1992; Prothero, 1994). The opening of the Drake Passage in the late Oligocene to early Miocene, ~28–23 Ma, and the consequent establishment of circum-antarctic circulation further reduced sea temperatures and isolated Antarctica and its benthic fauna (Lawver *et al.*, 1992; Prothero, 1994; Crame, 1999). Cooling in the late Eocene was thus the beginning of a long-term shift from the cool-temperate climate of the Eocene to the glaciated, polar climate found in Antarctica today (Lear *et al.*, 2000). Climatic changes in Antarctica and elsewhere during the late Eocene may have been related to extraterrestrial impacts, but causal connections have not yet been clarified (Clymer *et al.*, 1996; Poag, 1997). Climatic cooling directly or indirectly reduced predation pressure, causing a fundamental shift in the structure of benthic communities in Antarctica. Most of what we know about this critical time in the history of the antarctic benthos comes from studies of the La Meseta Formation at Seymour Island, off the Antarctic Peninsula.

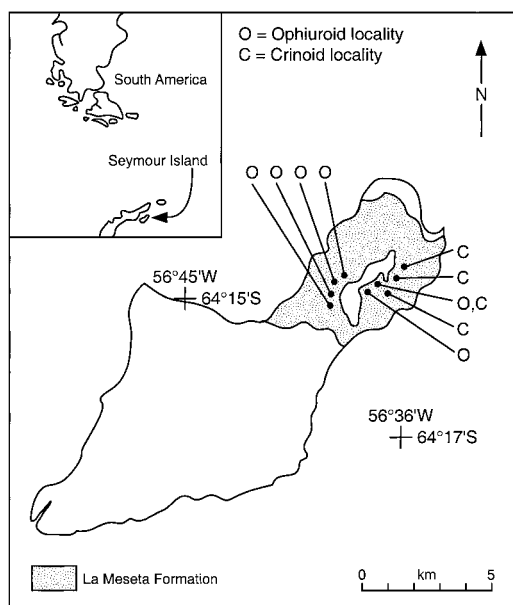


FIG. 2. Map of Seymour Island, showing the locations of dense assemblages of ophiuroids and crinoids. Reproduced from Aronson *et al.* (1997) by permission of the Geological Society of America.

Geology of the La Meseta Formation at Seymour Island

Seymour Island (64°15'S, 56°45'W) lies 100 km southeast of the tip of the Antarctic Peninsula. The La Meseta Formation, a marine deposit composed of siliciclastic sediments, forms a large plateau on the northern portion of the island (Fig. 2). The sediments are locally fossiliferous, constituting the most abundant source of Cenozoic marine fossils in Antarctica.

The La Meseta Formation was deposited in a complex of nearshore, shallow-water settings (Sadler, 1988). A high diversity of marine fossils throughout the formation and the absence of any clear indicators of fluvial deposition or subaerial exposure indicate fully marine conditions, possibly at the mouth or immediately seaward of a bay-like or estuary-like basin (see Elliott and Trautman, 1982; Marcellari, 1988; Sadler, 1988). Porębski (1995, 2000) interpreted the La Meseta as representing a series of three cycles of sedimentary deposition. The three stacked, sequence-stratigraphic units were produced by episodes of faulting, subsidence, and infilling.

Temporal correlation of the La Meseta Formation to regions outside Antarctica has proven problematic. The precise ages of the individual sedimentary units are not required for the present discussion, but it is critical that the depositional interval represent a time span that is sufficient to reflect climatically mediated ecological change. The La Meseta appears to span an interval as long as late early Eocene to early Oligocene, although the formation may only include the middle and late Eocene (Wrenn and Hart, 1988; Fordyce, 1989; Coccozza and Clarke, 1992; Gazdzicki *et al.*, 1992). Berggren *et al.* (1995) placed the early Eocene-middle Eocene boundary at 49.0 Ma, the middle Eocene-late Eocene boundary at 37.0 Ma, and the Eocene-Oligocene boundary at 33.7 Ma.

The important point is that the La Meseta Formation records the marine faunas that lived in shallow-water habitats off the Antarctic Peninsula during a period of abrupt cooling and expansion of ice sheets in the late Eocene or possibly early Oligocene, around 35 million years ago (Gazdzicki *et al.*, 1992; Lear *et al.*, 2000). During this time, a series of minor, climatically driven extinction events occurred around the world (Prothero 1989, 1994). Sea temperatures in the area of the Antarctic Peninsula fluctuated, but the overall trend was a decline of up to 9°C (Kennett and Warnke, 1992; Stilwell and Zinsmeister, 1992).

