

SYMPOSIA SERIES FOR UNDERSEA RESEARCH

NOAA'S UNDERSEA RESEARCH PROGRAM, VOL. 1 NO.1, 1983

The Ecology of Deep and Shallow Coral Reefs

Results of a Workshop on Coral Reef
Ecology held by the American Society
of Zoologists, Philadelphia, Pennsylvania,
December 1983

Edited by
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December 1983



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FISH GRAZING AND COMMUNITY STRUCTURE OF REEF CORALS AND ALGAE: A SYNTHESIS OF RECENT STUDIES

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ABSTRACT

This paper reviews major studies published over the past 5 years on the impact of fishes upon the major components of tropical reef benthos. With one notable exception, virtually no studies have demonstrated a strong effect of fish corallivores upon coral communities, although at least one coral genus is certainly affected by fish predation. On the other hand, herbivorous fishes strongly affect the distribution and abundance of reef algae, with recent studies elucidating temporal and spatial variations in herbivore impact. Of all reef fishes, territorial damselfish have especially widespread direct and indirect effects. By establishing and defending distinct algal mats, they affect: (1) coral growth, recruitment, and bioerosion; (2) algal abundance and local diversity; (3) local microfaunal abundance; and (4) nitrogen fixation by blue-green algae. These and other interactions are summarized on a synthetic flow-chart.

INTRODUCTION

The dominant benthic organisms on tropical reefs are scleractinian corals and various algae. That grazing fishes can affect the local distribution and abundance of such organisms was first demonstrated by the caging experiments of Stephenson and Searles (1960) and Randall (1961). More recently, ecologists have focused their attention on the role of fishes and large invertebrates in determining the structure of benthic communities, that is, how differential foraging can alter competitive relationships and thus the local species diversity of reef benthos. Recent reviews have been published on the impact of sea urchins (Lawrence and Sammarco 1982) and the crown-of-thorns seastar (Birkeland 1982). The goal of this paper is to briefly review and synthesize major studies on the effects of fishes upon the community structure of reef corals and algae published during the past 5 years (1978 through part of 1983). Due to textual constraints, this overview is necessarily of limited scope. Those seeking more comprehensive reviews of marine plant-herbivore interactions are referred to Ogden and Lobel (1978), Borowitzka (1981), and Lubchenco and Gaines (1981). Sheppard (1982) includes a general taxonomic review of corallivores.

FISHES AND CORALS

Despite observations that members of about ten families of fishes eat coral polyps (Randall 1974, Patton 1976), surprisingly few studies have demonstrated that such corallivores influence the distribution and abundance of hermatypic corals. For example, although butterflyfishes (Chaetodontidae) are apparently the major reef-fish corallivores (e.g., Reese 1977), recent data from the Red Sea suggest that these fishes consume a negligible portion of the total standing crop of live coral (Harmelin-Vivien and Bouchan-Navaro 1981). However, at least one coral genus, *Pocillopora*, is strongly affected by fish predation. Neudecker (1979) found that colonies transplanted from a relatively fish-free lagoon (1 m depth) to reef slopes (15-30 m depth) in Guam survived well when caged, but were

extensively fed upon by butterflyfishes and balistid triggerfishes when exposed. Using a similar experimental design, Wellington (1982) found that Pocillopora colonies exposed to predation by mainly tetraodontid pufferfishes off the Pacific coast of Panama suffered strongly reduced growth rates relative to protected controls. These studies suggest that Pocillopora colonies may be generally rare where fish corallivores are abundant.

Perhaps more important to coral distribution and abundance than direct predation by fishes are the indirect effects of certain damselfishes (Pomacentridae). These fish defend permanent individual territories about 1 m in diameter, resulting in locally decreased grazing by other fishes, and thus increased algal growth as distinct mats used as food sources and nesting sites (see next section). Field observations have shown that damselfish kill coral either directly by removing polyps, thus providing open substrate for their algal mats (Kaufman 1977, Wellington 1982), or indirectly by the reduced grazing within territories allowing algae to smother corals (Potts 1977). In either case, bioerosion of corals may be accelerated within territories, apparently because the algal mats provide refuges and/or food sources for settling boring organisms, which subsequently reduce the ability of the coral to withstand wave shock (Risk and Sammarco 1982). Thus, the algal mats within damselfish territories are generally detrimental to coral colonies (see also Lobel 1980). However, small corals located within the periphery of a territory but still outside the algal mat can be protected from corallivores by the resident damselfish (Wellington 1982).

