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A NOTE ON TROPHIC COMPLEXITY AND COMMUNITY STABILITY*

That "stability" is conferred approximately in proportion to the diversity of energy pathways characterizing any particular community is a widely held axiom among ecologists. As examples of this belief, one can read that "Stability increases as the number of links increase" (MacArthur, 1955, p. 535) or "a rich fauna and flora . . . tends to be very stable because of a multiplicity of ecological checks and balances" (Watt, 1964, p. 1434). There appears to be little or no sound evidence available to accept or reject these statements, because an operational definition of stability is lacking, as are data from the more complex associations. The most workable definition involves statements about the relative variability of population numbers in space and/or time, although limits on the extent of the spatial dimension are not usually stated, and collections of acceptable data through time are tedious to gather, and hence minimal. The basic data for a community tend to be species lists with comparisons and evaluations made between years on a presence or absence basis, an analysis providing a measure of predictability, not necessarily stability. At the population level the direction and magnitude of change in numbers, that is, a measure of the tendency to oscillate, may be adequate as a measure. Even impressions based on the intuitive understanding of a competent naturalist may prove acceptable. Any or all of these would suffice for the present purpose, although they fail to make the critical distinction between describing the relative continuity of a community, that static component which is relatively easily measured, and the ability of that community to withstand perturbation, the dynamic and presumably more fundamental component which is discernible only upon alteration. Thus, the

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compositional changes in two communities might be comparable, yet if the stresses they were subjected to were unequal, they could not be considered equivalent in stability.

These definitional difficulties need not be resolved now. What I wish to explore are the implications of two recent events in the marine littoral zone, especially as they bear on the contribution of food web complexity to the persistence and general appearance of the communities in which they occurred.

One of the most widely distributed sets of marine organisms occupies the exposed rocky intertidal from Alaska to Baja California, with many species being found throughout the entire range (Glynn, 1965). This is an association of moderate complexity for which some of the trophic pathways are documented (Paine, 1966), and also one that I have subjected to varying degrees of experimental manipulation. Significant changes in population density, species composition, and overt appearance are produced by the removal of a dominant carnivore, the starfish *Pisaster ochraceus*. Indirect evidence strongly suggests that equivalent changes do not appear with the exclusion of other consumers.

The other situation involves the current rapid decimation of parts of the Great Barrier Reef by a starfish, *Acanthaster planci* (New Zealand Herald, 1966; Barnes, 1966; Williamson, 1968). Tropical coral reefs are generally recognized as embodying the acme of complexity in marine communities (Wells, 1957), and, on an a priori basis, it seems unlikely that a carnivore of high trophic status could have reached plague proportions (local densities of almost one per square foot) within the last 5 years. *Acanthaster* feeds principally on stony corals (Goreau, 1964; Schoenberg, 1966), apparently exercising little food preference (Williamson, 1968), although some gastropods may also be consumed. It in turn is consumed by tritons (*Charonia* spp.), large gastropods popular as mementos of the reef. A case can be made for the hypothesis that on the pre-tourist reef both *Charonia* and *Acanthaster* were rare, forming a minor portion, both numerically and energetically, of the vast species complex dominated by corals. Subsequently, after continuous exploitation, *Charonia* becomes locally extinct, *Acanthaster* becomes patchily abundant, and the reef, in spite of its biological complexity, begins to be significantly altered (Barnes, 1966).

Within both these fairly or very complex systems the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time, that is, stability, are determined by their activities and abundances. They may be unimportant as energy transformers. The two keystone species discussed above have little in common. *Pisaster* is abundant and is somewhat of a trophic generalist; *Charonia* is rare and a food specialist. If *Charonia* was unimportant, and the plague of *Acanthaster* was due to other causes, then the comparison between the latter species and *Pisaster* reveals many common features. Both are

starfish feeding on a variety of prey, although both apparently prefer that species or category of prey that is capable of monopolizing the basic requisite in a space-limited system: mussels on the open coast of Washington and corals on the reef. The significance of these carnivores could not have been guessed beforehand, since other carnivores coexist with them. However, observations on, for instance, *Conus* spp. on the coral reefs and *Thais* spp. and *Leptasterias* on the open coast, suggest that variations in their abundance would produce no impact comparable to that produced by variations in the keystone species. Whatever, then, the significance of ecological complexity may be, it seems to have exercised little influence in ameliorating significant, short-term changes in these two communities, and hence has contributed minimally to stability.

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