Ecological changes in the late Eocene

Beginning in the late Eocene, declining temperatures accompanied by reduced shelf area due to glaciation altered the geographic and bathymetric ranges of a variety of antarctic taxa (Zinsmeister and Feldmann, 1984; Clarke and Crame, 1992; Meyer and Oji, 1993; Blake and Aronson, 1998). The effects of changing climate on fish and crabs are of particular interest because of their importance as predators in benthic communities. Isolated teleost bones are scattered throughout the La Meseta Formation but not in sufficient numbers to determine temporal patterns of abundance and diversity. Crabs are found throughout, but shark remains are concentrated in the lower (earlier) units (Feldmann and Wilson, 1988;

Long, 1992). The distribution of batoids through La Meseta time is not known, as skate teeth have been found at only one site, midway up the formation (Long, 1994). The early Tertiary teleost fauna probably went extinct in Antarctica sometime around the Eocene-Oligocene transition, and the current, endemic fauna of notothenioids and liparids radiated some time later (Eastman and Clarke, 1998). Likewise, crabs and sharks disappeared from Antarctica in association with late Eocene and subsequent cooling trends (Dayton *et al.*, 1994). At least one species of crab, however, survived into the early Miocene (Feldmann and Crame, 1998). Skates (Rajidae) apparently survived the post-Eocene climatic changes in Antarctica, and a few species persist to this day in shallow water (<100 m) (DeWitt, 1971; Long, 1994; Eastman and Clarke, 1998). Crabs and sharks are now absent from shallow benthic communities in Antarctica, and teleosts and rajids are minor players in terms of durophagous predation.

These faunal changes are correlated with declining temperatures. Since global cooling by itself was probably not sufficient to cause widespread extinction (Clarke, 1993), and since durophagous predation remains strong in the Arctic (Dayton, 1990), the causal connections in Antarctica must be complex and indirect. Climate-associated factors that could account for the loss of durophagous predators include faunal isolation, declining productivity, and/or changes in the seasonal intensity of productivity (Arntz *et al.*, 1994, 1997; Dayton *et al.*, 1994; Crame, 2000). Whatever the causes, the loss of skeleton-breaking predators in the late Eocene disrupted trophic linkages in shallow-water habitats, with profound and lasting consequences for community structure.

During expeditions to Seymour Island in the austral summers of 1986 and 1994, we found dense, monospecific concentrations of hundreds to thousands of ophiuroids and tens to hundreds of crinoids in the La Meseta Formation (Aronson *et al.*, 1997; Fig. 3). We located six assemblages of the ophiuroid *Ophiura hendleri* Blake and Aronson (order Ophiurida) and four assemblages of the crinoid *Metacrinus fossilis* Rasmussen (order Isocrinida). The good state of pres-

ervation of the fossils, their concentration within single horizons, the lack of bioturbation, and other sedimentological evidence indicate that the animals were buried rapidly and preserved in place, and not transported significant distances. These autochthonous fossil assemblages represent localized, short-lived populations.

All of the assemblages were found close to the central plateau (Fig. 2) within the upper few meters of the of the La Meseta Formation. This stratigraphic occurrence is near the top of the uppermost of Porebski's (1995, 2000) three sequence units. Their placement puts them close to the end of La Meseta time, when crabs and sharks had essentially disappeared and when teleosts may already have been in decline as well.

Brett *et al.* (1997) showed that rates of deposition vary during different phases of sedimentary cycles. Such variations affect the likelihood that echinoderm assemblages will be subject to rapid burial and autochthonous preservation. Sedimentation may have been more rapid near the top of the uppermost sequence-stratigraphic unit of the La Meseta Formation than further down in that unit, and the result would have been a sedimentological bias favoring the preservation of ophiuroid and crinoid assemblages near the top. This possibility could account for the vertical distribution of dense assemblages within the uppermost sequence-stratigraphic unit. It does not, however, explain why no dense assemblages were found anywhere within the lower two units. Those lower units would have shown the same bias toward preservation of echinoderms during the phases of their cycles in which sedimentation was rapid. An ecological explanation is more likely, particularly in light of our inferences about predation pressure.

The proportions of individuals with sublethal arm damage were extremely low in the fossil *Ophiura* and *Metacrinus* populations, indicating low predation pressure (Aronson *et al.*, 1997). The low incidence of regenerating arms is not an artifact of preservation; the zero and near-zero proportions of regenerations observed are not strongly affected by corrections for post-mortem arm breakage (see Aronson,

