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Interdecadal Variation in an Antarctic Sponge and Its Predators from Oceanographic Climate Shifts

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During the 1960s there was extensive formation of anchor ice to depths of 30 meters at McMurdo Station, Antarctica. During this period the sponge *Homaxinella balfourensis* was rare, as were its predators in that depth zone. Most of the existing sponges were killed by anchor ice. During the 1970s, anchor ice formation was reduced, and there was a massive recruitment of *Homaxinella*, which covered as much as 80 percent of the substrata in that zone. Many predators appeared but did not control the sponge population, and it continued to grow through that decade. The early 1980s were characterized by ice formation and almost all of the *Homaxinella* were eliminated, leaving an order of magnitude more predators in that zone. The interdecadal increases in anchor ice probably result from local upwelling of extremely cold deep water, possibly in response to shifts in the strengths of regional currents.

Large population fluctuations with frequencies exceeding a decade often are characteristic of fishery data (*1*). They also have been observed in a few benthic and pelagic systems in which there are episodic single recruitment events that may or may not involve biotic coupling, but which have very long-lasting consequences (*2*). In most cases climatological forcing functions are assumed, but except for El Niño–induced shifts, solid data on the causes of long-term population variation often is lacking (*3*). Antarctic benthic populations are often thought to be characterized by low recruitment and slow growth and mortality rates (*4*). Here I report massive interdecadal changes in the population of an Antarctic sponge and some of its predators.

These observations were at two sites, Cape Armitage and Hut Point, in the vicinity of McMurdo Station, on the southern end of Ross Island, McMurdo Sound, Antarctica. The benthic fauna is strikingly zoned (*5*). The shallow zone (0- to 10-m depth) is relatively bare of sessile animals because it is scoured by drifting sea ice and seasonally covered with a sheet of ice growing down from the shore. In addition, this shallow zone is regularly disturbed by anchor ice. Anchor ice is composed of ice platelets, which form aggregations that may be as large as 1 to 2 m in diameter and up to 0.7 m high. Eventually the aggregation floats free of the bottom, carrying sessile organisms away. A zone from an approximately 15- to 30-m depth is disturbed occasionally by anchor ice, and the sessile fauna in this zone usually is characterized by coelenterates that are either resistant to the anchor ice or have turnover rates fast enough to allow their populations to be maintained by recruitment, or both. The anchor ice disturbance rarely occurs below 30 m, and there is thus a deeper (30- to 45-m depth) zone dominated by long-lived sponges and their predators.

The demosponge *Homaxinella balfourensis* was very rare in the intermediate 15- to 30-m zone of both study areas in 1967. Eight individuals were recorded in the over 30,000-m^2 Cape Armitage study area and all were heavily fouled with anchor ice (Fig. 1); six *Homaxinella* were observed in over 20,000 m^2 at Hut Point. By 1968 all of the Cape Armitage individuals were gone, but, while damaged by anchor ice, those at Hut Point had reproduced, and there were perhaps 100 juveniles, most of which were fouled with anchor ice. All the small individuals were conspicuously clumped under the adults, suggesting that they might be branches that had fallen off the adults (*6*).

In 1974 a massive but patchy population explosion of *Homaxinella* had occurred at Hut Point, with local patches reaching 80% cover. Despite the fact that there were no *Homaxinella* at Cape Armitage in 1968, that area also had a striking recruitment in 1974, but it was more patchy than at Hut Point and never exceeded 50% cover. By 1975 it appeared that the 1974 population had at least doubled in both sites, and three permanent transects were established in each study area. The percent cover of *Homaxinella* more than doubled along these transects between 1975 and 1977 (Fig. 2). By following individuals on the photographs, it was found that the unbranched buds or "twigs" were in their first year, whereas the much larger adult "bushes" could be several years old. The ratio of twigs to bushes in 1977 varied from six to ten per bush; clearly a massive recruitment was still under way at that time (*7*).

