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EFFECTS OF GRAZING AND BROWSING FISHES ON THE ZONATION OF CORALS IN GUAM^{1, 2}

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Abstract. Controlled coral transplant experiments were used to determine the effect of piscine corallivores on growth, zonation, and distribution of scleractinian corals in Guam. *Pocillopora damicornis* L. generally occurs only on the reef flat, reef margin (crest), and in lagoon habitats of the Indo-West Pacific. Although *P. damicornis* grows in deeper reef habitats in the eastern Pacific, it is seldom found in fore reef zones of the Indo-West Pacific. Colonies were transplanted from a depth of 1.3 m in a barrier reef lagoon to depths of 15 and 30 m in fore reef zones of three fringing reefs, where *P. damicornis* was absent. All transplanted colonies were heavily fed upon and branch tips were removed primarily by chaetodontid and balistid fishes, but none of the colonies was killed. This feeding removed about one-fourth of the colony wet weight in 1 wk ($\bar{x} = 23.7\% \pm 2.4$, .99 confidence limits, $N = 118$). There was a very significant difference in the amount of fish feeding on transplants between three different study reefs ($F_s = 459.30$, $P < .001$). There was no significant difference in the amount of feeding between the two depths at each site on any one run. Polyp and mucus browsing by species which do not physically damage the coral skeleton was also substantial.

When colonies of *P. damicornis* from Apra Harbor (1.3 m) were transplanted with colonies of *Pocillopora* sp. from Fafai Reef (15 m) to Double Reef and attached to naturally occurring *Pocillopora verrucosa* colonies (15 m), fish discriminated between the three similar species and fed only on *P. damicornis*. While some authors have indicated that these species may comprise a species complex, the fish clearly discriminated between the species. Coral feeding by many reef fishes is a regular event and exerts great influence upon reef community structure. Although *P. damicornis* can survive and grow well in deeper habitats in fish exclusion cages, it generally does not occur in these zones in the Indo-West Pacific. It is therefore concluded that piscine corallivores are important in restricting the growth, local zonation, and general distribution of some coral species.

Key words: coral distribution; coral growth; piscine corallivores; *Pocillopora*; reef community structure; zonation.

INTRODUCTION

The importance of animals feeding on corals has been a point of contention in the literature. Some authors have concluded that corallivores are not important to coral survival and reef growth (Wells 1957, Yonge 1963, 1968, Stoddard 1969). Hiatt and Strasburg (1960) found it surprising that although corals dominated the living biomass of Marshallese reefs, they seldom appeared to enter the food web directly. However, Robertson (1970) listed fishes in twelve families and a host of invertebrates as coral predators. A review of the literature on fish predation may be found in Randall (1974). Quantitative measurements of feeding rates and population densities of predators indicated that corallivores may destroy about one-third of the annual growth of *Pocillopora* communities in Panama (Glynn et al. 1972). Evidence is accumulating that many more teleost species (Lassig 1977, Neudecker 1977a, Reese 1977) as well as many organisms of other phyla (Robertson 1970, Glynn and Stewart 1973, Pat-

ton 1974, 1976) utilize coral as a food resource and that the total biomass of living tissue consumed is considerable.

When several colonies of *Goniastrea aspera* Verrill were transplanted from their natural habitat, the middle of the reef flat, to the reef margin in Palau, all colonies were killed by excessive fish grazing (Motoda 1940). Maragos (1972) reported that fish feeding on transplanted specimens of *Montipora verrucosa* (Lamarck), *Porites lobata* Dana, *Porites compressa* Dana, *Fungia scutaria* Lamarck, and probably *Pocillopora damicornis* L. was probably important. Feeding of piscine corallivores was also reported on transplants of *P. damicornis* in the eastern Pacific (Glynn and Stewart 1973).

