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DISEASE-INDUCED MASS MORTALITY OF CRUSTOSE CORALLINE ALGAE ON CORAL REEFS PROVIDES RATIONALE FOR THE CONSERVATION OF HERBIVOROUS FISH STOCKS

Mark M. Littler and Diane S. Littler

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 U.S.A.

ABSTRACT

Because all coralline algae proved fatally susceptible to the bacterial pathogen, CLOD, the broad-scale infection provided a unique natural coralline-algal removal experiment. Two Fijian reef systems were studied for successional events after the CLOD epidemic. Nacalevu Reef, with low populations of herbivorous fishes, underwent a phase shift from coralline/coral domination to turf-algal domination. An important role of coralline algae was to inhibit the settlement of frondose algae by epithallium sloughing. However, at the highly grazed Butukoro Reef, the increased turf cover provided an attractive food source for herbivorous fishes (Scaridae and Acanthuridae). The resultant grazing opened up primary substrata for new coral recruits (mostly *Acropora* spp.) that had competitive advantage over algal turfs. Direct experimental evidence showed that large herbivorous fishes can reverse phase shifts from coral/coralline reefs to algal-turf dominated reefs, following coralline and coral mortality. We suggest that enough information has accrued to warrant the commercial protection of critical stocks of essential herbivores.

INTRODUCTION

Tropical reefs in high-energy environments depend on calcareous coralline algae for the maintenance of wave-resistant intertidal ridges (Littler and Doty 1975, Nunn 1993). Crustose coralline algae (Rhodophyta, Corallinales) are plants that deposit calcite, a particularly hard and environmentally resistant form of calcium carbonate. These marine plants bind surficial carbonate materials, debris, and other calcareous organisms to create stable substrata. Many crustose corallines have a prostrate-type growth form and are conspicuous as maroon, red, pink, and purple pavements covering large areas, whereas other forms develop vertically branching heads much like some corals. Crustose coralline algae, particularly *Porolithon*, are the principal binding agents that generate the structural integrity and shock resistance of the outer reef rim in high-energy systems. Coralline algae are important for the absorption of massive wave energy that would otherwise erode shoreward land masses (Nunn 1993) and for the facilitation of the development of many other sheltered shallow reef communities (Littler 1973).

A bacterial pathogen of coralline algae, designated coralline lethal orange disease (CLOD), was initially observed during June 1993 (Littler and Littler 1995b) and now occurs on South Pacific reefs that span a geographical range of over 10,000 km (i.e., Cook Islands to Mariana Islands). The occurrence of CLOD at Great Astrolabe Reef sites (Fiji) increased from zero percent in 1992 to 100 percent in 1993 (n=25, Littler and Littler 1995b). Because all taxa of Fijian coralline algae proved fatally susceptible to CLOD, the broad-scale epidemic provided a unique natural coralline-algal removal experiment. Consequently, we addressed the ecological role of crustose coralline algae on two reef systems with different herbivorous fish densities by monitoring successional events for a 4-yr period from the first appearance of CLOD in 1993.

MATERIALS AND METHODS

Two oligotrophic fringing reefs, with different densities of herbivorous fishes, were monitored for successional patterns following CLOD infection on the Great Astrolabe Reef, Fiji. Water-column levels of dissolved nitrogen and phosphorus were as low for environs adjacent to both study areas as they were in the open ocean (Yamamura *et al.* 1993). On Nacalevu reef (18° 46′S, 178° 31′ E), at the southwest end of Dravuni Island, monitoring of the benthic biota was conducted yearly from the first appearance of CLOD in 1993 to 1996. This site historically had low populations of herbivorous fishes due to spearfishing pressure from the nearby native village (personal observations). Unmanipulated , 1.0-m^2, photogrammetric quadrats provided an overview and served as control samples for potential large-scale stochastic events. Twenty-eight of these samples were taken annually during 1993 and 1994, and increased to 38 each year in 1995 and 1996. The 1.0-m^2 plots were deployed at haphazard intervals along 1.5 m-deep transects at right angles to the shoreline (90° magnetic, origins also selected haphazardly). On Butukoro Reef, at the northeast margin of Dravuni Island (18°45′S, 178°32′ E), where CLOD first appeared in 1994, similar sampling was done during 1995 and 1996. Because of the relatively large scale of the 1.0-m^2 samples, micro- and macro-algal cover were combined and quantified as frondose algae during the digitized scoring procedure.