How damselfish territoriality affects the recruitment of coral larvae is unclear. Previous work has shown that algal mats inhibit settlement by corals (e.g., Birkeland 1977). However, Sammarco and Carlton (1981) reported enhanced recruitment of mostly Acropora on substrates placed inside damselfish territories on the Great Barrier Reef for four months relative to caged substrates or those exposed to grazers outside territories. Unfortunately, the ultimate fates of these recruits were not followed. Using a similar experimental design in Hawaii, Hixon and Brostoff (in prep.) found the recruitment of Pocillopora over the course of a year on caged surfaces to be greater than that on exposed surfaces either inside or outside damselfish territories. However, there was indication of low survival of these recruits due to smothering by algae. Moreover, in a laboratory microcosm experiment at the same site, Brock (1979) found an inverse relationship between the density of grazing scarid parrotfishes and coral recruitment on exposed tank walls. Bak and Engle (1979) have also attributed the high mortality rates of juvenile corals to grazing by parrotfishes, which are typically excluded from damselfish territories. It appears that on open surfaces, coral recruits may initially experience enhanced survival where they are protected from extensive fish grazing, either inside cages or within damselfish territories, but will eventually be overgrown by algae. Those larvae settling where exposed to fish grazing may initially suffer high mortality, being consumed along with the fishes' other prey, but some individuals will eventually reach an invulnerable size class where they are both immune to incidental predation and freed from competition with algae (Birkeland 1977).

Very few data have been reported on how fishes alter competitive interactions between corals. Sammarco and Williams (1982) have hypothesized that the algal mats of damselfish territories may act as refuges for some rarer corals, thus increasing the local evenness of relative abundances among coral species. By far the most extensive published study of the effects of fishes on coral community structure is that of Wellington (1982), who worked on a fringing reef off the Pacific coast of Panama. In this system, branching Pocillopora spp. dominated shallow areas (0-6 m depth), while the massive Pavona gigantea dominated deeper areas (6-10 m depth). Using a clever series of experiments and observations,

Wellington discovered an interactive feedback loop whereby the damselfish Eupomacentrus acapulcoensis may directly and indirectly cause this zonation. When establishing territories in the shallow zone, damselfish differentially kill Pavona by polyp removal and maintain their algal mats on the exposed substrate; Pocillopora is apparently protected by its tightly branched morphology and rapid polyp regeneration. Moreover, as discussed above, Pocillopora colonies within the periphery of territories are protected from fish corallivores. These factors enhance the ability of Pocillopora to competitively dominate Pavona in shallow areas. The Pocillopora framework, in turn, provides the damselfish with shelter, a necessary requisite for a territory. In the deep zone, shelter sites and thus damselfish densities are low because overall coral cover (and thus inter-coral competition) is low, apparently due to physical factors. Here, transient fish corallivores (mostly puffers) differentially eat Pocillopora, whose branches they can ingest and masticate, leaving Pavona as the dominant coral. Overall, it seems that territorial damselfishes in general have a far greater impact on hermatypic corals than do true fish corallivores per se.

FISHES AND ALGAE

Considerably more data have been gathered on the effects of fishes on reef algae than on corals. This may reflect the fact that herbivorous fishes, especially parrotfishes (Scaridae), surgeonfishes (Acanthuridae) and territorial damselfishes (Pomacentridae), are together among the most diverse and abundant of reef fishes (e.g., Ogden and Lobel 1978). Indeed, Hatcher (1981) has empirically estimated that about half the net algal production on One Tree Reef, Australia, is consumed by fishes. Although some excellent studies have investigated the impact of these fishes on subtropical rocky reefs (e.g., Montgomery 1980a,b), I will necessarily limit this discussion to true coral reefs.

