

**TOWARD AN UNDERSTANDING OF COMMUNITY
RESILIENCE AND THE POTENTIAL EFFECTS OF
ENRICHMENTS TO THE BENTHOS AT
McMURDO SOUND, ANTARCTICA**

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INTRODUCTION

There is increasing concern about the potential effects of pollution on undisturbed Antarctic communities such as the nearshore benthic community of McMurdo Sound. Of particular interest are the potential effects on this community of organic enrichment from the sewage from McMurdo Station. In order to predict and evaluate these effects correctly and efficiently, it is necessary to understand clearly the sorts of mechanisms that are basic to maintenance of community organization and the methodology appropriate for determining how the particular organizing mechanisms respond to increased nutrients from an extended source. In the first section of this paper, I include a discussion and summary of ecological principles which have proven essential to understanding the basis of the resilience of some communities to outside perturbations. This discussion is necessary because ecologists often make statements about community organization which are based on measurements of irrelevant or insufficient parameters. In the second section I have applied some of these general insights to a specific consideration of the conservation problem at McMurdo Sound.

There is a pressing need for predictive powers at the community level in order to judge the potential effects of particular pollutants or disturbances on ecological communities. Because of the extreme complexities of most natural communities, such predictions are rarely possible. Often attempts at such predictions are confused by the use of the wrong approaches to community study. In the hierarchy of biological organization, populations and communities represent the two most complex levels amenable to study. Confusion has arisen because historically much biological training and research have been directed toward the study of the individual organism, its organ systems, and the physical and chemical interactions between and within its cells. It is a widely appreciated fact that communities are composed of interacting and variously interdependent components, but so far as determination of the organization of the community is concerned, the components are

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populations, not individuals. The effect of a perturbation on a community must be manifested through changes in such population parameters as mortality and natality rates. Physiological data can contribute to the prediction of the effects of such a perturbation only by yielding new information on changes in population rate phenomena.

Solely descriptive or structural approaches to community composition have also misplaced the emphasis of community organization; it is not possible to extrapolate a functional appreciation of community organization solely from species lists or distributions. Because populations are dynamic units with widely differing effects on other populations, such static description, regardless of how accurately compiled, can not predict the effects on the whole community of a given perturbation. As an example of how misleading a static description can be, an accurate map of certain parts of Australia today shows the cactus *Opuntia* to be quite rare and *Cactoblastis*, its caterpillar predator, even more rare; but in the same area, the *Opuntia* is known to have the potential to alter markedly much of the community, as it was at one time a serious pest which displaced much of the native vegetation (Dodd, 1940, reference not available).

Another well documented example involves the Klamath weed, *Hypericum perforatum*, which was introduced into California and became a serious economic pest. It was controlled by the beetle, *Chrysomela gemellata*. A careful descriptive study of infested fields today would probably not find any *Chrysomela* and would find *Hypericum* to be a rare species occurring only in shaded patches of the field. The conclusion from this static descriptive study might be that *Hypericum* is not a potentially important species to the community and is possibly shade adapted. In this case, however, it is known that *Hypericum* is able to displace the native species and that it thrives best in the sun. But *Chrysomela* is most effective in the sun; the fact that *Hypericum* is found in the shade is best explained by the fact that the beetle is less effective there, allowing *Hypericum* a partial refuge (Huffacker and Kennett, 1959). There are many examples of this kind of phenomenon, and it seems obvious that one could be badly misled about the potential importance of organisms in a community by static, descriptive studies.

Population Regulation and Biological Interactions

The interpretation of community structure depends upon an understanding of the factors determining population patterns of abundance and distribution in time and space. It is clear that a mechanistic appreciation of such community organization rests upon a knowledge of the functional roles of the various populations in the

growth and regulation of other populations in the community. There are two classically understood mechanisms by which the growth of populations is regulated. Populations may be limited when some requisite resource is in short supply, or they may be limited by disturbances operating somewhat independently of the resources which otherwise potentially limit the populations. In the former situation, the population is said to be limited by either intra- or interspecific competition. In the latter situation the disturbance limits the growth of the population before any resource becomes limiting.

Assuming no immigration or emigration, the two parameters necessary to describe the change in size of a population are the birth rate and the death rate. Any factor altering either of these rates can have important implications to the population. Changes in the birth rate frequently are much more difficult to evaluate and are much more important to the population than are changes in the death rate (Cole, 1954). Unfortunately it is true that in most cases a major effect of pollution is to alter the birth rate through various subtle physiological stresses on the individual. This can rarely be observed in the field and is an example of an area of interest in which physiological research has much to offer regarding the effects of pollution on the community.