Table 1. Successional changes in abundances of dominant cover organisms in unmanipulated, 1.0-m^2, haphazard photoquadrats on Nacalevu and Butukoro Reefs (Dravuni Island, Great Astrolabe Reef, Fiji). Values are mean percent cover (±S.E.).

	Nacalevu Reef					Butukoro Reef		
Organism group	A July1993	B June1994	C Mar1995	D Feb1996	Significance (P < 0.05)	C Mar1995	D Feb1996	Significance (P < 0.05)
CLOD	2.5 (±0.3)	1.0 (±0.8)	0.2 (±0.1)	0.1 (±0.05)	A>B,C,D	8.7 (±1.0)	<0.1	C>D
Coralline algae	75.8 (±3.1)	24.7 (±4.3)	14.8 (±1.5)	6.6 (±1.4)	A>B>C>D	54.8 (±3.9)	10.1 (±2.0)	C>D
Frondose algae	8.1 (±1.3)	73.3 (±2.1)	68.6 (±2.4)	78.6 (±2.1)	A<B,C<D	25.0 (±3.0)	53.5 (±3.0)	C<D
Corals	13.6 (±3.1)	12.0 (±1.0)	10.6 (±1.6)	8.5 (±1.6)	A,B>D	15.0 (±3.3)	9.9 (±2.0)	C,D
Quadrats (n)	28	28	38	38		38	38	

Table 2. Successional changes in abundances of dominant cover organisms and grazing scars in 108-cm^2 permanent photoquadrats after infection with CLOD on Nacalevu and Butukoro Reefs. Values are mean percent cover (±S.E., n=18).

Organism group	Nacalevu Reef						Butukoro Reef		
	A 13July1993	B 29July1993	C June1994	D Mar1995	E Feb1996	Significance (P < 0.05)	D Mar1995	E Feb1996	Significance (P < 0.05)
CLOD	<0.1	27.4 (±4.6)	0.7 (±0.5)	0.1 (±0.06)	0.1 (±0.04)	A,C,D,E<B	7.2 (±1.0)	0.3 (±0.2)	D>E
Coralline algae	76.3 (± 3.2)	52.1 (±4.9)	17.8 (±3.0)	14.7 (±2.2)	3.6 (±1.1)	A>B>C,D>E	44.2 (±4.6)	12.3 (±2.1)	D>E
Filamentous microalgae	4.1 (±0.6)	17.8 (±3.6)	43.4 (±6.1)	55.1 (±4.2)	78.4 (±3.7)	A<B<C,D<E	16.2 (±3.3)	56.6 (±2.7)	D<E
Frondose macroalgae	7.6 (±2.5)	10.1 (±2.6)	14.1 (±2.9)	17.8 (±2.8)	2.2 (±0.9)	A,B<C,D>E	10.3 (±2.5)	9.0 (±1.6)	D,E
Corals	11.2 (±3.5)	19.7 (±6.6)	1.5 (±0.5)	1.6 (±1.1)	2.8 (±1.2)	A,B>C,D,E	13.3 (±2.8)	6.6 (±2.5)	D>E
Grazing scars	0.0	0.0	0.0	0.0	0.0		3.1 (±0.6)	11.3 (±2.3)	D<E
Successful coral recruits	0.0	0.0	0.0	0.0	0.0		< 0.1	3.1 (±1.0)	D<E

Eighteen permanently marked experimental plots (108-cm^2 each) containing newly infected coralline crusts (about 50% *Porolithon onkodes* and 50% *Hydrolithon reinboldii*) also were established (haphazardly) 1.5-m deep on Nacalevu Reef during 13 July 1993. This scattered array permitted the fine-scale photogrammetric monitoring of subtle successional detail in identical plots following the demise of reef-building coralline algae. The 18 plots were rephotographed 16 days later and changes quantified by digitizing. One, two, and three years later, these plots were again rephotographed and digitized. A similar set of 18, 1.5 m-deep, newly infected plots (108-cm^2) were permanently marked on Butukoro Reef and quantified during March 1995 and February 1996. Changes in percent cover were arcsine transformed and analyzed using analysis of variance followed by the Bonferroni, *a posteriori* multiple classification test (SAS, 1985) for significance at $P<0.05$.