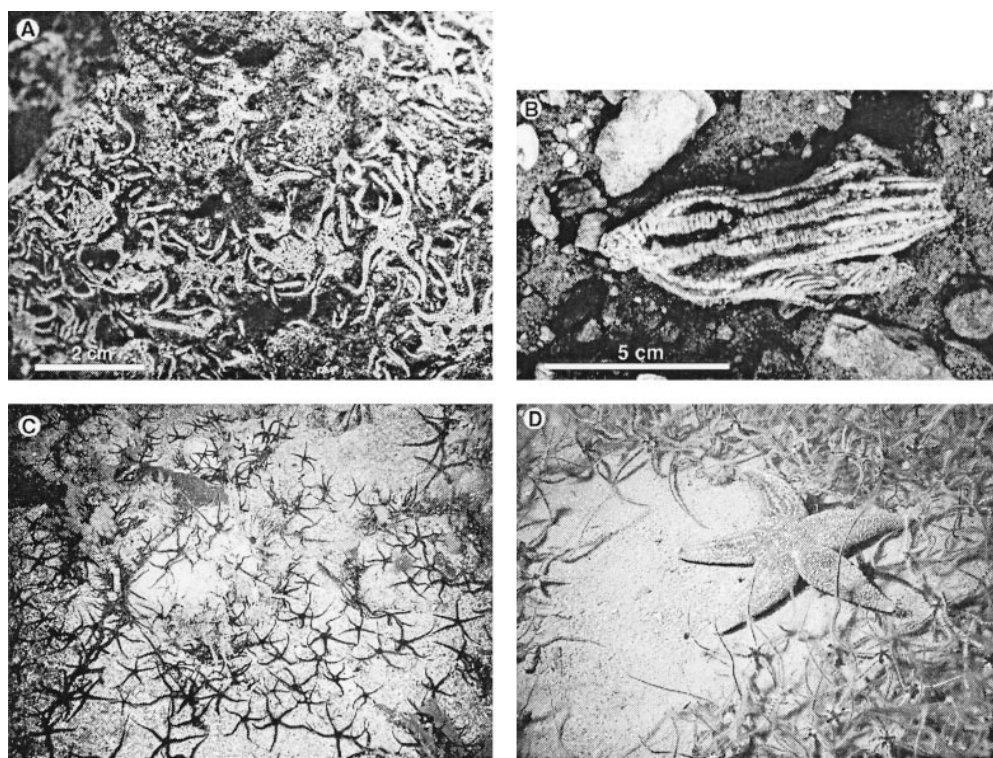


FIG. 3. (A) Part of a dense, autochthonous, shallow-water assemblage of ophiuroids, *Ophiura hendleri*, from the La Meseta Formation at Seymour Island. (B) An isocrinid crinoid, *Metacrinus fossilis*, from the La Meseta Formation. Although the genus *Metacrinus* may have evolved in shallow water in Antarctica during the Eocene and then spread to deep-water habitats elsewhere (Zinsmeister and Feldmann, 1984; Meyer and Oji, 1993), isocrinids in general have been excluded from shallow water since the middle Cretaceous (Oji, 1985). Unlike other isocrinids, *M. fossilis* had short, tapered stalks, which they probably used to anchor themselves in soft sediments. (C) Living, dense aggregation of ophiuroids, *Ophiocomina nigra* (Abildgaard), photographed in Loch Melfort, west coast of Scotland at 7 m depth in 1992. (D) Living, dense aggregation of ophiuroids, *Ophiothrix fragilis* (Abildgaard), in Loch Melfort, 9 m depth. Seastars, *Asterias rubens* Linnaeus, (center) are the primary predators in this community. The ophiuroids are retreating toward the right, producing a "bow wave" in front of the pursuing seastar.

1991b). Furthermore, physical damage was not an important cause of arm injury when the ophiuroids and crinoids were alive in the late Eocene. Modern, shallow-water ophiuroids in the Caribbean are not affected by even the most intense storm conditions (Aronson, 1991b). Injury levels in the fossil crinoids from Seymour Island were even lower than injury levels in a congeneric population currently living off Japan, in a deep-water habitat where both predation and physical damage are known to be extremely limited (Aronson *et al.*, 1997).

Clearly, the late Eocene ophiuroids and crinoids experienced little physical damage and limited predation pressure. The strati-

graphic distributions of the dense echinoderm populations and their predators and the data on sublethal damage strongly suggest that predation pressure was declining at the end of the Eocene or beginning of the Oligocene. Upwelling near the Antarctic Peninsula at that time (Mackensen and Ehrmann, 1992; Kennett and Warnke, 1992; Diester-Haass and Zahn, 1996) probably provided the nutrients necessary to produce the flux of phytoplankton required to feed the dense ophiuroid and crinoid populations (Aronson *et al.*, 1997; note that this upwelling argument is at variance with the hypothesis that predation levels were influenced by declining productivity).

Gastropod shells from the lower units of the La Meseta Formation are heavily sculpted compared to those from higher in the section (see Stilwell and Zinsmeister, 1992). Although this pattern is consistent with the hypothesis of declining predation pressure, it could also be a more direct result of declining temperature; calcified defensive sculpture carries a fitness cost that increases with decreasing temperature (Vermeij, 1978; Palmer, 1981). There is no information available on repaired shell damage in gastropods from the La Meseta Formation, and data on shell-drilling predation are sparse. In a preliminary comparison, Kelley *et al.* (1997) found that drilling frequencies were similar between late Eocene bivalves from Seymour Island and roughly contemporaneous bivalves from the U.S. Gulf Coast. This result cannot be easily interpreted at present, because the effects of late Eocene cooling on drilling predation in Antarctica have not been investigated.

MARINE COMMUNITIES PAST, PRESENT, AND FUTURE

Living, dense populations of *Ophiura* spp. and other ophiuroids occur worldwide, but they are found only in the deep sea and in a few shallow-water habitats where predation pressure is minimal (Aronson and Harms, 1985; Aronson, 1989a; Fujita and Ohta, 1990). Likewise, *Metacrinus* and the other isocrinids now occur only in deep water, where they too can form dense aggregations (Meyer and Macurda, 1977; Oji, 1996). These distributional restrictions are rooted in increasing levels of predation in the Mesozoic. The sudden, sporadic appearance of retrograde, Paleozoic-style, echinoderm-dominated communities in Antarctica in the late Eocene suggests strong, though probably indirect, climatic control of predation pressure.

