

Herbivory, Nutrients, Stochastic Events, and Relative Dominances of Benthic Indicator Groups on Coral Reefs: A Review and Recommendations

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ABSTRACT. Threshold levels (i.e., tipping points where the probability of community phase shifts is increased and the potential for recoverability is reduced) for critical bottom-up interactions of productivity (e.g., nutrients) and those for top-down disturbances (e.g., herbivory) must be known to manage the competitive interactions determining the health of coral-dominated reefs. We further posit that latent trajectories (reduced resiliencies/recoverability from phase shifts) are often activated or accelerated by large-scale stochastic disturbances such as tropical storms, cold fronts, warming events, diseases, and predator outbreaks. In highly diverse and productive reef ecosystems, much of the overall diversity at the benthic primary producer level is afforded by the interaction of opposing nutrient-limiting/nutrient-enhancing and herbivory controls with the local physical and spatial variability, such that a mosaic of environmental conditions typically occur in close proximity. Although the relative dominance model (RDM) appears straightforwardly simple, because of the nature of direct/indirect and stimulating/limiting factors and their interactions it is extremely complex. For example, insufficient nutrients may act directly to limit fleshy algal domination (via physiological stress); conversely, abundant nutrients enhance fleshy algal growth, with the opposite effect on reef-building corals (via toxic inhibition or increased diseases). Furthermore, the effects of controls can be indirect, by influencing competition. Even this seemingly indirect control can have further levels of complexity because competition between algae and corals can be direct (e.g., overgrowth) or indirect (e.g., preemption of substrate). High herbivory (via physical removal) also acts indirectly on fleshy algae through reduced competitive ability, whereas lowered herbivory and elevated nutrients also indirectly inhibit or control corals and coralline algae by enhancing fleshy algal competition. Other ecologically important bottom-up factors, such as reduced light, abrasion, allelopathy, disease vectoring, and sediment smothering, also result from indirect side effects of fleshy algal competition. These factors tend to selectively eliminate the long-lived organisms in favor of weedy fast-growing species, thereby reducing desirable complexity and biodiversity.

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INTRODUCTION

There has been an exhaustive debate in the coral reef literature over the relative importance of forces that regulate community structure and resilience (i.e., the potential to resist stresses and to recover following disturbances). The expansion of the human population and associated increases in destructive fishing

(Hughes, 1994) and nutrient loading (Lapointe, 1999), compounded with ocean warming (Hoegh-Guldberg, 1999) and stochastic environmental effects (Precht et al., 2005), have been broadly debated to explain the increasing degradation of coral reefs worldwide. Because human population growth is not expected to abate, discriminating among various stressors is critical to determine conservation strategies and to eventually ameliorate the accelerating degradation of coral reefs. What has been lacking is the ability to rigorously test and differentiate among the possible acute versus chronic stressors—leading to ongoing controversy. In an attempt to address this problem, several workers (Mora, 2008; Burkepile and Hay, 2006) have conducted broad correlative and statistical assessments of communities over large regional scales. These studies have suggested a clear interaction between eutrophication in conjunction with declining herbivorous organisms as direct causes for maintaining present undesirable phase shifts on coral reefs.

Such phase shifts have been devastating to the many uniquely specialized benthic photosynthetic symbionts dominating tropical reefs, which are responsible for some of the most productive natural ecosystems known. Four major space-occupying groups of benthic primary producers combine to create high coral-reef primary productivity: reef-building corals (containing symbiotic algae), crustose coralline algae, algal turfs (fleshy filamentous and low-growing prostrate forms, and frondose macroalgae. Of these, photosynthetic corals create much of the structural heterogeneity and complexity and, with coralline algae, are primarily responsible for accretion of CaCO_3 into the reef matrix—making them the most desirable functional groups from a management perspective.

A basic objective in management ecology is to determine the mechanisms by which natural and anthropogenic factors maintain or alter structure and interactions in biotic communities. Anthropogenic eutrophication and destructive overfishing (i.e., herbivore removal by trapping, netting, poisoning, blasting) are the most tractable factors correlated with the marked global decline in tropical reef communities over the past two decades (see reviews in Ginsburg, 1994; Birkeland, 1997; papers in Szmant, 2001). The theoretical framework involving “top-down” regulation by predators and “bottom-up” control by resource availability in terrestrial systems was first proposed by Hairston et al. (1960), concepts that were later used (Atkinson and Grigg, 1984) to describe mechanisms that regulate the structure of coral-reef communities. These factors provide a valuable perspective (Figure 1) to assess and manage the human activities that affect the interac-

tive mechanisms controlling stable states, tipping points, phase shifts, and recovery among the dominant functional groups of primary producers on tropical reefs.