Fish transects were made at both Nacalevu Reef and Butukoro Reef during February 1996 by photographing (parallel to the substratum, 50-mm Nikonos RS) so as to record fish populations at 10-m intervals. A similar transect using video (15-mm Sony Handicam) was carried out at Nacalevu Reef in July 1992. Herbivorous fishes were counted in the laboratory using the photographs or stop-action video (n=36) to compare relative abundances between the two study sites.

RESULTS

CLOD was first noted in Fijian waters in 1993 (Littler and Littler 1995b) and doubled its cover by 1994. During 1993, the large-scale (1.0-m^2) unmanipulated control quadrats (Table 1) on Nacalevu Reef contained 2.5% CLOD cover, which declined to 1.0% one year later ($P<0.05$). At the same time, coralline algal cover dropped precipitously from 75.8 to 24.7%, with a concomitant sharp rise in frondose algae from 8.1 to 73.3% cover (both significant at $P<0.05$, Bonferroni test). Throughout 1994 to 1996, coralline cover continued to show a 50% rate of annual decline (Table 1, $P<0.05$) while CLOD also decreased to trace levels during this same period. Continuing into 1995 and 1996, frondose algae dominated the biotic cover at Nacalevu Reef (68.6 and 78.6%, respectively). Coral populations in the 1.0-m^2 control quadrats declined steadily from 1993 to 1996 (Table 1).

The 1.0-m^2 control quadrats at Butukoro Reef showed a pattern similar to the 1993-1994 changes at Nacalevu Reef (Table 1). CLOD decreased from 8.7% cover to trace levels from 1995 to 1996 ($P<0.05$). At the same time, coralline algae underwent a 5.4-fold reduction, while frondose algae doubled in cover (both significant at $P<0.05$, Table 1). Coral cover at Butukoro Reef was similar to that recorded at Nacalevu Reef and also decreased (by one third, not significant) between 1995 and 1996.

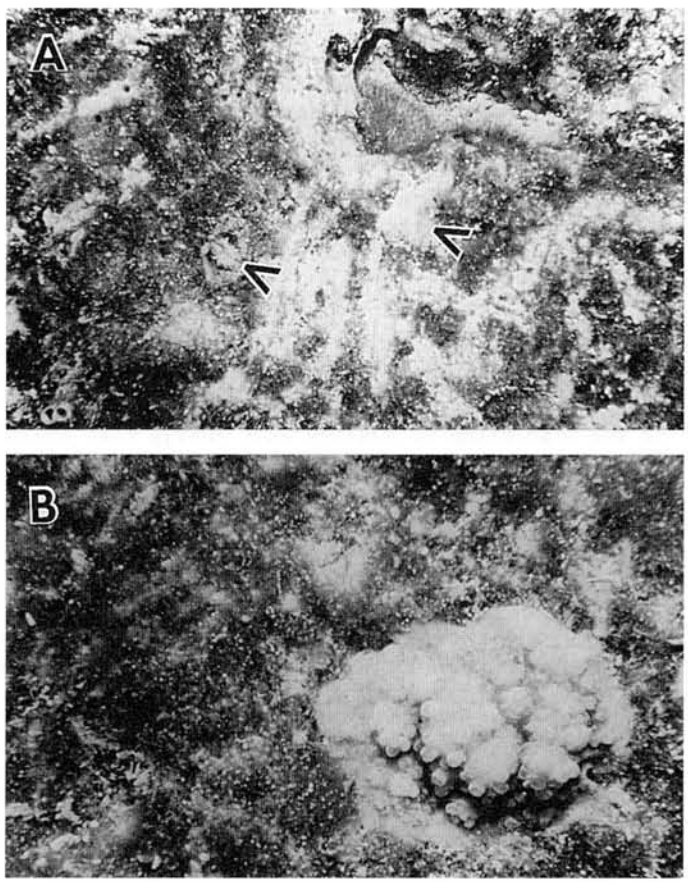

Fig. 1. A. Photoquadrat of small *Acropora* colonies (arrows) newly recruited onto grazing scars in algal turfs. This phenonenon occurred in 12 of 18 permanent quadrats on Butukoro Reef during 1995-1996. B. Note the example of overgrowth of established algal turf by the rapidly expanding margins of the competitively superior young coral colonies.