Assuming that it is possible to describe a perturbation and identify its immediate or proximal effect on a given population, in addition we usually wish to predict its effect on the integrated community. Such a prediction must be based on a knowledge of the functional roles in the community of the affected populations in terms of their effects on the growth and regulation of other populations in the community. Unfortunately, because of the very long generation times of most of the species in many communities, such roles are usually impossible to define experimentally. Insights into these roles can be deduced, however, by classifying the component populations of communities into trophic levels linked by food webs which tend to be the basis for organization of the components into functional relationships.

In summary, then, the central goal of research concerning the ecological effects of a given pollutant is to predict the ultimate effect on the community (or, eventually, the ecosystem) of the particular population changes caused by the pollutant. Realizing this goal involves a knowledge of what the pollutant will do to the affected populations and how resilient the community will be to the changes. Since different pollutants will have different effects on different species, I cannot generalize about these effects; rather, I will direct my discussion to the general question of community resilience, and will then discuss certain specific and predictable effects of enrichment on the benthic community at McMurdo Sound.

Community Resilience and the Foundation Species

Two overlapping but somewhat different concepts of community stability should be differentiated at this point. The first and most common concept is that which considers a high level of stability to mean that the system is relatively constant through time — that is, the relative abundances of the populations do not have large, random fluctuations over time. By this view, a stable system is one in which the natural periodicity is predictable over time. The second concept concerns the ability of the community to resist and recover from external perturbations. The second concept is clearly related to but does not necessarily follow from the first, and although it is much more complex, I think that it is also more useful, as it recognizes the fact that all populations naturally undergo long- and short-term fluctuations and that it is often very difficult to differentiate natural flux due to demographic time lags from population changes resulting from an external perturbation. In this view, then, no community is stable in the sense that it does not change. Rather the relative sizes of the populations and the magnitudes of their interactions are in constant flux; but so long as the changes and fluxes remain within certain bounds, the system persists.

One of the generalizations resulting from the few existent experimental community studies is that most of the communities so studied have key or foundation species which have roles in the maintenance of the community disproportionate to the abundance or biomass of the species. For example, Dodson (1970) has found that the composition of species which he finds in certain alpine lakes depends on the presence or absence of one key species. In this case the key species is a salamander whose larvae are very effective size-selective predators. This selective predation by the salamander excludes the larger prey from the lakes and allows the existence of suboptimal, smaller prey, which apparently are replaced by the preferred larger prey in the absence of the salamander larvae. The presence of the salamander larvae with the concurrent presence of the smaller prey favors the presence of a second, dependent predator. Thus the population of salamander larvae structures the entire planktonic community. Similar planktonic dependence upon fish predators in experimental ponds was demonstrated by the intensive study of Hall, Cooper, and Werner (1970).

Another well-studied community is that of the rocky intertidal zone where competitive dominants and their predators have been well delineated. In Millport, Scotland, *Balanus balanoides* is a dominant competitor for space but is a preferred prey species of *Thais lapillus* (Connell, 1961a,b). In the Washington state intertidal community Paine

(1966) and I (1971) have found a well-defined competitive hierarchy in which *Balanus cariosus* dominates both *B. glandula* and *Chtamalus dalli*, while *B. glandula* also dominates *C. dalli* in the competition for space. In the upper intertidal all the barnacles dominate the space competition with algae. The mussel, *Mytilus californianus*, requires a secondary substrate (algae or barnacles) for settlement, but once established, it dominates the primary space in the higher intertidal in the exposed outer coast community by overgrowing the barnacles and the algae. Paine has demonstrated in this area that by preferentially preying on *Mytilus*, the asteroid *Pisaster ochraceus*, is responsible for the continued coexistence of *Mytilus* and the other sessile species. There are also areas in the community more exposed to wave action where the *Mytilus* have, at least temporarily, grown too large for *Pisaster* to prey upon them effectively. There are other more protected areas where neither *Mytilus* nor *Pisaster* is abundant, and here *Balanus cariosus* has an escape in growth from its predators and potentially dominates the competition for space. In both areas free space is maintained as a result of bashing by drift logs (Dayton, 1971). Thus in this community a number of species, including the competitive dominants, *Balanus cariosus* and *Mytilus californianus*, and the disturbances provided by *Pisaster* and logs, which prevent the monopolization of space, are key factors in the continued maintenance of the observed community. There are well over 93 species of macroscopic organisms in this community (Glynn, 1965), yet the maintenance of the observed structure of this community depends upon the populations of relatively few species. Because of its important role, Paine (1969) has called *Pisaster* a "keystone" species; following this example, I will refer to the group of critical species which define much of the structure of a community as "foundation" species.