Recent studies have substantiated earlier caging experiments (e.g., Stephenson and Searles 1960; Randall 1961) showing that herbivorous fishes strongly affect the distribution and abundance of reef algae. Typically, heavily grazed dead coral surfaces become dominated by grazer-resistant crustose coralline algae (e.g., Vine 1974; Wanders 1977; Brock 1979; Hixon and Brostoff 1981, 1982), while caged but otherwise identical surfaces become covered by high standing crops of erect algae (e.g., above studies plus: Lassuy 1980, Miller 1982, Sammarco 1983), which apparently competitively exclude corallines. While grazing algae, fishes also affect interspersed assemblages of sessile animals (e.g., Day 1977, 1983). Attention has shifted lately to temporal and spatial variations in these general patterns. Hatcher and Larkum (1983) demonstrated that algal standing crops at One Tree Reef were controlled by grazing fishes all year (autumn and spring) on the reef slope (10 m depth), but only during spring in the lagoon (2 m depth). In autumn, inorganic nitrogen limited the standing crop of lagoon algae despite the continued presence of fishes.

In addition to seasonal variations, an apparently general trend within reefs is that the spatial distribution of fish grazing intensity varies inversely with tidal exposure and/or wave action (e.g., Van den Hoek *et al.* 1978) and directly with the availability of shelter for the herbivores from predatory fishes (e.g., Hay 1981a, Hay *et al.* 1983). Thus, as documented in Guam (Nelson and Tsutsui 1981) and the Caribbean (Hay *et al.* 1983), the depth distribution of grazing intensity may often be unimodal: low in very shallow water due to limited accessibility by fishes, high at intermediate depths due to high accessibility and shelter, and low in deep reef areas, where the abundance of coral shelter typically decreases. This pattern may explain the bimodal zonation of erect algal cover found on reefs such as those in Curacao (Van den Hoek 1978): high cover in the eulittoral zone (0-1 m depth), low on the upper reef slope (1-30 m),

and high again on the lower slope (30-50 m). The lack of shelter for grazing fishes probably also explains the existence of extensive algal plains occurring on sand bottoms below and between reefs (e.g., Hay 1981b, Hay et al. 1983).

As might be expected, the impact of fish herbivory strongly influences the community structure of reef algae. Hay (1981b) and Hay et al. (1983) suggested that selection for resistance to grazing may compromise competitive ability. They found that, off the Caribbean coast of Panama, fishes prevent competitively dominant (but highly palatable) sand-plain species from displacing competitively subordinate (but grazer-resistant) reef algae. This dichotomy may act to maintain between-habitat diversity in algae (Hay 1981b).

Within-habitat algal diversity is strongly affected by territorial damselfishes. As discussed in the previous section, these fishes establish and maintain dense mats of mostly filamentous algae on dead coral surfaces by defending small individual areas against other herbivores, including sea urchins (Williams 1980, 1981). By differentially grazing these mats (Irvine 1982, Hixon and Brostoff in prep.) and/or by "weeding" undesirable species (Lassuy 1980), damselfishes can affect the local diversity of algae. This effect has been demonstrated by three similar experiments in Guam (Lassuy 1980), Hawaii (Hixon and Brostoff 1981, 1982, 1983), and Australia (Sammarco 1983). Each experiment compared algal diversity on substrates exposed to three different treatments: accessible to mostly damselfish grazing inside territories, accessible to intense grazing by other herbivores outside territories, and protected within fish-exclusion cages outside territories. Although strict comparisons are precluded by differences in experimental design and laboratory analyses, some general patterns do emerge. For both damselfish species he studied, Lassuy (1980) found that, of the three treatments, caged surfaces exhibited the greatest algal diversity after 2 months. Both Hixon and Brostoff (1981, 1983) and Sammarco (1983) obtained the same result from samples taken after 2 to 6 months and 3 months, respectively. However, after a year both these studies found that algal diversity was greatest inside damselfish territories. These data, combined with the fact that Sammarco studied one of the same species as Lassuy, suggest that Lassuy's (1980) samples may have represented early successional stages. In any event, Hixon and Brostoff (1982, 1983) further showed that grazing intensity was of intermediate intensity inside territories relative to the other two treatments. These results thus supported the "intermediate-disturbance hypothesis" (sensu Connell 1978). At low levels of grazing disturbance within cages, a few dominant competitors (especially the red alga Tolypocladia in the Hawaii study) were capable of locally excluding most other species. At high levels outside territories, many local extinctions occurred. Algal diversity thus peaked at intermediate grazing intensity inside damselfish territories, where the coexistence of many species was maintained because their densities were apparently kept below levels where resources became limiting. Note, however, that not all damselfishes enhance local algal diversity; some species maintain near monocultures within their territories (e.g., Montgomery 1980a,b).