There are many taxonomic uncertainties about *Pocillopora damicornis*. Some of these uncertainties relate to the effects of fish grazing on the morphology of colonies (Randall 1976). Several researchers (Vaughan 1907, 1918, Crossland 1952, Rosen 1971, Wells 1972) have indicated that many *Pocillopora* species may constitute continuous series. Wells (1972) reported that the intraspecific variation in this genus is so great that the 40 or so described species may constitute only 10 to 15 true species. In a recent revision of *Pocillopora*, Veron and Pichon (1976) recognized only four species in all of eastern Australia.

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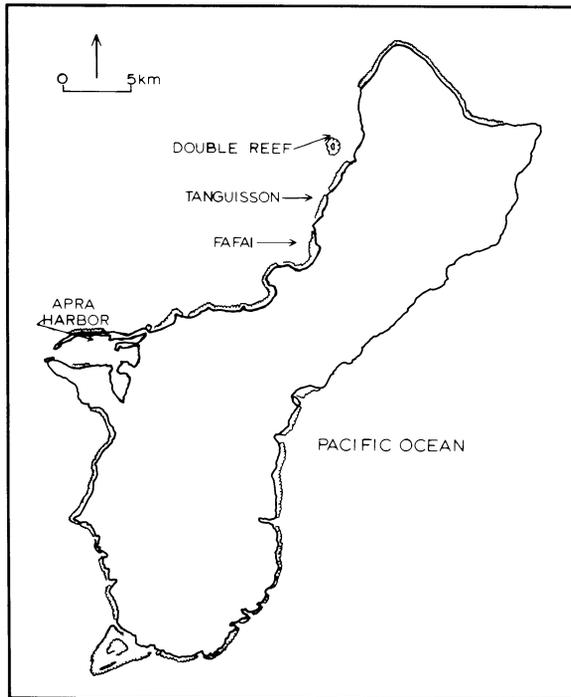


FIG. 1. Map of Guam, showing study sites.

The zonation of *Pocillopora damicornis* on Indo-Pacific reefs is generally restricted to the reef flat, margin, and lagoon environments, although it is tolerant of a wide range of environmental parameters. This restricted zonation is evident in the Marshall Islands (Wells 1954), the Marianas (Randall 1973a, b), the Gilberts (Banner and Randall 1952), American Samoa and Fiji (Hoffmeister 1925), the Seychelles (Rosen 1971), and also in the Indian Ocean at Sri Lanka (Mergner and Scheer 1974), the Maldives (Davies et al. 1971), and the Laccadives (Pillai 1971). *Pocillopora damicornis* has been observed in deeper fore reef zones, but this is uncommon.

Although *P. damicornis* is a dominant hermatype on eastern Pacific reefs, occurs in fore reef zones (Glynn et al. 1972, Porter 1972, Glynn and Stewart 1973), and can grow in fish exclusion cages in the Indo-West Pacific fore reef zones (Neudecker 1977a), it is not a principal reef builder or dominant species in fore reef zones of Indo-Pacific reefs. This species is often one of the few corals found in recently disturbed areas in Hawaii (Grigg and Maragos 1974). It recruits well (Connell 1973) and is a pioneer species on new or artificial substrata (Maragos 1972). Even though this species is very tolerant, recruits in abundance, can colonize harsh and unpredictable environments, and quickly regenerates lost material, it may not be a strong competitor with the other 100 or so common species in fore reef zones on most Indo-West Pacific reefs. While some of the life history traits of *Pocillo-*

pora damicornis are well adapted for colonization and competitive ability, its actual abundance and distribution may be determined more by the effects of piscine corallivores than by recruitment or competition.

