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The Ecology of Coral Reefs

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OVERVIEW: CORAL REEF COMMUNITY STRUCTURE AND FUNCTION

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This paper summarizes an open discussion session which took place during the "Coral Reef Ecology Workshop" held at the annual meeting of the American Society of Zoologists in Philadelphia on December 27, 1983. Due to either sampling error or a genuine bias in current research emphasis, most of the participants in this session studied herbivory and grazing patterns on reefs. Consequently, most of the discussion centered around two related topics: (1) the recently discovered mass mortality of urchins in the Caribbean and (2) the relative importance of urchins vs. fishes in structuring benthic reef communities in areas facing different fishing pressures. A third more general topic was discussed briefly toward the end of the session: approaches to research on the community structure of reef systems. I will cover each of these topies in turn, extending discussion on the final topic with an overview of future needs in the study of coral reef communities.

MASS MORTALITY OF CARIBBEAN URCHINS

One of the major herbivores on Caribbean reefs is the long-spined urchin *Diadema antillarum*. In November 1983, a letter published in *Science* reported unprecedented mass mortalities of this species that were sweeping the Caribbean (Lessios, *et al.*, 1983). Haris Lessios (Smithsonian Tropical Research Institute) attended the session and provided both a description of the effects of the apparent pathogen (the origin or nature of which was currently unknown) and an updated account of the spread of the calamity.

The apparent disease runs a 4- to 5-day course, beginning with the urchins emerging from coral cover and climbing up any available substrate. The urchins then discolor, gradually lose their attachment capabilities, and ultimately lose their spines and die. Up to 98% mortality has been reported in some populations, with apparently resistant individuals remaining. Curiously, no other species of urchin has been affected.

The outbreak was first noted near the Caribbean entrance of the Panama Canal in January 1983. Urchin mortalities were observed subsequently in Colombia, Costa Rica, and Grand Cayman by June; in Jamaica, Belize, Cancun (Mexico), and Key Largo (Florida) by July; in the Bahamas by August; in the Dry Tortugas and Bermuda by September; in Grand Turk and Haiti by October; and throughout the Greater and Lesser Antilles, including Curacao, Bonnaire, and part of the coast of Venezuela, between November 1983 and January 1984.

Initially, the spread of the die-off appeared to follow prevailing ocean currents. However, certain exceptions, such as the outbreak in Barbados in October (a full month or two before the remainder of the Antilles), suggested a more complex situation. At present, Lessios reports that the entire Caribbean, except for much of Venezuela, Tobago, and the area between Guadaloupe and the British Virgin Islands, has been affected, although these areas could be affected by the time this report is published.

Mark Hay (University of North Carolina at Chapel Hill) noted that, despite the die-off of Diadema in the Florida Keys, algal abundance on reefs there was not unusually high 2 months after the die-off. He suggested that either herbivorous fishes were sufficiently abundant to check algal growth or 2 months may not have been enough time to detect a noticeable change.

Douglas Morrison (University of Georgia) summarized his quantitative data on the effects of the die-off on a Jamaican reef. Mean densities of urchins 1 year before the die-off were about 15 per m^2 at 5 m depth and about 2 per m^2 at 16 m. Several months after the die-off, mean densities had declined to about 1 per m^2 at 5 m depth, and no urchins were apparent at 16 m. After the urchin die-off at the shallow site, the coverage of crustose coralline algae (an indicator of high grazing intensity) declined from 45% to about 18%. Replacing the corallines, coverage by fleshy macroalgae quadrupled (from 7% to about 28%) and coverage by filamentous algae nearly tripled. These patterns were corroborated by earlier urchin-removal experiments conducted before the die-off; in the experimental absence of grazing, crustose corallines were replaced by upright macroalgae. In contrast, the die-off had little apparent effect upon algal growth at the deep site, where urchin densities were normally low, and macroalgal abundance remained relatively high (73% cover). The macroalgae that increased in abundance at the shallow site are known to be resistant to fish grazing but not to urchin grazing. These included members of the genera Lobophora, Caulerpa, and Dictyota.

Whatever its cause, the mass mortality of Diadema throughout the Caribbean provides an excellent (although uncontrolled) "natural experiment" for determining the impact of urchins on entire reef systems. Where adequate baseline data are available, observations following the die-off will test the widespread applicability of previous experimental analyses of small patch-reef systems (e.g., Ogden, et al., 1973) and help to resolve the controversy discussed in the next section.