The effects of climatic cooling in Antarctica have led to a near-absence of skeleton-breaking predators, an emphasis on predation by slow-moving invertebrates, and the occurrence of communities with a distinctly archaic, deep-sea character in shallow-water habitats. These features are important reasons why today's shallow-water, benthic communities in Antarctica are

different from those at temperate and tropical latitudes. As mentioned earlier, however, the taxa themselves are not necessarily archaic, and many are highly derived. Many species of antarctic invertebrates employ chemical defenses against predation by other invertebrates (McClintock and Baker, 1997, 1998), a fact that is not at variance with the evidence for minimal predation by fish and no predation by crabs. Furthermore, not all aspects of food web dynamics are reminiscent of those of the Paleozoic. The potentially strong influence of drilling predation is a trophic link made possible by the post-Paleozoic diversification of shell-drilling gastropods.

Another modern trophic relationship in Antarctica is the consumption of algae by regular echinoids. Interestingly, Vermeij and Lindberg (2000) identified high-latitude, shallow-water benthic communities as Paleozoic-like anachronisms in the sense that herbivory is supposedly low. Whether this generalization is correct remains to be seen, but in Antarctica the sea urchin *Sterechinus neumayeri* (Meissner) can be found in abundance in rocky subtidal habitats, feeding on macroalgae and diatoms (McClintock, 1994; Brey *et al.*, 1995). The reason echinoids occur in dense populations in Antarctica no doubt has to do with the low diversity and biomass of durophagous predators. At lower latitudes, human fishing activity has released sea urchins from predation (Aronson, 1990, 1994). Thus, dense populations of regular echinoids indicate that predation pressure from fish and decapods is low, whether naturally low in Antarctica or anthropogenically reduced in the temperate zone and the tropics.

Understanding the evolution of trophic relationships in Antarctica makes it possible to predict the ecological consequences of the current phase of global climate change. Changes in sea temperature of only a few degrees Celsius can have significant impacts on predator-prey relationships, with profound ecological consequences. Sanford (1999) showed that a temperature drop in the rocky intertidal of Oregon, related to El Niño-intensified upwelling, markedly reduced predation by the seastar *Pisaster ochraceus* (Brandt). El Niño events appear

to be increasing in frequency (McGowan *et al.*, 1998), so the effects of upwelling/cooling should become more prominent over the next several decades. Upwelling/cooling in many temperate and subtropical areas may also intensify on a time scale of centuries as the result of the continued atmospheric accumulation of greenhouse gases (Bakun, 1990).

If reduced predation pressure in temperate upwelling zones is a general consequence of current trends in global climate change, and if that reduction in predation pressure extends to the activity of fish and decapods, we predict major changes in local community structure. Communities in areas of upwelling will be increasingly characterized by dense aggregations of suspension-feeding echinoderms, which will be released from predation pressure and fed by the productivity associated with the upwelling. Furthermore, we expect a decline in gastropod shell sculpture, and increase in shell-drilling predation, and other ecological patterns associated with low predation pressure in Antarctica.

ACKNOWLEDGMENTS

We thank Jim McClintock, Bill Baker, and Chuck Amsler for organizing the symposium and for facilitating field work by R.B.A. at McMurdo Station. Our paleontological work was made possible through the generous cooperation of the Argentine Air Force's 1994 summer contingent at Base Marambio, Seymour Island. Comments from Chuck Amsler, Alistair Crame, Paul Dayton, Rich Mooi, David Pawson, Andrew Smith, and two anonymous reviewers clarified a number of issues relating to this paper. Thad Murdoch and Carolyn Wood prepared the illustrations. This work was funded by National Science Foundation grants OPP-9413295 and OPP-9908828 to R.B.A., and OPP-9315297 and OPP-9908856 to D.B.B. This is Contribution No. 316 from the Daphin Island Sea Lab.