Regardless of whether or not damselfishes enhance local diversity, the greatly increased standing crop of erect algae within their territories has important secondary effects on reef communities. The algal mat serves as a refuge for invertebrate microfauna and/or various epiphytes (Lobel 1980, Hixon and Brostoff 1982 and in prep.). Also, because accretion by coralline algae adds to the reef framework and such algae (along with corals, see above) are overgrown by the algal mat, damselfish territories are probably sites of weakened reef structure (Vine 1974, Lobel 1980). Finally, damselfish territories may indirectly affect nitrogen fixation on reefs, although available data are somewhat contradictory. During the same study as Sammarco (1983) described above, Wilkinson and Sammarco (1983) found that nitrogen fixation by blue-green algae was positively correlated

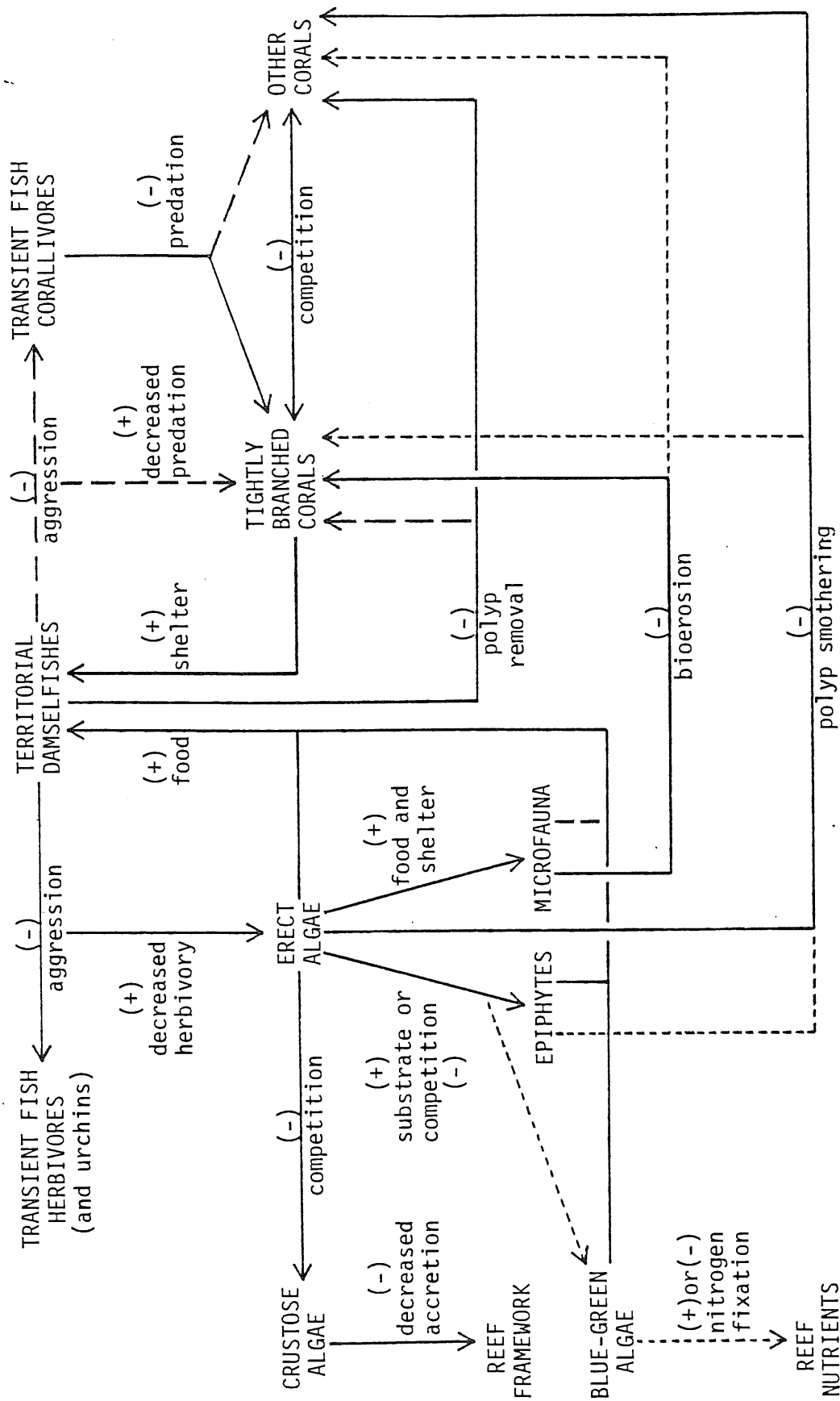


Figure 1. Flowchart summarizing interactions between fishes and benthos on a "typical" coral reef where territorial damselfishes are abundant. Arrows indicate the direction of interaction; (+) and (-) indicate positive and negative effects, respectively. Dashed lines indicate relatively weak interactions, and dotted lines indicate interactions that are poorly documented and/or controversial. Where damselfishes are rare, some of these interactions reverse. In particular, erect algae and their associates often are replaced by grazer-resistant crustose algae and their associates. See text for further explanation.

with grazing intensity on the Great Barrier Reef, being lowest within cages, intermediate within damselfish territories, and greatest outside territories. However, both Lobel (1980) and Hixon and Brostoff (in prep.), working in Hawaii, found considerably more blue-green algae inside than outside territories. These discrepancies suggest possible regional differences in local distributions of blue-green algae. In any event, herbivorous fishes, especially territorial damselfishes, extensively affect reef algae in a variety of ways.