ARE URCHINS IMPORTANT GRAZERS ON UNFISHED REEFS?

Hay summarized a study that was in press at the time of the workshop (Hay, 1984). He noted that most of the studies of the impact of urchin grazing on reef benthos have occurred at two sites: Teague Bay, St. Croix (e.g., Ogden, et al., 1973) and Discovery Bay, Jamaica (e.g., Sammarco, 1980). Such studies have led some to believe that urchins are the most important grazers on "typical" coral reefs. However, Hay suggested that these particular sites are atypical in that they have been heavily fished, indirectly resulting in unusually high densities of urchins which have been freed from predation by (and perhaps competition with) fishes. Using pieces of the seagrass Thalassia testudinum as a field bioassay for the intensity of herbivory on macrophytes, he found that eight lightly fished sites scattered throughout the Caribbean (including Salt River on St. Croix) showed decreasing grazing intensity with increasing depth and that almost all herbivory was due to fishes. Moreover, urchin abundances were low at these sites. In contrast, Haiti and Teague Bay on St. Croix, both heavily fished areas, showed the traditional opposite patterns. Hixon added that Hay's general observation that urchins are often rare where large urchin-eating fishes are abundant is evident on Hawaiian reefs. Where fishing is prohibited on marine reserves, such as Hanauma Bay and Coconut Island on Oahu, urchins appear to be relatively rare.

Hay stressed that his major point was that many patterns documented on human-impacted reefs may be recent, having prevailed only for the past few hundred years. Because herbivory by fishes may select for different evolutionary responses in algae than herbivory by urchins, attempts to extract evolutionary implications from ecological data gathered on heavily fished reefs is not justified.

Les Kaufman (New England Aquarium) objected to a number of Hay's assertions, particularly the idea that urchins on heavily fished reefs necessarily are freed from predation by fishes. He took issue with Hay's data which indicated, on one hand, a decrease in grazing intensity with increased depth at Salt River on St. Croix but, on the other hand, an increase in grazing intensity with increased depth at nearby Teague Bay on the same island. Based on his diving experience at these sites, Kaufman felt that both areas supported fishes capable of eating urchins. Thus, other factors besides the overall abundance of fishes may explain the patterns that Hay attributed to fishing pressure. Further, Kaufman felt that Hay failed to consider the importance of juvenile mortality in urchin populations. He suggested that predation by wrasses on juvenile urchins may be considerable on heavily fished reefs, such as Teague Bay (St. Croix) and Discovery Bay (Jamaica), so that fishing pressure on larger fish species may not ultimately affect urchin densities.

Substantial discussion centered on the adequacy of Thalassia as a bioassay of grazing intensity. Robert Carpenter (University of Georgia) suggested that different measures of grazing could produce different depth profiles of grazing intensity (see also Steneck, 1983). Carpenter felt that the Thalassia technique measured mostly parrotfish grazing and that a more general measure of grazing is provided by counting the number of herbivore bites per unit reef area. Hixon agreed, noting that bite marks by fishes from different families (e.g., parrotfishes vs. surgeonfishes) can be individually identified and counted on flat substrates (e.g., Hixon and Brostoff, 1983). Morrison also concurred and suggested that, instead of Thalassia, a food readily consumed by all herbivores should be used to measure overall grazing intensity. Based on his own and other's work, Morrison indicated that filamentous algae seem to be preferred by urchins and nearly all herbivorous fishes (especially parrotfishes and damselfishes).

Sara Lewis (Duke University) noted that some algal species (e.g., Lobophora variegata) are differentially susceptible to grazing on different reefs. She suggested that these within-species differences may represent geographical variation in the development of plant defensive compounds. Hay agreed, noting that herbivory on a local level possibly could induce the production of chemical defenses. He went on to stress the problem of interpreting data from herbivore food-preference observations. Data on food preferences provide information on the responses of herbivores to different plants, but not necessarily on the selective pressure that herbivores impose upon the plants. Clearly, more information will be required to elucidate the reciprocal interactions between reef herbivores and algae.

STUDYING COMMUNITY STRUCTURE IN REEF SYSTEMS

Eldredge Bermingham (University of Georgia) introduced this general topic toward the end of the session by suggesting what he believed to be a major problem with coral reef community ecology. He felt that reef ecologists were often academic descendants of bird ecologists, but failed to follow their ornithological forefathers' passion for detailed natural history data. He stressed that lack of solid baseline data on coral reefs inhibits our ability to understand these systems.