In the lower intertidal on the Washington coast, Paine and Vadas (1969) and I (1972) determined that such foundation species also exist in the algal community. Here there is one clear competitive dominant in most areas, *Hedophyllum sessile*, which, depending on the exposure to wave action, dominates the algal association. Further, the presence of *Hedophyllum* allows the existence of a group of "obligate understory" species which depend on *Hedophyllum* for protection from desiccation; in the absence of *Hedophyllum* these are replaced by a sequence of many algae which behave as fugitive species (Hutchinson, 1951). While there are many herbivore species, the only animal capable of over-exploiting *Hedophyllum* as a food source is the sea urchin, *Strongylocentrotus purpuratus*. The grazing of large (to 30 m²) and dense (to 264/m²) aggregations of these sea urchins in some areas prevents the growth of any algae except one or two species of

encrusting coralline algae. However, clear areas in the urchin patches are provided by *Pycnopodia helianthoides*, the urchin's asteroid predator. After being cleared of sea urchins, these patches are recolonized by algal species. So again, this community is most critically structured by identifiable foundation species, including the competitive dominant, *Hedophyllum sessile*, its only effective herbivore, *Strongylocentrotus purpuratus*, and the most important predator upon urchins, *Pycnopodia helianthoides*. And again, there are at least 40 species of algae and 12 species of molluscan herbivores whose patterns of distribution and abundance are largely dictated by the effects of these foundation species.

The most important point for the present discussion is that in all the communities which have been experimentally manipulated, one can demonstrate that certain foundation species are disproportionately important to the continued maintenance of the existent community structure. These foundation species usually include those species actually contributing most of the spatial structure of the community, the competitive dominants, and the disturbers preventing their domination. In most communities these foundation species strongly influence the boundaries of the normal drift and flux of the population densities in the community. Thus, perturbations to the community have the most serious consequences if they affect the birth rates or death rates of these foundation species. It is obviously important that ecologists, when studying the effects of pollution, identify the foundation species and evaluate the effects of the perturbation on their populations.

Identification of Foundation Species at McMurdo Sound

The benthic community between 33 and 60 m at Cape Armitage, McMurdo Sound, is composed primarily of many species of sponges and their various asteroid and molluscan predators (Dayton, Robilliard, and Paine, 1970). It is also characterized by an extremely predictable physical environment (Littlepage, 1965; Dayton, Robilliard, and DeVries, 1969). The predictability of the physical environment suggests that biological interactions have been and continue to be the dominating factors in the evolution and maintenance of the community. This community is of particular ecological interest because most of the conspicuous sessile species share primary substratum as their most important potentially limiting resource. The successful utilization of the resource can easily be quantified in a two dimensional sense. The community appears to be amendable to accurate food chain quantification because the important predators are molluscs and asteroids which move and digest slowly; this facilitates the quantification of their abundances, distributions, and diets.

Our cage studies, designed to quantify the effects of predation in the McMurdo Sound benthic community, generally yielded inconclusive results over the period of one year because of the very slow growth and consumption rates. However, one predator exclusion cage demonstrated that one species of sponge *Mycale acerata*, has a much faster growth rate than other sponge species. This implies that *M. acerata* is potentially the dominant species in competition for primary substratum. In support of this hypothesis, we have many observations of this sponge having grown over and apparently either having killed or been in the process of killing other sponges such as *Rossella nuda*, *R. racovitzae*, *Scolymastra joubini*, *Haliclona dancoi*, *Polymastia invaginata*, *Kirkpatrickia variolosa*, and *Calyx arcuarius*, the anemones *Hormathia lucunifera* and *Artemidactis victrix*, and the solitary tunicate *Cnemidocarpa verrucosa*. While it seems quite probable that *Mycale* is potentially the dominant space consumer in the community, it is nevertheless rare, comprising less than 2% of the total sponge cover and less than 3% of the biomass. *Mycale* is a minor component of the diets of *Odontaster validus*, *O. meridionalis*, and *Acodontaster conspicuus*, but a major prey item of *Perknaster fuscus antarcticus*. It seems likely that *Perknaster* and *Acodontaster* predation is largely responsible for preventing *Mycale* from dominating the space resource (Dayton, Robilliard, Paine, and Dayton, 1972). Representative examples of a number of these molluscs and asteroids, including some of their interactions, are shown in Figures 1-7.