REFERENCES

- Allmon, W. D., J. C. Neih, and R. D. Norris. 1990. Drilling and peeling of turritelline gastropods since the Late Cretaceous. *Palaeontology* 33:595–611.
- Amsler, C. D., J. B. McClintock, and B. J. Baker. 1999. An antarctic feeding triangle: Defensive interactions between macroalgae, sea urchins, and sea anemones. *Mar. Ecol. Prog. Ser.* 183:105–114.
- Arntz, W. E., T. Brey, and V. A. Gallardo. 1994. Antarctic zoobenthos. *Oceanogr. Mar. Biol. Ann. Rev.* 32:241–304.
- Arntz, W. E., J. Gutt, and M. Klages. 1997. Antarctic marine biodiversity. In B. Battaglia, J. Valencia, and D. W. H. Walton (eds.), *Antarctic communities: Species, structure and survival*, pp. 3–14. Cambridge University Press, Cambridge, England.
- Aronson, R. B. 1987. Predation on fossil and Recent ophiuroids. *Paleobiology* 13:187–192.
- Aronson, R. B. 1988. Palatability of five Caribbean ophiuroids. *Bull. Mar. Sci.* 43:93–97.
- Aronson, R. B. 1989a. Brittlestar beds: Low-predation anachronisms in the British Isles. *Ecology* 70:856–865.
- Aronson, R. B. 1989b. A community-level test of the Mesozoic marine revolution theory. *Paleobiology* 15:20–25.
- Aronson, R. B. 1990. Onshore–offshore patterns of human fishing activity. *Palaios* 5:88–93.
- Aronson, R. B. 1991a. Ecology, paleobiology and evolutionary constraint in the octopus. *Bull. Mar. Sci.* 49:245–255.
- Aronson, R. B. 1991b. Predation, physical disturbance, and sublethal arm damage in ophiuroids: A Jurassic–Recent comparison. *Mar. Ecol. Prog. Ser.* 74:91–97.
- Aronson, R. B. 1992. Biology of a scale-independent predator-prey interaction. *Mar. Ecol. Prog. Ser.* 89:1–13.
- Aronson, R. B. 1994. Scale-independent biological processes in the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 32:435–460.
- Aronson, R. B., D. B. Blake, and T. Oji. 1997. Retrograde community structure in the late Eocene of Antarctica. *Geology* 25:903–906.
- Aronson, R. B. and C. A. Harms. 1985. Ophiuroids in a Bahamian saltwater lake: The ecology of a Paleozoic-like community. *Ecology* 66:1472–1483.
- Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* 247:198–201.
- Bambach, R. K. 1993. Seafood through time: Changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* 19:372–397.
- Berggren, W. A., D. V. Kent, C. C. Swisher III, and M.-P. Aubry. 1995. A revised Cenozoic geochronology and chronostratigraphy. In W. A. Berggren, D. V. Kent, M.-P. Aubry, and J. Hardenbol (eds.), *Geochronology, time scales and global stratigraphic correlation*, pp. 129–212. SEPM Spec. Pub. 54, Tulsa.
- Blake, D. B. and R. B. Aronson. 1998. Stelleroida of the late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *J. Paleont.* 72:339–353.
- Bottjer, D. J. and W. I. Ausich. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology* 12:400–420.
- Bottjer, D. J. and D. Jablonski. 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* 3:540–560.
- Brett, C. E., H. A. Moffat, and W. L. Taylor. 1997. Echinoderm taphonomy, taphofaces, and Lagerstätten. In J. A. Waters and C. G. Maples (eds.),