In an effort to evaluate the effect of anchor ice, 30 large *Homaxinella* were marked with adjacent permanent tags in 1975. By 1977 all but four had either disappeared or were badly damaged. Anchor ice damage, in which the flesh is present but discolored, is readily differentiated from predation, which

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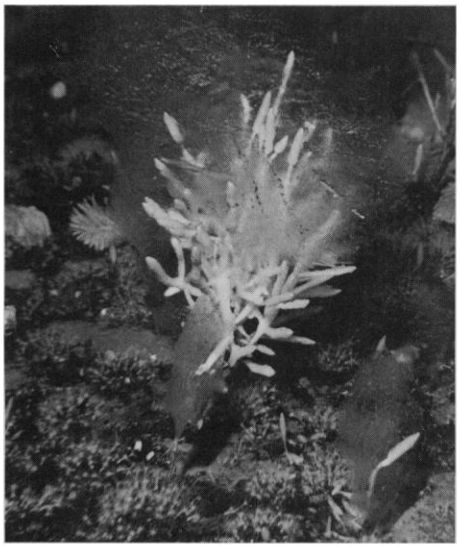

Fig. 1. Anchor ice fouling *Homaxinella balfourensis*. The white bush-like structure is the sponge and the opaque platelets are the ice.

leaves a clean spongin skeleton. Although sponges being killed by predators were observed, 87% of the tagged sponges had been lost or damaged by anchor ice in the preceding 2 years. Nevertheless, the local population was at least four times as dense as it had been 2 years earlier (7). Thus there was continuing mortality from the ice and predation, but the population continued to grow at a rate much faster than the mortality rate.

In 1984 heavy anchor ice formation was reminiscent of the 1960s, and the *Homaxinella* population was essentially eliminated, existing only as scattered individuals or small patches. Sponge percent cover on the permanent transects was very close to zero (Fig. 2). There was a 5 to 30% cover of anchor ice to depths of 25 m, and at least 60% of the bottom of the sea ice overhead had clumps of uplifted anchor ice with *Homaxinella*. More than 90% of the remaining *Homaxinella* were covered with ice. It was clear that a massive resurgence of anchor ice had almost eliminated the *Homaxinella*. In November 1988 there was very little anchor ice. There were a few areas in which it appeared that *Homaxinella* recruitment was under way, but there was not much recruitment along the actual transects (their percent cover ranging from 0.2 to 2.1%). If the low anchor ice conditions continue, the *Homaxinella* population may explode again.

The most important predators of *Homaxinella* are the asteroids *Odontaster meridionalis*, *O. validus*, and young *Perknaster fuscus antarcticus*. During the 1960s little predation on the rare *Homaxinella* was observed, and except for *O. validus* (density of 2.7 per square meter), the asteroids were rare. Only one *O. meridionalis* was seen in depths shallower than 30 m in the 1960s. All the rest of this relatively rare and small asteroid were in the deeper sponge zone (7). Similarly, only five *Perknaster* were recorded in the area. In fact, *Homaxinella* was so rare in 1967 and 1968 that we did not discuss its loss from predation. By 1974 almost half the *O. validus* were eating *Homaxinella*, and there were up to four juvenile *Perknaster* per 100 m^2; *O. meridionalis*, previously rare in the deeper zone and essentially nonexistent in the *Homaxinella* zone, ranged from two to eight per 100 m^2 in the *Homaxinella* zone in 1974. In 1977 the calculated standing crop of *Homaxinella* was 7 to 8 kg/m^2 (2000 kcal/m) (6). These were very conservative estimates, and the real values may have been almost double that. Nevertheless it is at least an order of magnitude more than the predators eat in a year (7). These asteroids eat one branch at a time and almost always leave some branches intact; thus, unless they are eating a small first-year *Homaxinella*, they usually do not kill the sponge. Even though a few other predators such as *Acodontaster conspicuus* and the nemertean *Parborlasia (=Lineus) corrugatus* had switched their diets to include *Homaxinella*, it was clear that the sponge population had escaped the functional (8) responses of their predators.