While the abundance of *Mycale* appears to be held at a low level (relative to its ability to dominate in competition) by predation, one group of rossellid sponges (*Rossella racovitzae*, *R. nuda*, and *Scolymastra joubini*) comprises 82% of the sponge cover and 89% of the biomass. The opisthobranch *Austrodoris McMurdoensis* and the asteroid *Acodontaster conspicuus* commonly prey on these sponges which contribute so importantly to the biomass and the structure of the community. A cage inclusion experiment demonstrated that three *A. conspicuus* are capable of killing within one year a large rossellid sponge, probably *Scolymastra joubini* (which was not differentiated from *R. nuda* in the field). Our energetics data demonstrate that because of its abundance and size, *A. conspicuus* could be a very effective predator of the rossellid sponges. Yet it is clear that these particular sponges are not being overexploited. Most of the other sponges appear to be fully exploited by their respective predators. The important question, then is: What regulates the growth of *Acodontaster conspicuus* population?

Our observations suggest the hypothesis that the small but ubiquitous asteroid, *Odontaster validus*, is partially responsible for



Figure 1. Photograph of the sponge community at 60 m at Cape Armitage, McMurdo Sound. The two round sponges in the foreground are *Tetilla leptoderma*; all the other recognizable sponges are members of the family Rossellidae. The large rossellid (probably *Scolymastra joubini*) was 2 m tall by 1.5 m wide.

Figure 2. Photograph of the asteroid *Acodontaster conspicuus* eating a *Tetilla leptoderma*.

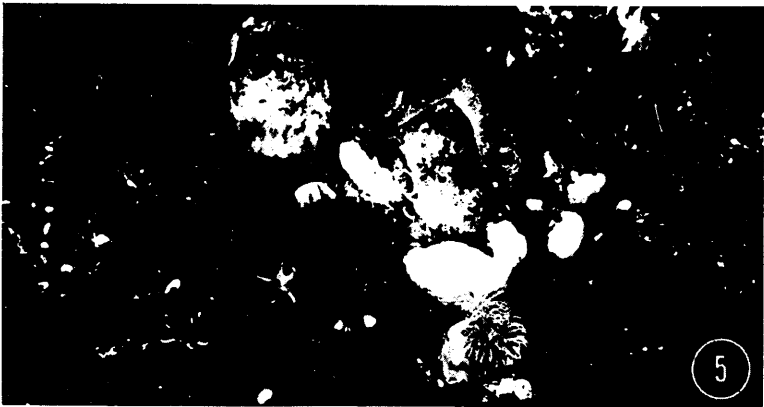


Figure 3. Photograph of the asteroid *Acodontaster conspicuus* eating an unidentified rossellid sponge.

Figure 4. Photograph of a large *Mycale acerata* growing over the side of a rossellid sponge. We observed situations in which the *Mycale* apparently have killed other sponges.

Figure 5. The asteroid *Perknaster fuscus antarcticus* eating the last of a *Mycale acerata*.