The purpose of this study was to measure the amount of fish feeding on transplanted colonies of *Pocillopora damicornis* and to determine the effects of the feeding on coral growth, zonation, distribution, and reef community structure. Although fish in the families Balistidae (triggerfishes), Canthigasteridae (sharp-nose puffers), Chaetodontidae (butterfly fishes), Diodontidae (porcupine fishes), Ephippidae (spadefishes), Gobiidae (gobies), Labridae (wrasses), Monacanthidae (filefishes), and Tetraodontidae (puffers) are known to eat corals (Robertson 1970, Reese 1973, 1975, 1977, Patton 1974, 1976), not much is known about the quantity or importance of this predation. The mode of coral feeding varies among species of piscine corallivores (which remove only a portion of the living coral, sensu Glynn et al. 1972), and can be divided into three feeding types (modified from Hiatt and Strasburg 1960). Coral browsers bite off individual polyps above the level of the corallite. Grazers crop the polyps so closely that they scrape off part of the corallite and therefore incidentally ingest some skeletal material. Corallum feeders bite off chunks or branches and ingest considerable amounts of CaCO_3 .

METHODS AND MATERIALS

Colonies of *Pocillopora damicornis* living at a depth of 1.3 m of clear water on pier pilings in a barrier reef lagoon were collected without aerial exposure and placed in plastic buckets filled with seawater. Initially five unweighed transplant runs ($N = 15$) were made to 15 and 30 m at the Tanguisson study site (Fig. 1). Invertebrate associates were not removed and no tags were attached to the transplants. All of these colonies were heavily grazed and all of the exposed branch tips were bitten off. While these runs varied in length from 14 to 70 d, none of the colonies was killed. For this experiment, a variety of colony sizes were collected for each of the eight transplant runs. All of the colonies ($N = 118$) were of the same growth form and showed no evidence of skeletal damage from fish predation.

The colonies ranged in wet weight (removed from water) from 11.0 to 195.2 g with most colonies in a size class of 25–50 g range. Each colony was carefully examined (with a minimum of handling) and macroinvertebrate associates such as xanthid crabs (*Trapezia*), alpheid shrimps, and coralliophilid gastropods (*Coralliophila*) were removed. Each coral was then allowed to shed excess water for ≈ 10 –20 s and weighed on a triple beam balance. Weights were recorded on small mylar tags which were threaded onto 14-gauge plastic-coated copper attachment wire. Total exposure was always less than 1 min.

The colonies were transported in buckets to the boat

ramp and then taken by boat to the study sites. Total time in the buckets was always <2.5 h and the water was changed at least once during the trip. As with other transplant experiments with *P. damicornis*, no significant ill effect was exhibited by the transplants (Maragos 1972, Glynn and Stewart 1973, Neudecker 1977a). Nevertheless, the amount of trauma in all transplants is assumed to be about the same.

Fig. 1 is a map of the collection and transplant sites. The fringing reefs on Fafai and Tanguisson exhibit similar zonation. The 15-m stations were on the submarine terrace while the 30-m stations were in the seaward slope zone. The differences between these study sites are in the degree of wave exposure (Fafai is more protected) and in the species composition of coral communities. The Double Reef study site has a different submarine topography. The 15-m stations were in the fore reef zone on a coral ridge flanking a sand channel and the 30-m stations were in the seaward slope zones. Qualitatively, the Double Reef study sites had the more diverse and abundant fish communities. The major difference between the 15- and 30-m stations at all study sites was that the coral coverage was more continuous at the shallower stations and sediments were more abundant at the deeper stations. *Pocillopora damicornis* has not been found in fore reef zones of any of the study sites.

Replicate transplant runs 1, 2, and 3 were wired, in a line, to steel communication cables and were suspended about 0.6 m above the bottom. Possible artificial effects from suspension above the reef and the even distribution of the first transplants were evaluated by securing colonies of the remaining five runs directly to in situ corals or to the reef substratum in a random fashion. The initial transplants demonstrated that the presence of invertebrate associates or the absence of mylar tags would not stop fish grazing. Several colonies were left untagged and unwired to test for a possible advertisement effect of the green wire. In addition to these multiple controls, a run was made to test for grazing elicited by transplantation. *Pocillopora* sp. was collected from the reef front (15 m) of Fafai Beach and transplanted along with *P. damicornis* colonies from Golf Pier to the Double Reef study sites. Replicates of one colony of each of these transplanted species were tied to naturally occurring colonies of *Pocillopora* sp. and *Pocillopora verrucosa* Ellis and Solander at 15 and 30 m at Double Reef.