By 1984 the density of *O. validus* was about 5 per square meter, the juvenile *Perknaster* was at least 15 per 100 m^2, and the *O. meridionalis* was as high as 17 per 100 m^2. These are minimal estimates from photographic transects, and small asteroids may have been missed. More importantly, these data grossly underestimate the actual asteroid recruitment because many, perhaps most, of the asteroids that did recruit into the *Homaxinella* zone were lost when the anchor ice carried away the sponges they were on. In 1974 a small sample of *O. meridionalis* in the *Homaxinella* zone were about the same size ($\bar{x}$ 3.1 grams wet weight, SD 1.7; n = 13) as they had been in the sponge zone in the 1960s (Fig. 2B). However, in addition to causing an appar ent increase in the populations of these predators, the population explosion of *Homaxinella* also affected the sizes of these relatively tiny asteroids. Most of the individual *O. meridionalis* in the *Homaxinella* zone are almost an order of magnitude larger than those in the deeper sponge zone (Fig. 2C). It is not clear that this growth is necessarily the result of consuming *Homaxinella*, because some of the sea stars may have migrated to that site. Considering the distances involved, it seems most likely that they settled as larvae. Irrespective, the size differences are dramatic. This is interesting because *O. meridionalis* in the sponge zone had a broad diet (6), but in the *Homaxinella* zone they are more abundant and bigger and specialize on *Homaxinella*. *Odontaster validus* and especially *Perknaster* have very important community roles (6), and this strong recruitment and growth could have broad ramifications on the sponge community.

Homaxinella recruited mainly on hard substrata in the shallow zone and not on the

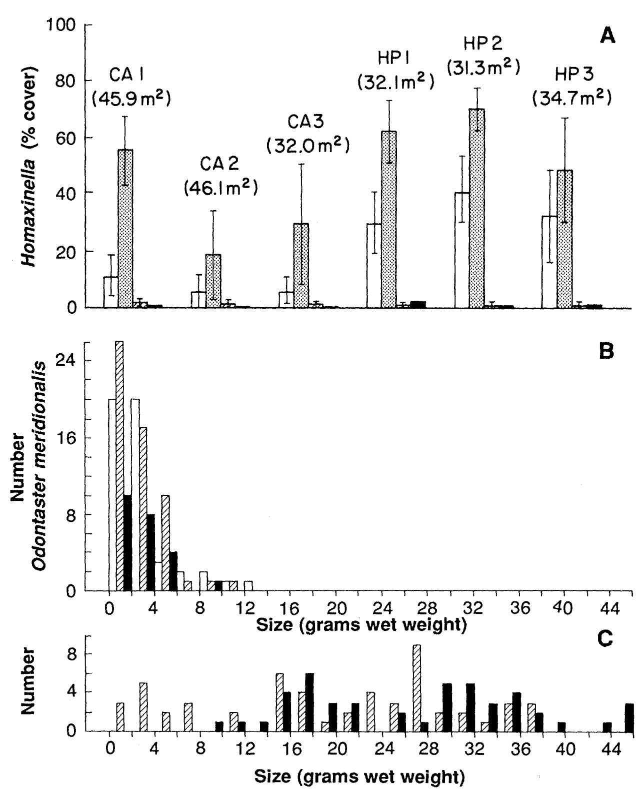

Fig. 2. (**A**) Mean percent cover of *Homaxinella* in 1975 (open bars), 1977 (stippled bars), 1984 (hatched bars), and 1988 (solid bars). Data are from ten permanent quadrats on each of three Cape Armitage (CA) and three Hut Point (HP) transects. Error bars are SD. The total transect area is listed above the histogram in parens. There were no *Homaxinella* in any of these transect areas in 1967 or 1968. (**B**) and (**C**) Size frequency of *Odontaster meridionalis* in the sponge spicule mat (B) and in the *Homaxinella* zone (C) in 1968 (open bars), 1984 (hatched bars), and 1988 (solid bars).

patches of available soft substrata in their habitat. In addition, although we had earlier thought that *Homaxinella* had limited dispersal, we have now seen at Cape Armitage in 1974 that they are very effective colonizers with at least some level of long-distance larval dispersal. In 1974 we established settling plates in all our study areas. These plates were established on the bottom and at various levels above the bottom, including many that were suspended from floats as much as 30 m above the bottom. Anchor ice virtually eliminated the *Homaxinella* from their adjacent natural habitat by 1984, but they had recruited in great numbers on the floating substrata. Whereas this is very suggestive of effective planktonic larval dispersal, it is significant that none of the settling plates had *Homaxinella* during the 1970s when they colonized the natural benthic habitat so heavily. An alternative hypothesis could be that the *Homaxinella* have demersal larvae that were released by those sponges already uplifted by the anchor ice. During strong uplifting episodes such as we observed in 1984, there can be a high cover of uplifted anchor ice with the *Homaxinella* in the platelet layer above, presumably able to release larvae that, even if demersal, could rain down on the settling plates below. The larvae should also settle on the sponge spicule mat, but fail to survive there, perhaps because of predators living in the mat.