- Geobiology of echinoderms*. Paleont. Soc. Pap. 3: 147–190.
- Brey, T. and A. Clarke. 1993. Population dynamics of marine benthic invertebrates in antarctic and sub-antarctic environments: Are there unique adaptations? *Antarctic Sci.* 5:253–266.
- Brey, T., C. Dahm, M. Gorny, M. Klages, M. Stiller, and W. E. Arntz. 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarctic Sci.* 8:3–6.
- Brey, T., J. Pearse, L. Basch, J. McClintock, and M. Slattery. 1995. Growth and production of *Sterechinus neumayeri* in McMurdo Sound, Antarctica. *Mar. Biol.* 124:279–292.
- Cadée, G. C., S. E. Walker, and K. W. Flessa. 1997. Gastropod shell repair in the intertidal of Bahía la Choya (N. Gulf of California). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 136:67–78.
- Clarke, A. 1983. Life in cold water: The physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Ann. Rev.* 21:341–453.
- Clarke, A. 1993. Temperature and extinction in the sea: A physiologist's view. *Paleobiology* 19:499–518.
- Clarke, A. and J. A. Crame. 1992. The Southern Ocean benthic fauna and climate change: A historical perspective. *Phil. Trans. Roy. Soc. Lond. B* 338: 299–309.
- Clymer, A. K., D. M. Bice, and A. Montanari. 1996. Shocked quartz from the late Eocene: Impact evidence from Massignano, Italy. *Geology* 24:483–486.
- Cocozza, D. and C. M. Clarke. 1992. Eocene microplankton from La Meseta Formation, northern Seymour Island. *Antarctic Sci.* 4:355–362.
- Crame, J. A. 1999. An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. *Sci. Mar.* 63 (Suppl. 1):1–14.
- Crame, J. A. 2000. Evolution of taxonomic diversity gradients in the marine realm: Evidence from the composition of Recent bivalve faunas. *Paleobiology* 26:188–214.
- Dayton, P. K. 1990. Polar benthos. In W. O. Smith, Jr. (ed.), *Polar oceanography*, Part B: *Chemistry, biology, and geology*, pp. 631–685. Academic Press, San Diego.
- Dayton, P. K., B. J. Mordida, and F. Bacon. 1994. Polar marine communities. *Amer. Zool.* 34:90–99.
- Dayton, P. K. and J. S. Oliver. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197:55–58.
- Dayton, P. K., G. A. Robilliard, R. T. Paine, and L. B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* 44:105–128.
- Dearborn, J. H. 1977. Foods and feeding characteristics of antarctic asteroids and ophiuroids. In G. A. Llano (ed.), *Adaptations within antarctic ecosystems*, pp. 293–326. 3rd SCAR Symp. on Antarctic Biology, Smithsonian Institution, Washington, D.C.
- Dell, R. K. 1972. Antarctic benthos. *Adv. Mar. Biol.* 10:1–216.
- DeWitt, H. H. 1971. Coastal and deep-water fishes of the Antarctic. *Antarctic Map Folio Ser.* 15:1–10.
- Diester-Haass, L., and R. Zahn. 1996. Eocene-Oligocene transition in the Southern Ocean: History of water mass circulation and biological productivity. *Geology* 24:163–166.
- Dudley, E. C. and G. J. Vermeij. 1978. Predation in time and space: Drilling in the gastropod *Turritella*. *Paleobiology* 4:436–441.
- Eastman, J. T. and A. Clarke. 1998. A comparison of adaptive radiations of Antarctic fish with those of nonAntarctic fish. In G. di Prisco, E. Pisano, and A. Clarke (eds.), *Fishes of Antarctica: A biological review*, pp. 3–26. Springer-Verlag Italia, Milan.
- Elliot, D. H. and T. A. Trautman. 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula. In C. Craddock (ed.), *Antarctic geoscience*, pp. 287–297. University of Wisconsin Press, Madison.
- Feldmann, R. M. and J. A. Crame. 1998. The significance of a new nephropid lobster from the Miocene of Antarctica. *Palaeontology* 41:807–814.
- Feldmann, R. M. and M. T. Wilson. 1988. Eocene decapod crustaceans from Antarctica. In R. M. Feldmann and M. O. Woodburne (eds.), *Geology and paleontology of Seymour Island, Antarctic Peninsula*, pp. 465–488. *Geol. Soc. Am. Mem.* 169, Boulder.
- Fell, H. B. 1961. The fauna of the Ross Sea. Part 1. Ophiuroidea. *N.Z. Dept. Sci. Ind. Res. Bull.* 142: 1–79.
- Fell, H. B., T. Holtzinger, and M. Sherraden. 1969. Ophiuroidea. *Antarctic map folio ser.* 11:42–43.
- Fordyce, R. E. 1989. Origins and evolution of Antarctic marine mammals. In J. A. Crame (ed.), *Origins and evolution of the Antarctic biota*, pp. 269–291. *Geol. Soc. Spec. Pub.* 47, London.
- Fratt, D. B. and J. H. Dearborn. 1984. Feeding biology of the antarctic brittle star *Ophionotus victoriae* (Echinodermata: Ophiuroidea). *Polar Biol.* 3:127–139.
- Fujita, T. and S. Ohta. 1990. Size structure of dense populations of the brittle star *Ophiura sarsii* (Ophiuroidea: Echinodermata) in the bathyal zone around Japan. *Mar. Ecol. Prog. Ser.* 64:113–122.
- Gazdzicki, A., M. Gruszczynski, A. Hoffman, K. Malkowski, S. A. Marensi, S. Halas, and A. Tatur. 1992. Stable carbon and oxygen isotope record in the Paleogene La Meseta Formation, Seymour Island, Antarctica. *Antarctic Sci.* 4:461–468.
- Graus, R. R. 1974. Latitudinal trends in the shell characteristics of marine gastropods. *Lethaia* 7:303–314.
- Hansen, T. A. and P. H. Kelley. 1995. Spatial variation of naticid gastropod predation in the Eocene of North America. *Palaaios* 10:268–278.
- Harper, E. M. 1991. The role of predation in the evolution of cementation in bivalves. *Palaeontology* 34:455–460.
- Hutchinson, G. E. 1961. The biologist poses some problems. In M. Sears (ed.), *Oceanography*, pp. 85–94. American Association for the Advancement of Science, Washington, D.C.
- Jablonski, D. 1989. The biology of mass extinction: A paleontological view. *Phil. Trans. Roy. Soc. Lond. B* 325:357–368.
- Jablonski, D. 1993. The tropics as a source of evolutionary novelty through geological time. *Nature* 364:142–144.
- Jablonski, D. and D. J. Bottjer. 1983. Soft-bottom epi-