After 1 wk, the colonies were recovered and weighed. Grazing was measured as the percent loss of colony wet weight after 7 d. Research specimens were deposited in the University of Guam Marine Laboratory Museum. Although corals were allowed to shed excess water, water remained in cavities and as a thin film. The relative amount of added weight was assumed to be constant. This quantity does not imply that all weight loss was due to consumption by corallivores. Since broken branch tips were occasionally

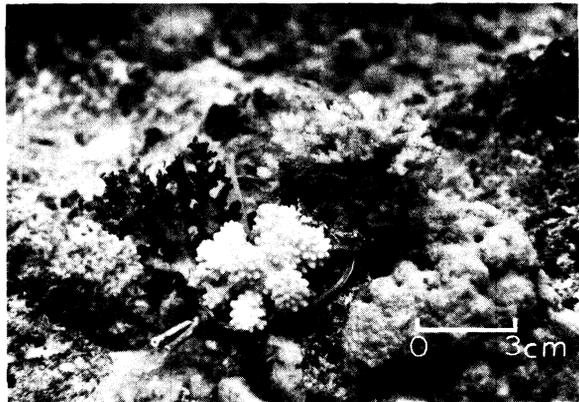


FIG. 2. Effects of transplantation were tested by transplanting *P. damicornis* (left) from 1.3 m in Apra Harbor along with *Pocillopora* sp. from 15 m at Fafai Reef to 15 m at Double Reef and attaching them to naturally occurring colonies of *P. verrucosa*.

found near the transplants, some of the weight loss is surely due to damage from large fish and not feeding. Even though some branches were alive, this damage still represents loss to that single colony and is important to its growth. The measured weight loss is therefore a combination of all of these factors. If loss from each feeding type could be segregated, browsing would be underestimated since the colonies regenerated some lost material within 7 d.

Mann Whitney *U* tests were made on each run to see if there was a significant difference between corals at the two depths. For statistical comparisons, the measurement of percent loss of colony weight was transformed by the angular transformation (Sokal and Rohlf 1969). The depths were subsequently pooled and an analysis of variance was used to determine the probability that there was no difference between the study sites. Ninety-nine percent confidence limits were calculated and the limits were retransformed to percent loss of wet skeletal weight.

RESULTS AND DISCUSSION

All of the transplant colonies ($N = 118$) of the eight experimental runs were grazed, but none was killed. There was no significant difference in the amount of grazing between the 15- and 30-m stations on any run. All of the untagged and unwired controls were also grazed, and none was killed. Nearly all of the exposed branch tips (Figs. 2 and 3) were bitten off; the only ungrazed branches were those that were down inside the colony, protected by other branches and physically difficult for the fish to reach.

Several species were actually observed eating the transplant colonies. In addition to the previously published list (Neudecker 1977a), two more *Chaetodon* species, *Chaetodon ornatissimus* Cuvier and Valenciennes and *C. puntatofasciatus* Cuvier and Valen-



FIG. 3. Seven days after transplantation, piscine corallivores had removed about one-fourth of *P. damicornis* colony while *P. verrucosa* showed no signs of skeletal damage and the *Pocillopora* sp. had three small bite marks.

ciennes, were observed eating transplant and other corals.

The two depths on each run were pooled and ANOVA was used to test for differences in the amount of fish grazing on corals between the three study reefs (Table 1). Ninety-seven percent of the total variance was due to differences between the reefs, while only 3% was due to intrareef differences. A similar ANOVA was performed to account for the total variance in grazing between the two depths when all runs were pooled (Table 2). Virtually all of the variance, 99%, was due to differences within depths. When all the data were pooled, the mean percent loss in wet weight after 7 d was 23.7 ± 2.4 , .99 confidence limits.