A more perplexing example of dispersal was observed in the oligotrophic New Harbor (*9*) site in 1984. It is mostly a soft-bottom habitat where, despite extensive work in the 1970s, we observed no *Homaxinella* on the bottom. Between 1974 and 1977 our settling plate arrays at New Harbor collected nothing but two serpulid polychaetes, and the plates were reported to be bare in 1979 (*10*). But in 1984 all of the settling surfaces were heavily covered with several species of bryozoans, hydroids, soft corals, and sponges, including *Homaxinella balfourensis*, for which the only local source of larvae was the few small sponges that had fouled the pectinid *Adamussium colbecki* or the cidarid sea urchin, *Austrocidaris canaliculata*. We have no documentation of this epizoic *Homaxinella* density, but we do maintain transects that cover over 1000 m^2 at this site, and there were never any *Homaxinella* seen on these transects, so their density seems very low to be the source for such heavy recruitment. These observations suggest a strongly swimming larva and a shift in the currents, which advect larvae from another source area. But then why was there not any *Homaxinella* on the settling plates at McMurdo Station during the 1970s, when there was such strong recruitment on the nearby benthos? One hypothesis is that the larvae are demersal, but are susceptible to resuspension and transport by benthic storms and strong wind-driven currents that may have been absent during the 1970s and strong during the early 1980s, or both. Some form of internal waves (*11*) may also have contributed. There are no physical data to evaluate these hypotheses.

This sort of population explosion followed by catastrophic decline has never been observed for sponge populations. In this case the apparent *Homaxinella* augmentation of the predator populations may have at least some local community effect because some of the asteroids have important community roles (*6*). Anchor ice is also well known to have important biological and geological roles in the Arctic (*12*) and is probably the main cause of the *Homaxinella* cycle. The early 1960s were marked by exceptionally heavy ice conditions, and in 1963 the annual sea ice in this region had not broken loose in at least 3 years (*13*). The subice platelet layer was as much as 2 to 3 m thick in 1963 and 1964 and 1967 and 1968, and anchor ice was an obvious and active disturbance agent in depths above 30 m (*5*). In the 1970s there was virtually no subice platelet layer and although anchor ice was always seen, it was at least an order of magnitude less abundant. The thickness of the subice platelet layer correlates with abundance of anchor ice, and the subice platelet layer was reported to be almost nonexistent in 1980 and 1981, but thick (1 to 2 m) in 1982 and 1983 (*14*). Thick platelet ice and anchor ice in 1984 was reminiscent of the 1960s. In contrast, there was less anchor ice in 1988 than I have ever seen.

Physical processes ultimately cause most episodic events; here, shifts in ocean climate are controlling benthic biological dynamics. The formation of frazil ice and anchor ice in this region is a result of cooling of the water by contact or proximity to the Ross Ice Shelf at depth, then freezing out as the water mass moves into shallow depths where the release in pressure raises the in situ freezing point (*15*). It may be significant that Lewis and Perkin (*16*) calculated a mean northward flow for the east Sound in November 1982, whereas Barry and Dayton observed a mean southward flow in 1984 and argued that this may be the more general pattern. The currents of McMurdo Sound are dominated by oscillatory tidal flows, but there is no straightforward explanation why net northward flow of cold deep water, apparently resulting in heavy anchor ice formation, dominated the 1960s and early 1980s, but not the 1970s. Although tidal currents should not have that much interannual variation, geostrophic and other aperiodic currents, such as the East Wind Drift (and its associated coastal flow along the Ross Ice Shelf), reflect large-scale atmospheric and oceanic dynamics that have considerable interannual variation. Barry and Dayton speculate that changes in zonal winds associated with the 1982 to 1983 El Niño–Southern Oscillation (ENSO) event modified the circulation pattern within McMurdo Sound during that period. This may account for the strong northward flow seen by Lewis and Perkin, which coincided with the beginning of strong platelet ice formation after a decade of low anchor ice and platelet ice formation. This could be an example of large-scale physical processes exerting profound biological effects over long time periods.

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