Both John Ebersole (University of Massachusetts at Boston) and Hixon agreed in turn that detailed observational data are essential for any convincing ecological study. In particular, long-term baseline data illustrating the constancy or variability of observed patterns are needed. However, Hixon questioned whether most (or even many) reef ecologists were academic descendants of bird ecologists and, more importantly, noted that reef ecologists have conducted far more rigorous experimental studies than most bird ecologists. This disparity is understandable. On one hand, many terrestrial systems (especially many avian communities) are amenable to long-term observation but not to experimental manipulation. On the other hand, most coral reefs are both geographically distant from most research institutions and difficult to observe for long periods due to diving constraints. However, some reef systems are small enough or the associated organisms sedentary enough to allow direct experimentation, as evidenced by the papers in this symposium. Moreover, artificial reefs constructed from either natural or manmade materials allow researchers to rigidly control the age and structure of reef habitats, allowing powerful experimental designs (e.g., Shulman, _et al._, 1983; Fitz, _et al._, 1983; Wolf, _et al._, 1983).

SYNTHESIS AND PROSPECTUS

It seems appropriate to close this paper with an overview of our future needs in the study of coral reef communities. It is clear that, despite the knowledge that has accrued since the first professional ecologists donned SCUBA gear in the 1950's, we have only begun to scratch the surface of the complexities of coral reef systems. The number of research possibilities is infinite; the field is wide open. Thus, rather than suggesting _what_ we need to study in particular, I would like to review the ideas suggested during this workshop on _how_ we might improve future studies.

Based on criticisms leveled at current studies and pleas for future changes aired at various times during this workshop, three basic needs are evident. First, the complexities of coral-reef community structure cannot be elucidated without more extensive use of properly controlled field experiments. This suggestion is not new (e.g., Connell, 1974), and many reef ecologists have embraced experimentation enthusiastically. However, any experiment, no matter how elegantly designed and executed, cannot stand alone. As discussed above, detailed observational knowledge of a system is essential before field experiments can be properly interpreted.

This brings us to a second need: long-term field studies. Because (1) most coral reefs are located far from universities and other research institutions, (2) most researchers cannot spend large blocks of time away f home, and (3) travel costs are becoming prohibitive, few current studies ha followed long-term variations in reef systems. Moreover, current policy di that most research grants are limited to durations of several years at most The net result is that most ecological studies are relatively static "snaps of intrinsically dynamic systems. Thus, our ability to understand the long range consequences of various ecological interactions, and especially major environmental events (such as the urchin die-off discussed above), becomes severely limited. Likens (1983) recently has characterized the establishme and funding of long-term ecological studies in general to be a major priori for the future. Perhaps reef systems will one day be included in the Natio Science Foundation's Long-Term Ecological Research Program. In any event, t establishment and funding of facilities for detailed studies in prescribed l areas (such as NOAA's HYDROLAB in Salt River Canyon, St. Croix) or in local regions (such as NOAA's MAKALI'I submersible program in Hawaii and Johnston Island, the JOHNSON SEA-LINK submersible program in Florida and the Bahamas, and the submersible now available at the Discovery Bay Marine Laboratory, Jamaica) represent important first steps toward obtaining long-term data on deep reef systems.

The third need is for future studies to include several study areas in order to determine the ubiquity of observed patterns. Most present studies occur at single sites, making widespread generalizations about coral reefs based on a single study tenuous at best (although this fact rarely stops us) This problem can be rectified by a single project being conducted at a numbe of locations, either sequentially by a single research team or simultaneousl by several teams using standardized methods. Present controversies, such as the importance of urchins as grazers discussed above, could be resolved by su an approach. NOAA's proposal to establish a saturation facility which can be moved among different geographical locations for comparative surveys of reef biota and processes should facilitate standardized studies.

Unfortunately, enacting these last two proposals may require changes in the current policies of granting agencies. The present system seems geared toward a fast-turnover "results-now" policy. While programs such as HYDROLAB provide the potential for long-term studies of reef systems, few such facilit exist presently, precluding detailed comparative studies among a number of study sites. In any case, should the majority of reef ecologists concur that these needs are important, long-term observational and experimental studies over wide areas will be realized eventually.

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Note added in proof: A recent update on the mass mortality of urchins can be found in:

Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. "Spread of Diadema Mass Mortality Through the Caribbean." Science 226:335-337.