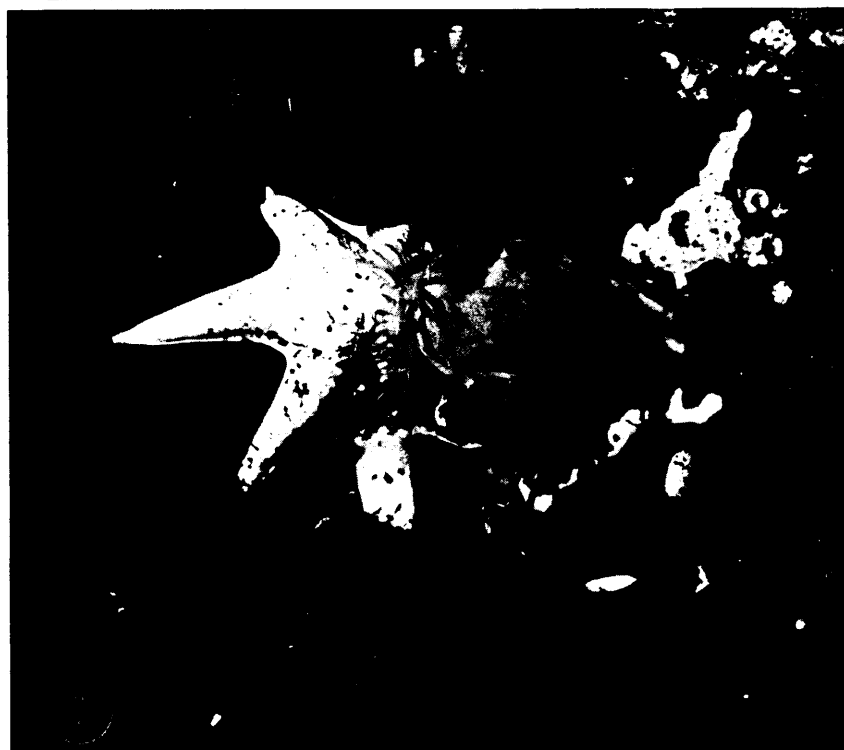


Figure 6. An aggregation of the asteroid *Odontaster validus* at Cape Evans.

Figure 7. The asteroid *Acodontaster conspicuus* being eaten by the sea-anemone *Urticinopsis antarcticus*.

limiting the population of this predator. *Odontaster* may exert this effect in two ways. First, since it is a relatively abundant detritus-feeder, it almost certainly consumes the settling larvae of this and other predators. An indication that this consumption has an important effect on the *A. conspicuus* population is the fact that *A. conspicuus* has a size-frequency distribution skewed far toward the larger sizes. Since we know from tagging studies that the growth rate is too slow to account for the scarcity of smaller individuals, it seems likely that it is caused by a disproportionately heavy mortality of the larvae or smaller size classes. But since this species probably has a very long life span, one would expect that the larvae and recently metamorphosed individuals that occasionally escape the predation of *O. validus* would, over time, cause the population of adults to build to a density sufficient to totally exploit their food resources. However, *Odontaster* also kills the adult *A. conspicuus*. This is a relatively rare event which we have seen only a few times; nevertheless, it does occur naturally and if it were to occur as frequently as the larvae escape, it would be sufficient to maintain the density of *Acodontaster conspicuus* at a constant level. If mortality caused by *Odontaster* and other factors such as occasional blundering into an anemone were to occur at a higher rate than that at which the larvae escape, the population of *A. conspicuus* would decrease. In most predator-prey systems, a decrease in the prey populations eventually has a negative feedback on the predator populations. However, this system is almost unique in that the *Odontaster* (in this case, predator) population density probably is controlled by the availability of the detritus from which they can derive the bulk of their energy (Pearse, 1965) rather than by the abundance of the *Acodontaster conspicuus* and other asteroids and molluscs (in this case, prey), which are relatively minor components of their diet. Therefore, the *Odontaster* predation on *A. conspicuus* could cause severe reduction of the latter's population without much feedback on the *Odontaster* population.

Since the abundance of detritus is directly related to the primary productivity, it seems likely that the density of the *Odontaster* population is directly related to the amount of primary productivity. Thus an increase in primary productivity with a resultant increase in *Odontaster* density should promote a decrease in the density of *A. conspicuus* and other sponge predator populations, with an associated increase in the amount of their sponge prey, particularly of *Mycale acerata* and of the rossellid family. Since 30% of the *Odontaster* diet is composed of sponge prey, this qualitative model would predict that the *Odontaster* might eventually over-exploit the sponges as well, so that in the areas of very high primary productivity, all the sponge populations might be reduced, leaving *Odontaster* to numerically dominate the community.

DISCUSSION

A number of foundation species can be identified in this shallow Antarctic community. There is a competitive dominant, *Mycale acerata* which is rare, apparently because of efficient predation by a specialized carnivore, *Perknaster fuscus antarcticus*, and a generalized carnivore, *Acodontaster conspicuus*, which, because of its abundance and high ingestion rate is an important consumer of *M. acerata*. The rossellid sponge species, which comprise most of the biomass and structure in the community, have escaped over-exploitation, probably because their most efficient predator, *Acodontaster conspicuus*, is in turn preyed upon by *Odontaster validus*.

While we know of no factors other than availability of food which might limit the distribution and abundance of *Perknaster* at Cape Armitage, the bounds or limits to the normal population fluxes of most of the species in this community are probably determined either directly or indirectly by the abundance of *Odontaster validus*. A decrease in the *Odontaster* density would probably first result in an increased larval recruitment of many species and eventually in a higher population of *Acodontaster conspicuus*, which would consume the rossellid sponges and *Mycale*. An increase in the *Odontaster* density would probably result in a decrease of all predator recruitment and an increase in the mortality of *Acodontaster*. Since *Odontaster* also eats sponges, all of the sponge populations might later be reduced, leaving *Odontaster* to dominate the community. What appears to be such a situation can be found at Cape Evans, 22 km to the north where there is considerably more primary productivity than at Cape Armitage (Pearse, 1965). Here there are very heavy concentrations of *Odontaster* and almost no other animals.