In the experimental plots intentionally inoculated with CLOD (Table 2), trace levels (i.e., a single propagule per quadrat) of infected coralline cover increased to 27.4% cover (significant at P<0.05, Bonferroni) during the first 16 days at Nacalevu Reef. One year later, bleached coralline plus CLOD-infected area averaged only 0.7% cover in these same quadrats (significantly less, P<0.05). At the same time, there was a 13-fold decrease in coral cover, a 10-fold increase in filamentous microalgae, a 3-fold decline in living cover of coralline algae, and a doubling in frondose macroalgae (all four changes significant at P<0.05, Table 2). The resurvey during March 1995 showed similar changes with further decreases in CLOD and coralline algae, along with increases in both filamentous microalgae and frondose macroalgae. Filamentous microalgal turf at Nacalevu Reef, following 4 yrs of succession, consisted of approximately 45% *Polysiphonia* sp., 42% *Spermothamnion* sp., 3% *Enteromorpha chaetomorphoides*, and 2% each of the following: *Gelidiella* sp., *Lyngbya* sp., *Anatrichum* sp., *Centroceras minutum* , and *Ceramium flaccidum*. Frondose macroalgae were mostly *Dictyosphaeria versluysii*, *Halimeda* spp., and *Laurencia* spp. as was the case at Butukoro Reef. Corals did not show significant changes in cover (1.6% vs. 1.5%, P>0.05) from 1994 to 1995. The following year (1996), filamentous microalgae became even more predominant at 78.4% cover, while coralline algae continued their decline to 3.6% cover (both changes significant at P<0.05). Frondose macroalgae also decreased significantly (P<0.05) from 17.8 to 2.2% cover between 1995 and 1996, whereas cover of CLOD and corals remained unchanged at low levels. It should be emphasized that throughout the four years of monitoring at Nacalevu Reef, no fish-grazing scars or new coral recruits were recorded in the quadrats.

The permanent experimental plots at Butukoro Reef showed trends similar to those recorded at Nacalevu Reef, with some important differences (Table 2). The changes that occurred during the year following infection by CLOD resulted in a 24-fold decline in CLOD, a 3.6-fold decrease in coralline algae, and a 2.0-fold reduction in established coral cover (all significant at P<0.05, Bonferroni). Frondose macroalgae showed no significant changes, whereas filamentous microalgae increased 3.5-fold (P<0.05). Filamentous microalgal turf at Butukoro Reef, after 1 yr of succession, consisted of about 40% *Dichothrix* sp., 20% *Lyngbya* sp., 15% brown algal crust, 10% *Pseudolithoderma* sp., 3% *Lyngbya majuscula*, 2% *Ceramium* sp., 2% *Gelidiella* sp., and <1% of each of the following: , *Derbesia marina*, *Ceramium* cf. *fastigiatum*, *Boodlea compositae*, *Polyphysa moebii*, *Cladophora* sp., *Griffithsia* sp., *Laurencia* sp., *Delesseria* sp., and *Codium* sp. Most importantly, fish-grazing scars in this microalgal turf (Fig. 1A) increased by a factor of 3.6 (significant at P<0.05), which resulted in significantly greater (P<0.05) coral recruitment on the newly grazed reef rock (Fig. 1A). New coral recruits showed a conspicuous increase in 12 of the 18 quadrats (< 0.1 vs. 3.1% cover) and consistently overgrew the previously established algal turf (e.g., Fig. 1B).

Populations of Scaridae and Acanthuridae combined were 16-times greater (significant at P<0.05) at Butukoro Reef (13.0 ±2.0 fish per sample, n=36) than at Nacalevu Reef (0.8 ±0.3, n=36). Numbers of these two fish families were equally low (1.0 ±0.5, P>0.05) at Nacalevu Reef in July 1992.