When colonies of *Pocillopora* sp. (possibly a new species, being described by Richard Randall) from Fafai were transplanted along with *P. damicornis* from Apra Harbor and attached to *Pocillopora* sp. and *P. verrucosa* at Double Reef, all *P. damicornis* were grazed (Figs. 2 and 3). The in situ *Pocillopora verrucosa* colonies were not grazed at all and four of the six *Pocillopora* sp. from Fafai had a few small bite marks. These results suggest that transplantation alone does not significantly increase the susceptibility of the corals to predation, and the few small bite marks

TABLE 1. Analysis of variance for the percent loss of colony wet weight per week in *Pocillopora damicornis* colonies transplanted to seven different study sites. Analysis by arc-sine transformation.

Source of variation	df*	MS*	F_s^*	% of s^2 †
Between reefs	7	14 482.33	459.30***	96.9
Within reefs	10	31.53		3.1

* df = degrees of freedom; MS = mean square error; F_s = sample statistic of F-distribution.

† Percent of total variance.

*** $P < .001$.

TABLE 2. Analysis of variance to determine the probability that grazing is the same for both depths at all study sites.*

Source of variation	df	MS	F_s	% of s^2
Between depths	1	16.43	0.4051 ns	<1
Within depths	116	40.50		99

* See Table 1 for explanations of symbols.

may suggest that fish discriminate between the corals by taste. Also, while some taxonomists may consider *P. damicornis* and *Pocillopora* sp. to be synonymous, the fish distinguish between the two.

Randall (1974) pointed out that many coral-eating fish are among the most highly evolved of modern teleosts. Observations during these experiments indicate that many *Chaetodon* species regularly feed on coral. Coral polyps and mucus probably constitute an important proportion of the diet of eleven species that were frequently seen eating transplanted colonies and other corals in situ. Observations and collections from numerous Indo-West Pacific reefs revealed browsing, grazing, and corallum feeding by manifold teleost species on many scleractinian species including *Acropora*, *Favia*, *Fungia*, *Lobophyllia*, *Montipora*, *Pocillopora*, *Porites*, *Seriatopora*, and *Stylophora*. The hydrozoan coral, *Millepora*, is also often eaten. This grazing removes a significant amount of biomass and may be a selective pressure accentuating protective mechanisms in corals.

Bakus (1964, 1967) reported that grazing by herbivorous reef fishes profoundly influenced the benthic biota, and suggested that this activity constituted a major selective force enhancing development of protective structures and cryptic behavior of certain benthic marine invertebrates. While grazing by fishes may limit the distribution of some invertebrates, it provides adequate settlement surfaces for others (Vine 1974) and increases coral recruitment success by controlling algal competitors (Birkeland 1977). Benthic flora show differential grazing susceptibilities (Ogden et al. 1973) and some contain certain toxins which may be effective repellents (Randall 1961, Doty and Santos 1966, Santos and Doty 1968). Perhaps fish feeding on corals has led to the development of similar biochemical defense mechanisms as well as morphological adaptations to minimize grazing. Nematocysts of corals may also serve antipredatory functions.

Fishes that prey on sessile marine invertebrates are highly evolved diurnal species which have specialized feeding structures and behavior that cope with various noxious or toxic defenses of their prey (Hobson 1974). The adaptability of perciform feeding has led to a wide variety of forms that have diverged from one another mainly on the basis of differing food resources; much of this diversity has arisen from adaptations that deal

with specific defense mechanisms of the prey (Bakus 1964, Hobson 1974).