Implications of Pollution

There are three general sources of pollution in this benthic community. Heated sea water is released from the nuclear-powered distilling plant, but the quantity of the effluent is not sufficient to have much effect. Inorganic material such as trash and discarded equipment litters the bottom from McMurdo Station 6 miles north to the Cinder Cones. This material could eventually smother the benthos; however, this does not seem to be an immediate problem.

Because it probably has major effects on the foundation species, the organic pollution in the vicinity of McMurdo Station is presently the most dangerous pollution threat. The organic enrichment to the benthos resulting from the introduction of food wastes and sewage affects the foundation species in a number of ways. It is reasonable to predict several possible results of continued or increased pollution of

this type. If this introduced organic material is utilized by the sponges, it could increase the growth rate differential between *Mycale* and the other sponges and thus add to the competitive edge of *Mycale*. A more likely effect of organic pollution on the McMurdo foundation species would be an increase in the population of the detritus-feeding asteroid, *Odontaster validus*, with the numerous consequences discussed above. In this way it is likely that organic pollution will alter the bounds of normal fluxes and oscillations of the populations of foundation species in the shallow benthic communities in McMurdo Sound or any other sites on the Antarctic continental shelf where this community occurs and where future organic pollution persists.

CONCLUSION

A primary objective of studies designed to predict the effects of pollution on a community is the recognition of the foundation species — those which have a disproportionately important influence on the structure of the community. Once the foundation species are identified, it is easier to consider the effects of the pollutant on them and thus indirectly on the rest of the community than to attempt to define the effect on each species in the community separately. Obviously this is only the first step, as potential information is lost with the restriction of the study to selected species. However, in contrast to the almost hopeless task of defining the normal population fluctuations and interactions of all the species in the community so as to predict accurately the total effect of the pollutant, the identification and consideration of a few foundation species is a logical beginning.

At McMurdo Sound, *Mycale acerata*, the rossellid sponges, *Perknaster fuscus antarcticus*, *Acodontaster conspicuus* and *Odontaster validus* appear to be the foundation species. The form of pollution most likely to affect this community is organic enrichment and eutrophication from the garbage dump and sewer outfall (Dayton & Robilliard, 1971).

Any perturbation affecting the interaction between *Mycale* and its two major predators, *Perknaster fuscus antarcticus* and *Acodontaster conspicuus* would probably have a relatively rapid and dramatic impact on the community. *Odontaster validus* is the "keystone" (Paine, 1969) to the rossellid sponge-*Acodontaster* interaction, and the detritus-feeding *O. validus* population is almost certain to respond to organic enrichment with a sharp rise in numbers. There are predictable and important consequences to such a response, which will radically alter the facies of the community.

As *Odontaster* and the rossellid sponges are common in other parts of the Antarctic (Koltun, 1970; Propp, 1970; Arnaud, 1970) and

Acodontaster is at least present, it is probable that this group of foundation species, perhaps with different population levels, is a generally recurrent group over much of the Antarctic continental shelf. Thus, the pollution caused by organic enrichment could be a general problem eventually facing all the coastal Antarctic stations.

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GENERAL DISCUSSION

Searles: Paul, could you indicate in what respect your marine benthic community is a unique one? Or would you say that it is characteristic of relatively deep bottom communities generally?

Dayton: I believe that the principles I discussed are generally true as I supported them with examples from terrestrial communities, lakes, and intertidal community, as well as the benthos at McMurdo Sound. There is evidence summarized in Hedgpeth (1971, Perspectives of benthic ecology in Antarctica. *Research in the Antarctic*. AAAS publication) that at least certain aspects of the benthic community at McMurdo are found around the Antarctic continent. This would have implications to other Antarctic shore stations which are adding organic pollutants.

SPECIAL FIGURE. *Euphausia superba* (=krill) (Courtesy of George Llano).



SPECIAL FIGURE. TOP: Harpooning of whale (Photo by W. J. McCarthy); BOTTOM: DeLury method – Imaginary example of its application to an exploited and declining population of whales [Both from: Mackintosh, *The Stocks of Whales*, 1965, Fishing News (Books) Ltd., London; Courtesy of The Buckland Foundation].