DISCUSSION

An important role of coralline algae on pristine tropical reefs was to inhibit the settlement and subsequent dispersal of frondose algae. This resulted from the sloughing of upper epithallial layers, which reduces (see Fig. 2, Masaki *et al.* 1984; Johnson and Mann 1986; Keats and Knight 1996) fouling processes in many crustose corallines. Our frequent observations of incipient fouling of living corallines followed by the detachment of large epiphyte loads during synchronous sloughing of epithallial layers in the cases of genera such as *Porolithon* and *Neogoniolithon* (e.g., Fig. 2), as well as diffuse epithallial cell shedding in genera such as *Porolithon* and *Hydrolithon*, indicated the widespread importance of this phenomenon under field conditions. Conversely, once coralline crusts were killed by CLOD, they became rapidly colonized (i.e., within days, Table 2) by microalgae. After the majority of dead substrata became covered by filamentous microalgae, algal turfs expanded their growing margins by trapping sediments (cf. Steneck 1996) and encroaching and interfering significantly with living coralline algae, corals, and large macroalgae (Tables 1 and 2). We particularly noted the entanglement of branched corals by microalgae (especially Cyanophyta, see Fig. 3), which often led to decreases in coral cover following necrosis and death of the polyps.

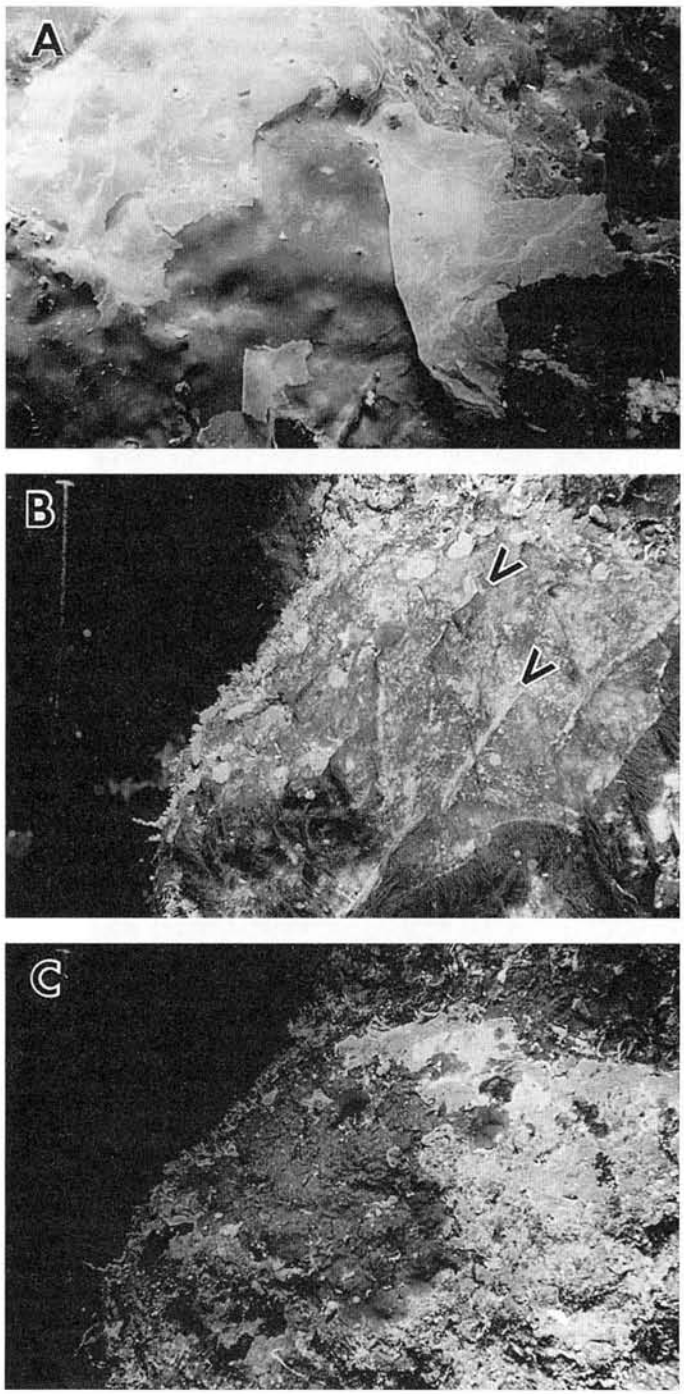

Fig. 2. A. Synchronous epithallial cell sloughing in *Neogoniolithon fosliei*. B. Example of algal turf (Cyanophyta-dominated) fouling of underlying healthy crustose coralline algae, with large sheets of sloughing epithallial cells visible as lines of folding (arrows). C. Same view as Fig. 2B following vigorous swirling of water to remove algal turf attached to sloughed cells.