Fringing reefs on Guam have probably been more or less continuous since the Eocene (Richard Randall, *personal communication*). Since this amount of time has been sufficient for feeding specializations by several corallivores (Robertson 1970, Randall 1974), it has also been sufficient to allow corals to evolve antipredatory mechanisms. Perhaps the morphological adaptations of species to certain environments (Maragos 1972), such as closely set heavy branches instead of an open, finely branched morphology, have a selective advantage in habitats where fish grazing is high. Over ecological time, the stout appearance of a particular colony may be a more direct result of the feeding activity of corallivores.

Hobson (1974) reported scleractinian corals to be a major food resource of many Kona butterfly fishes, and Reese (1975, 1977) classified 16 Chaetodontid species as either facultative or obligate coral feeders. While it has been generally accepted that Monacanthidae is the only family which can be characterized as being composed of coral specialists, Reese (1977) listed six *Chaetodon* species as coral specialists and Patton (1974) and Lassig (1977) reported on four species of *Paragobiodon* (Gobiidae) that were totally dependent upon corals for food and shelter. *Chaetodon ornatissimus* is unique among the butterfly fishes studied in that it specializes on energy-rich coral mucus (Hobson 1974, Reese 1975, 1977). Since Chaetodontids are abundant at all of my study sites (14 common species) and 11 of these have been observed to eat transplants as well as naturally occurring colonies, the total coral biomass removed by these fish is probably quite large.

The ability of corals to regenerate lost material quickly has been widely reported (Kawaguti 1937, 1943, Bosch 1967, Franzisket 1970, Loya 1976). This response is very rapid in *P. damicornis*, and not only prevents settlement of fouling organisms, but minimizes the effects of grazing. Since several scleractinian species are known to regenerate lost material rapidly, coral feeding, which is temporally and spatially partitioned, can constitute either a large portion or the entire diet of these teleost species. Only corals that can quickly regenerate lost material can withstand much grazing pressure.

While light intensity and water temperature are important factors influencing coral zonation and distribution, neither of these parameters excludes *P. damicornis* from the fore reef zones; colonies in protective cages grew well on the submarine terrace (15 m) and on the seaward slope (30 m) (Neudecker 1977a). In fact, transplanted caged colonies at 15 m grew significantly more (6.5 mm in 63 d) than did colonies left in situ in 1.3 m of water (5.9 mm in 68 d) (Neudecker 1977b). With several species of fish jointly eating an average of one-fourth of the colony weight, it is ap-

parent that these predators would make it extremely difficult for *P. damicornis* to recruit to and colonize the fore reef zones. The importance of fish in influencing the growth of corals, their abundance, and the community structure of reefs has been underestimated. The amount of living biomass removed is large and coral is not an uncommon food resource for reef inhabitants. This study indicates that the presence or absence of certain corals on reefs may be directly related to piscine corallivores. While the fish distinguish between closely related corals in nature, the implications for the species complex remain uncertain.

Some chaetodontid fishes of tropical reefs in all oceans feed primarily on corals. Relationships between the fishes and corals appear to be highly co-evolved. The fish have specialized morphology and behavior that maximize their feeding ability (Hobson 1974, Reese 1977), while the scleractinians have specialized mechanical defenses, modified morphology, and behavior (e.g., nocturnal polyp extension) that minimize grazing. In the Marshall Islands, stomachs of generalized *Chaetodon* species which partly ate coral polyps always contained a considerable calcereous fraction, whereas specialized congeners did not (Hiatt and Strasburg 1960). Piscine corallivores exert considerable influence upon the growth, abundance, and distribution of corals. Their effect also influences coral systematics and scientific estimates of reef accretion. A better understanding of the influence of corallivores will lead to a better understanding of coral reefs system in general.