SYNTHESIS

Attempting to synthesize the above studies into a single conceptual framework can be done only at the realized risk of over-generalization and over-simplification. So be it. In general, fishes appear to strongly influence the community structure of reef algae, much more so than that of corals. This difference may be due to coral polyps and their surrounding calcareous skeletons being less available, palatable, and productive than many algae. Indeed, Randall (1974) has indicated that truly corallivorous fishes are among the most highly evolved of fishes, suggesting that this form of predation has appeared only recently in evolutionary time. However, many algae are inferior sources of nutrition (e.g., Montgomery and Gerking 1980), and chemical defenses in algae are being discovered at an increasingly rapid rate (e.g., Norris and Fenical 1982, Paul and Fenical 1983).

In any event, while transient grazing fishes certainly control the distribution and abundance of many algae and some corals, the direct and indirect effects of territorial damselfishes appear to strongly alter a variety of components of reef benthos. These fishes truly can be considered "keystone species" (sensu Paine 1969) where they are abundant (Williams 1980, Hixon and Brostoff 1983). I thus submit Figure 1 as a flowchart summarizing the general scheme of fish-benthos interactions on a "typical" coral reef where damselfishes are common. Some of these interactions are well documented; others are not. This "synthesis" should therefore be considered a set of working hypotheses rather than a list of facts. All that can be stated unequivocally is that, first, fishes do indeed affect benthic community structure on tropical reefs, and second, more data on this important topic clearly are needed.

ACKNOWLEDGMENTS

Many thanks to F. Lynn Carpenter for her eleventh-hour review and Pam McDonald for her twelfth-hour typing of the manuscript.

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