- faunal suspension-feeding assemblages in the Late Cretaceous: Implications for the evolution of benthic paleocommunities. In M. J. S. Tevesz and P. L. McCall (eds.), *Biotic interactions in Recent and fossil benthic communities*, pp. 747–812. Plenum Press, New York.
- Jablonski, D. and D. J. Bottjer. 1990. Onshore-offshore trends in marine invertebrate evolution. In R. M. Ross and W. D. Allmon (eds.), *Causes of evolution: A paleontological perspective*, pp. 21–75. University of Chicago Press, Chicago.
- Jablonski, D. and D. J. Bottjer. 1991. Environmental patterns in the origins of higher taxa: The post-Paleozoic fossil record. *Science* 252:1831–1833.
- Kabat, A. R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32:155–193.
- Kelley, P. H. 1991. Apparent cannibalism by Chesapeake Group naticid gastropods: A predictable result of selective predation. *J. Paleont.* 65:75–79.
- Kelly, P. H. and T. A. Hansen. 1993. Evolution of the naticid gastropod predator-prey system: An evaluation of the hypothesis of escalation. *Palaaios* 8: 358–375.
- Kelly, P. H. and T. A. Hansen. 1996. Naticid gastropod prey selectivity through time and the hypothesis of escalation. *Palaaios* 11:437–445.
- Kelley, P., C. Thomann, T. Hansen, R. Aronson, and D. Blake. 1997. A world apart but not so different: Predation by naticid gastropods in Antarctica and the U.S. Gulf Coast during the Eocene (abstract). *Geol. Soc. Am. Abst. Prog.* 29:A107.
- Kennett, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the Circum-Antarctic Ocean, and their impact on global paleoceanography. *J. Geophys. Res.* 82:3843–3860.
- Kennett, J. P. and D. A. Warnke. (eds.) 1992. *The Antarctic paleoenvironment: A perspective on global change*, Part 1. Antarctic Res. Ser. 56. American Geophysical Union, Washington, D.C.
- Kitching, J. A., L. Muntz, and F. J. Ebling. 1966. The ecology of Lough Ine. XV. The ecological significance of shell and body forms in *Nucella*. *J. Anim. Ecol.* 35:113–126.
- Lawver, L. A., L. M. Gahagan and M. F. Coffin. 1992. The development of paleoseaways around Antarctica. In J. P. Kennett and D. A. Warnke (eds.), *The Antarctic paleoenvironment: A perspective on global change*, Part 1, pp. 7–30. Antarctic Res. Ser. 56. American Geophysical Union, Washington, D.C.
- Lear, C. H., H. Elderfield, and P. A. Wilson. 2000. Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science* 287:269–272.
- Leighton, L. R. 1999. Possible latitudinal predation gradient in middle Paleozoic oceans. *Geology* 27: 47–50.
- Long, D. J. 1992. Paleoecology of Eocene antarctic sharks. In J. P. Kennett and D. A. Warnke (eds.), *The Antarctic paleoenvironment: A perspective on global change*, Part 1, pp. 131–139. Antarctic Res. Ser. 56. American Geophysical Union, Washington, D.C.
- Long, D. J. 1994. Quaternary colonization or Paleogene persistence?: Historical biogeography of skates (Chondrichthyes: Rajidae) in the Antarctic ichthyofauna. *Paleobiology* 20:215–228.
- Mackensen, A. and W. U. Ehrmann. 1992. Middle Eocene through early Oligocene climate history and paleoceanography in the Southern Ocean: Stable oxygen and carbon isotopes from ODP sites on Maud Rise and Kerguelen Plateau. *Mar. Geol.* 108:1–27.
- Marcellari, C. E. 1988. Stratigraphy, sedimentology, and paleoecology of Upper Cretaceous/Paleocene shelf-deltaic sediments of Seymour Island. In R. M. Feldmann and M. O. Woodburne (eds.), *Geology and paleontology of Seymour Island, Antarctic Peninsula*, pp. 25–53. *Geol. Soc. Am. Mem.* 169, Boulder.
- Martin, R. E. 1998. *One long experiment: Scale and process in earth history*. Columbia University Press, New York.
- McClintock, J. B. 1994. Trophic biology of antarctic shallow-water echinoderms. *Mar. Ecol. Prog. Ser.* 111:191–202.
- McClintock, J. B. and B. J. Baker. 1997. A review of the chemical ecology of antarctic marine invertebrates. *Amer. Zool.* 37:329–342.
- McClintock, J. B. and B. J. Baker. 1998. Chemical ecology in antarctic seas. *Am. Sci.* 86:254–263.
- McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281: 210–217.
- Meyer, D. L. 1985. Evolutionary implications of predation on Recent comatulid crinoids from the Great Barrier Reef. *Paleobiology* 11:154–164.
- Meyer, D. L. and D. B. Macurda, Jr. 1977. Adaptive radiation of the comatulid crinoids. *Paleobiology* 3:74–82.
- Meyer, D. L. and T. Oji. 1993. Eocene crinoids from Seymour Island, Antarctic Peninsula: Paleobiogeographic and paleoecologic implications. *J. Paleont.* 28:250–257.
- Nichols, D. 1996. Evidence for a sacrificial response to predation in the reproductive strategy of the comatulid crinoid *Antedon bifida* from the English Channel. *Oceanol. Acta* 19:237–240.
- Oji, T. 1985. Early Cretaceous *Isocrinus* from northeast Japan. *Palaentology* 28:629–642.
- Oji, T. 1996. Is predation intensity reduced with increasing depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution. *Paleobiology* 22:339–351.
- Oji, T. and T. Okamoto. 1994. Arm autotomy and arm branching pattern as anti-predatory adaptations in stalked and stalkless crinoids. *Paleobiology* 20: 27–39.
- Palmer, A. R. 1979. Fish predation and the evolution of gastropod shell sculpture: Experimental and geographical evidence. *Evolution* 33:697–713.
- Palmer, A. R. 1981. Do carbonate skeletons limit the rate of body growth? *Nature* 292:150–152.
- Pearse, J. S. and I. Bosch. 1994. Brooding in the Antarctic: Östergren had it nearly right. In B. David, A. Guille, J.-P. Féral, and M. Roux (eds.), *Echinoderms through time*, pp. 111–120. Balkema, Rotterdam.
- Picken, G. B. 1980. Reproductive adaptations of Ant-