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LITERATURE CITED

- Bakus, G. J. 1964. The effects of fish grazing on invertebrate evolution in shallow tropical waters. Occasional Papers 27, Allan Hancock Foundation, University of Southern California Press, Los Angeles, California, USA.
- . 1967. The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesica* 3:135–149.
- Banner, A. H., and J. E. Randall. 1952. Preliminary report on marine biology study of Onotoa Atoll, Gilbert Islands. Part. 1. Atoll Research Bulletin 13:1–42.
- Birkeland, C. 1977. The importance of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proceedings of the Third International Coral Reef Symposium 1:15–21. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- Bosch, H. 1967. Growth rates of *Fungia scutaria* in Ka-

- neoh Bay, Oahu. Thesis. University of Hawaii, Honolulu, Hawaii, USA.
- Connell, J. H. 1973. Population ecology of reef-building corals. Pages 247–268 in O. A. Jones and R. Endean, editors. *Biology and geology of coral reefs*. Academic Press, New York, New York, USA.
- Crossland, C. 1952. Madreporaria, Hydrocorallina, Heliopora and Tubipora. Great Barrier Reef Expedition, 1928–1929, Science Reports. British Museum of Natural History 6:86–257.
- Davies, P. S., D. R. Stoddard, and D. C. Sigg. 1971. Reef forms of Addu Atoll, Maldives Islands. *Symposia of the Zoological Society of London* 28:217–259.
- Doty, M. S., and G. A. Santos. 1966. Caulerpicin, a toxic constituent of *Caulerpa*. *Nature* 211:990.
- Franzisket, L. 1970. The atrophy of hermatypic reef corals maintained in darkness and the subsequent regeneration in light. *Internationale Revue gesamten Hydrobiologie* 55:1–12.
- Glynn, P. W., and R. H. Stewart. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. *Limnology and Oceanography* 18:367–379.
- Glynn, P. W., R. H. Stewart, and J. E. McCosker. 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Geologischen Rundschau* 61:483–519.
- Grigg, R. W., and J. E. Maragos. 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55:387–395.
- Hiatt, R. W., and D. W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* 30:65–127.
- Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fisheries Bulletin* 72:915–1031.
- Hoffmeister, J. E. 1925. Some corals from American Samoa and the Fiji Islands. Publication 343, Carnegie Institution of Washington, Washington, District of Columbia, USA.
- Kawaguti, S. 1937. On the physiology of reef corals II. The effect of colour and form of reef corals. *Palao Tropical Biological Station Studies* 1:199–208.
- . 1943. Growth form of corals in relation to water currents. *Journal of the Natural History Society of Taiwan* 33:263–267.
- Lassig, B. R. 1977. Socioecological strategies adopted by obligate coral dwelling fishes. *Proceedings of the Third International Coral Reef Symposium* 1:565–570. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- Loya, Y. 1976. Skeletal regeneration in a Red Sea scleractinian coral population. *Nature* 261:490–491.
- Maragos, J. E. 1972. A study of the ecology of Hawaiian reef corals. Dissertation. University of Hawaii, Honolulu, Hawaii, USA.
- Mergner, H., and G. Scheer. 1974. The physiographic zonation and ecological conditions of some South Indian and Ceylon coral reefs. *Proceedings of the Second International Coral Reef Symposium* 1:213–231. Great Barrier Reef Committee, Brisbane, Australia.
- Motoda, S. 1940. The environment and life of massive reef coral, *Goniastrea aspera* Verrill, inhabiting the reef flat in Palao. *Palao Tropical Biological Station Studies* 2:61–104.
- Neudecker, S. 1977a. Transplant experiments to test the effect of fish grazing on coral distribution. *Proceedings of the Third International Coral Reef Symposium* 1:317–323. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- . 1977b. Development and environmental quality of coral reef communities near the Tanguisson Power Plant. Technical Report 41, University of Guam Marine Laboratory, Agana, Guam.