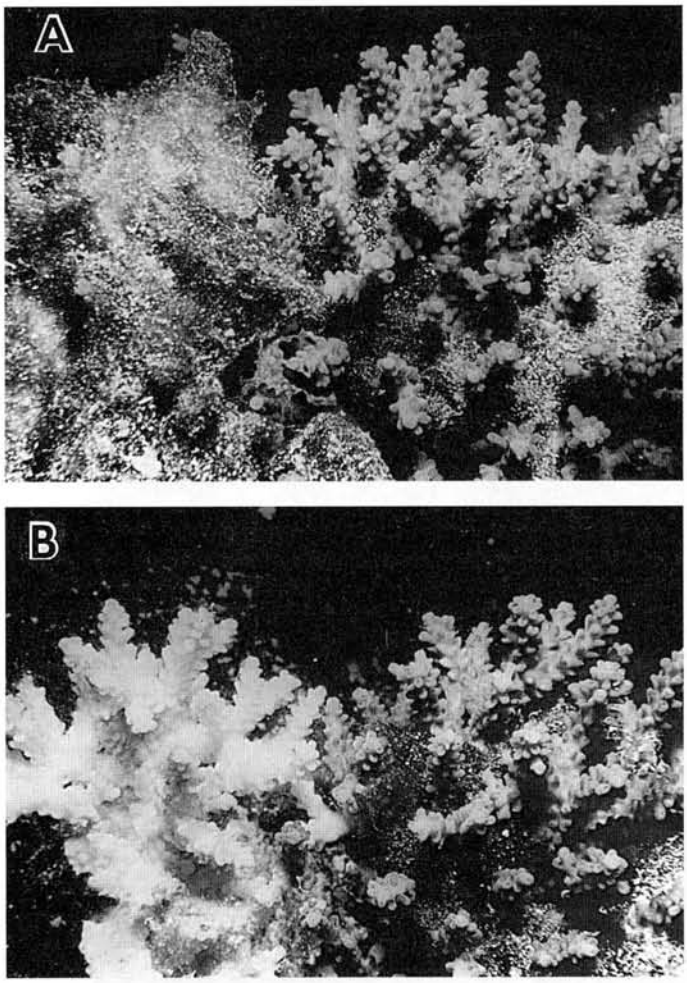

Fig. 3. A. Example of young algal turf (Cyanophyta-dominated) entangled on established *Acropora* coral at left side of colony. B. Same view as Fig. 3A following the careful removal of algal turf showing dead coral skeleton.

Low cover values do not necessarily reflect the importance or long-term impact of a mobile pathogen. CLOD was less abundant in 1994-1996 (< 1% cover) than it was in July 1993 (27% cover) in permanent successional plots at Nacalevu Reef (Table 2), because the local community composition had been altered from a preponderance of crustose corallines and corals to domination by overgrowths of fleshy algae. The same explanation applies to the considerable reduction in CLOD on Butukoro Reef from 1995 to 1996 (from 8.7% to trace coverages). We calculated from an initial abundance of only several percent cover of CLOD, in conjunction with its mean lateral rate of increase [1.5 mm per day (Littler and Littler 1995b)], that up to 50% of the total coralline algal population of an entire reef could be decimated within a single year (assuming contiguous contact of all coralline crusts). However, our data (Tables 1 and 2) documented a somewhat higher mortality of corallines than this (mean coralline mortality = 60% • yr^{-1}), which we hypothesize was due to enhanced dispersal by the production of globule-like propagules. The propagules sank rapidly (1.6 cm per second for 3-mm diameter propagules) and were highly infective (Littler and Littler 1995b). This showed that CLOD can have a large localized impact while never reaching high levels of cover. Dispersal effects were also seen in the fact that coralline regrowths, surviving from cryptic pits and depressions following the passage of CLOD bands, often became infected as well (see photograph 3 of Littler and Littler 1995a).