- arctic benthic marine invertebrates. *Biol. J. Linn. Soc.* 14:67–75.
- Picken, G. B. 1985. Marine habitats—benthos. In W. N. Bonner and D. W. H. Walton (eds.), *Key environments—Antarctica*, pp. 154–172. Pergamon, Oxford.
- Poag, C. W. 1997. Roadblocks on the kill curve: Testing the Raup hypothesis. *Palaos* 12:582–590.
- Porebski, S. J. 1995. Facies architecture in a tectonically-controlled incised-valley estuary: La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula. *Stud. Geol. Polon.* 107:7–97.
- Porebski, S. J. 2000. Shelf-valley compound fill produced by fault subsidence and eustatic sea-level changes, Eocene La Meseta Formation, Seymour Island, Antarctica. *Geology* 28:147–150.
- Poulin, É. and J.-P. Féral. 1996. Why are there so many species of brooding antarctic echinoids? *Evolution* 50:820–830.
- Prothero, D. R. 1989. Stepwise extinctions and climatic decline during the later Eocene and Oligocene. In S. K. Donovan (ed.), *Mass extinctions: Processes and evidence*, pp. 217–234. Columbia University Press, New York.
- Prothero, D. R. 1994. *The Eocene-Oligocene transition: Paradise lost*. Columbia University Press, New York.
- Raup, D. M. and D. Jablonski. 1993. Geography of end-Cretaceous marine bivalve extinctions. *Science* 260:971–973.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M. L. and R. D. McCord. 1991. Incumbent replacement: Evidence for long-term evolutionary progress. *Paleobiology* 17:202–213.
- Sadler, P. M. 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. In R. M. Feldmann and M. O. Woodburne (eds.), *Geology and paleontology of Seymour Island, Antarctic Peninsula*, pp. 303–320. *Geol. Soc. Am. Mem.* 169, Boulder.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095–2097.
- Schoener, T. W. 1979. Inferring properties of predation and other injury-producing agents from injury frequencies. *Ecology* 60:1110–1115.
- Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc. Nat. Acad. Sci., U.S.A.* 83:6897–6901.
- Sepkoski, J. J., Jr. 1991. Diversity in the Phanerozoic oceans: A partisan view. In E. C. Dudley (ed.), *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*, Vol. 1, pp. 210–236. Dioscorides Press, Portland, Oregon.
- Signor, P. W., III and C. E. Brett. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10:229–245.
- Sih, A. 1985. Evolution, predator avoidance, and unsuccessful predation. *Am. Nat.* 125:153–157.
- Smith, A. B. 1994. *Systematics and the fossil record*. Oxford, Blackwell.
- Stanley, S. M. 1977. Trends, rates and patterns of evolution in the Bivalvia. In A. Hallam (ed.), *Patterns of evolution as illustrated by the fossil record*, pp. 209–250. Elsevier, Amsterdam.
- Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9:44–61.
- Stilwell, J. D. and W. J. Zinsmeister. 1992. *Molluscan systematics and biostratigraphy: Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula*. Antarctic Res. Ser. 55, American Geophysical Union, Washington, D.C.
- Thies, D. and W.-E. Reif. 1985. Phylogeny and evolutionary ecology of Mesozoic Neoselachii. *N. Jb. Geol. Paläont., Abh.* 169:333–361.
- Vermeij, G. J. 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology* 3:245–258.
- Vermeij, G. J. 1978. *Biogeography and adaptation: Patterns of marine life*. Harvard University Press, Cambridge, Massachusetts.
- Vermeij, G. J. 1982. Unsuccessful predation and evolution. *Am. Nat.* 120:701–720.
- Vermeij, G. J. 1987. *Evolution and escalation: An ecological history of life*. Princeton University Press, Princeton.
- Vermeij, G. J. 1989a. The origin of skeletons. *Palaos* 4:585–589.
- Vermeij, G. J. 1989b. Interoceanic differences in adaptation: effects of history and productivity. *Mar. Ecol. Prog. Ser.* 57:293–305.
- Vermeij, G. J. 1995. Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* 21:125–152.
- Vermeij, G. J., E. C. Dudley, and E. Zipser. 1989. Successful and unsuccessful drilling predation in Recent pelecypods. *Veliger* 32:266–273.
- Vermeij, G. J. and D. R. Lindberg. 2000. Delayed herbivory and the assembly of marine benthic ecosystems. *Paleobiology* 26:419–430.
- Vermeij, G. J., D. E. Schindel, and E. Zipser. 1981. Predation through geological time: Evidence from gastropod repair. *Science* 214:1024–1026.
- West, K., A. Cohen, and M. Baron. 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: Implications for lacustrine predator–prey coevolution. *Evolution* 45:589–607.
- White, M. G. 1984. Marine benthos. In R. M. Laws (ed.), *Antarctic ecology*, Vol. 2, pp. 421–462. Academic Press, London.
- Wrenn, J. H. and G. F. Hart. 1988. Paleogene dinoflagellate cyst biostratigraphy of Seymour Island, Antarctica. In R. M. Feldmann and M. O. Woodburne (eds.), *Geology and paleontology of Seymour Island, Antarctic Peninsula*, pp. 321–448. *Geol. Soc. Am. Mem.* 169, Boulder.
- Zinsmeister, W. J. and R. M. Feldmann. 1984. Cenozoic high latitude heterochroneity of Southern Hemisphere marine faunas. *Science* 224:281–283.