- Ogden, J. C., D. P. Abbott, and I. Abbott. 1973. Studies on the activity and food of the echinoid *Diadema antillarum* Philippi on a West Indian patch reef. *Special Publications in Marine Biology* 2, West Indies Laboratory, Fairleigh Dickinson University, Teaneck, New Jersey, USA.
- Patton, W. K. 1974. Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. Pages 219–243 in W. B. Vernberg, editor. *Symbiosis in the sea*. University of South Carolina Press, Columbia, South Carolina, USA.
- . 1976. Animal associates of living reef corals. Pages 1–36 in O. A. Jones and R. Endean, editors. *Biology and geology of coral reefs*. III(Biology). Academic Press, New York, New York, USA.
- Pillai, C. S. 1971. Composition of the coral fauna of the southeastern coast of India and the Laccadives. *Symposia of the Zoological Society of London* 28:217–259.
- Porter, J. W. 1972. Patterns of species diversity in Caribbean reef corals. *Ecology* 53:745–748.
- Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. *Ecology* 42:812.
- . 1974. The effect of fishes on coral reefs. *Proceedings of the Second International Coral Reef Symposium* 1:159–166. Great Barrier Reef Committee, Brisbane, Australia.
- Randall, R. H. 1973a. Reef physiography and distribution of corals at Tumon Bay, Guam before crown-of-thorns starfish *Acanthaster planci* (L.) predation. *Micronesica* 9:119–158.
- . 1973b. Coral reef recovery following extensive damage by the "crown-of-thorns" starfish *Acanthaster planci* (L.). *Publications of the Seto Marine Biological Laboratory* 20:469–489.
- . 1976. Some problems in coral reef taxonomy. *Micronesica* 12:151–156.
- Reese, E. S. 1973. Duration of residence of coral reef fishes on "home" reefs. *Copeia* 1:145–159.
- . 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. *Zeitschrift für Tierpsychologie* 37:37–61.
- . 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. *Proceedings of the Third International Coral Reef Symposium* 1:267–274. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- Robertson, R. 1970. Review of the predators and parasites of stony corals with special reference to symbiotic prosobranch gastropods. *Pacific Science* 24:43–54.
- Rosen, B. R. 1971. Principal features of reef coral ecology in shallow water environments Mahe, Seychelles. *Symposia of the Zoological Society of London* 28:163–183.
- Santos, G. A., and M. S. Doty. 1968. Chemical studies on three species of the marine algal genus *Caulerpa*. Pages 219–227 in H. D. Freuderthal, editor. *Drugs from the sea*. Washington Marine Technical Society, Washington, District of Columbia, USA.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Stoddard, D. R. 1969. Ecology and morphology of recent coral reefs. *Biological Reviews* 44:433–498.
- Vaughan, T. W. 1907. Recent madreporaria of the Hawaiian Islands and Laysan. *Bulletin United States National Museum* 59:1–427.
- . 1918. Some shoal-water corals from Murray Island, Cocos-Keeling Islands and Fanning Island. *Publications of the Carnegie Institution of Washington* 51:213–234.
- Veron, J. E. N., and M. Pichon. 1976. Scleractinia of eastern Australia. Australian Institute of Marine Science. Monograph 1:1–86.
- Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohol* on coral-reef ecology. *Marine Biology* 24:131–136.

- Wells, J. W. 1954. Recent corals of the Marshall Islands. Professional Papers United States Geologic Survey **260-I**:385–486.
- . 1957. Coral reefs. Pages 609–631 *in* J. Hedgepeth, editor. Treatise on marine ecology and paleoecology. Memoirs of the Geological Society of America 67, University of Kansas Press, Lawrence, Kansas, USA.
- . 1972. Notes on Indo-Pacific scleractinian corals. Part 8. Scleractinian corals from Easter Island. Pacific Science **26**:183–190.
- Yonge, C. M. 1963. The biology of coral reefs. Pages 209–260 *in* F. S. Russell, editor. The biology of coral reefs. Academic Press, London, United Kingdom.
- . 1968. Living corals. Proceedings of the Royal Society of London B Biological Sciences **169**:329–344.