The impact of CLOD during this 5-yr study was unexpectedly great--so great that unmanipulated control plots ultimately showed the same successional patterns as the experimental plots inoculated with CLOD (cf. Tables 1 and 2). This suggested a high fitness of the pathogen, as measured by the large number of hosts infected (see Ewald 1994), which, in turn, revealed the importance of reef-building crustose corallines in maintaining a balance of accreting versus erosive processes on tropical reefs (Littler *et al.* 1995). The pathogen affected a broad spectrum of reef-building coralline algae (Littler and Littler 1995b), in particular the dominant builder of Pacific algal ridges, *Porolithon onkodes*. Other Corallinales that were readily infected by CLOD included the jointed forms *Amphiroa* spp. (six species), *Jania* spp. (two species), and *Corallina* sp., as well as the crustose reef-building genera, *Hydrolithon, Neogoniolithon, Lithophyllum, Mesophyllum, Sporolithon,* and *Lithothamnion*. Because of the critical role played by coralline algae in forming reef rims throughout the Indo-Pacific (Nunn 1993) and because reef-building coralline algae extend to much greater latitudes and depths than hermatypic corals (Littler *et al.* 1985), this pathogen has the potential to greatly influence coral reef ecology and reef-building processes.

On the Great Astrolabe Reef as a whole, CLOD increased from 0% in 1992 to 100% frequency at the same sites in 1993 (Littler and Littler 1995b), where it also doubled in percent cover by 1994. However, at Nacalevu Reef, CLOD declined during 1993 to 1996 (Table 2), as was also the case at Butukoro Reef between 1995 and 1996, because neither of the study sites retained an abundance of coralline hosts. Pathogen-induced alterations of population and community structure (Table 2) may be more common on coral reefs than suspected, but overlooked or attributed to other causes if the growth rates and successional events are extremely rapid or restricted to small dense patches of host taxa.

A related study (Littler *et al.* 1995) also showed that once turf communities achieve dominance over corallines, they become an attractive food source for large powerful herbivorous fishes. The scraping and rasping action of such fishes (mainly Scaridae and Acanthuridae) led to detrimental rates of bioerosion and reduction of accretion by intertidal corallines. However, the present study demonstrated an additional "beneficial role" of powerful grazing fishes on subtidal coral reefs, by significantly altering the successional patterns via enhanced recruitment of fast-growing corals.

Most reef managers and ecologists would agree that coral/coralline-dominated biotic reefs are "more desirable" than fleshy-algal dominated systems. The former have greater spatial heterogeneity, are architecturally more pleasing, provide one of the world's most diverse communities, and accrete vertical structure in response to rising sea-level changes. At Nacalevu Reef, where populations of Scaridae and Acanthuridae were low, the reef underwent a phase shift from coralline/coral domination to what appeared to be a turf-algal dominated alternative stable state, following coralline mortality by CLOD.

However, the results for the highly grazed Butukoro Reef (with 16 times greater numbers of Scaridae and Acanthuridae) were different. As turf cover increased, it provided an attractive food source for herbivorous fishes (as evidenced by a 3.6-fold increase in grazing scars, Table 2). The resultant grazing (Fig. 1A) opened up primary substrata for new coral recruits, which concomitantly increased from trace levels to 3% cover (Table 2, significant at $P<0.05$). Furthermore, it was apparent (Fig. 1B) that the newly recruited corals (mostly rapid-growing *Acropora* spp.) had competitive advantage over established algal turfs, since all examples (i.e., n=12) showed laterally spreading coralla margins overtopping the underlying filamentous algal forms. We interpret this alteration in successional patterns as the begining phase toward recovery of a more desirable coral-dominated stable state.

The present study provides direct experimental evidence showing the role of large mobile herbivorous fishes of the families Acanthuridae and Scaridae in reversing or preventing phase shifts on oligotrophic coral/coralline reefs to algal-turf dominated systems (see also Littler and Littler 1994; Hughes 1994). We suggest that enough predictive information has accumulated to justify consideration by reef and fisheries managers for the commercial protection of these critical stocks of essential herbivores.

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