In healthy coral-dominated reefs, nutrient concentrations are extremely low and attachment space is occupied by a broad diversity of three-dimensional overgrowing organisms. Given these conditions, the major tenets of the management model proposed by Littler and Littler (2006: fig. 1, relative dominance model [RDM]) are (1) that competition for space and light is crucial in determining the relative abundances of major benthic photosynthetic organisms, and (2) that the outcome of competition for these resources is most often, but not exclusively, controlled by the complex interactions of biological factors (top-down controls such as grazing) and environmental factors (bottom-up controls such as nutrient levels). As suggested by Grime (1979) for terrestrial plants and expanded for marine macroalgae (Littler and Littler, 1984; Steneck and Dethier, 1994), primary producer abundance and evolutionary strategies are controlled by physical disturbances (i.e., factors that remove biomass) coupled with physiological stresses (i.e., factors that limit metabolic production). In the conceptual relative dominance model (RDM; see Figure 1), grazing physically reduces biomass (top-down) and nutrients control production (bottom-up). The complex natural interactions between herbivory and nutrients are most dramatically impacted by large-scale catastrophic disturbances such as tropical storms (Done, 1992), warming events (Macintyre and Glynn, 1990; Lough, 1994), cold fronts (Precht and Miller, 2007), diseases (Santavy and Peters, 1997), and predator outbreaks (Cameron, 1977). These events serve to trigger or accelerate the ultimate long-term phase shifts postulated in the RDM. Such stochastic events selectively eliminate the longer-lived organisms in favor of faster-growing fleshy macroalgae, which are often competitively superior (Birkeland, 1977). However, nutrients and herbivory, in the absence of large-scale disturbances, are both sufficient to maintain phase shifts independently or in concert (Smith et al., 2001; Armitage and Fong, 2004; Littler et al., 2006a).

On undisturbed oligotrophic coral-reef habitats, the effects of well-documented top-down physical controls via intense herbivory prevail, where changes in grazing intensity often show acutely rapid effects. Conversely, bottom-up stimulatory controls are more chronic, the result of lack of nutrient availability, overcompensation by grazers, and a slower growth response, compared with acute physical destruction by herbivory. However, under persistent elevated nutrient conditions (relative to low [near-undetectable] concentrations), consistent coral declines can occur, con-

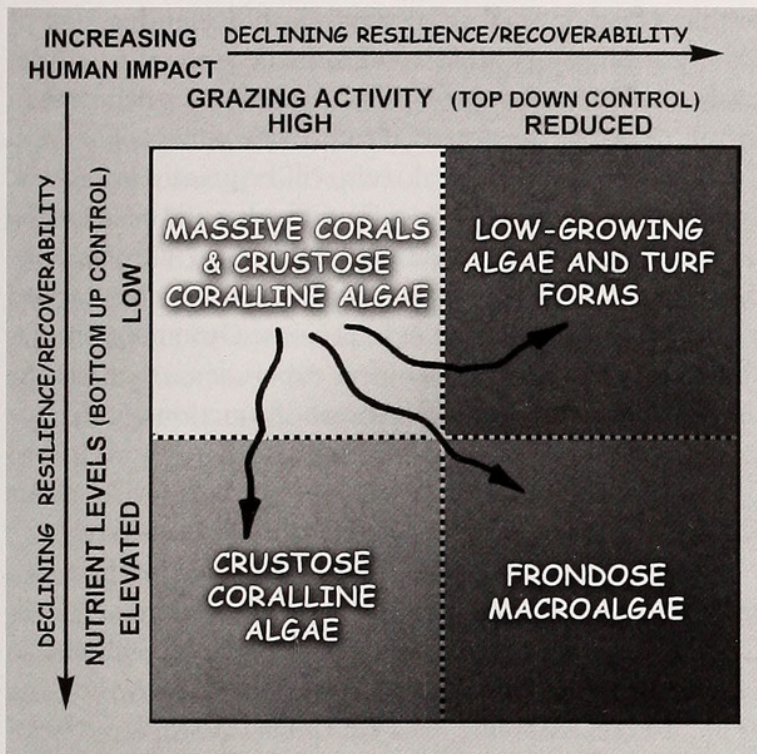


FIGURE 1. The competition-based relative dominance model (RDM). All the functional indicator groups occur under the conditions of every compartment of the model; however, the RDM predicts which group will most often *dominate*. Light to dark shading indicates declining desirability of each functional group from a management perspective. Crustose coralline algae are posited to be competitively inferior and dominate mainly by default, that is, where fleshy algae are removed by herbivores and some corals are inhibited by nutrients. The dashed lines approximate tipping points where declining herbivory and increasing nutrients reach critical levels that begin to reduce resilience to and recoverability from phase shifts. One vector can partially offset the other; for example, high herbivory can delay the impact of elevated nutrients, or low nutrients may offset the impact of reduced herbivory. As a baseline for healthy coral-reef habitats, herbivore population abundances and diversity should be high and palatable test plants should show at least greater than 50% loss 6 h^{-1} (i.e., $<6 \text{ h}$ half-life) during a replicated series of midday in situ exposures. Hypothetical nutrient tipping points (i.e., thresholds that sustain algal growth) are thus far indicated to be quite low (i.e., $\sim 0.1 \mu\text{M}$ soluble reactive phosphorus [SRP], $\sim 1.0 \mu\text{M}$ dissolved inorganic nitrogen [DIN]), as suggested by laboratory growth experiments, case studies for macroalgal overgrowth of coral reef communities, and in situ experimental nutrient enrichment research (Bell, 1992; Bell and Elmetri, 1995; Lapointe et al., 1993; Bell et al., 2007). We further posit that latent trajectories (reduced resilience/recoverability from phase shifts) are often triggered or accelerated by large-scale stochastic disturbances such as tropical storms, cold fronts, warming events, diseases, and predator outbreaks. Although these are events from which coral reefs have recovered for millions of years in the absence of humans, when tipping points remain surpassed, less-desirable stable states can persist.

comitant with algal increases that may lead to enduring states throughout all combinations of herbivory (Littler et al., 2006a). Changes in bottom-up controls and their interactions not only alter the dominance patterns of the major benthic functional groups on coral reefs but, hypothetically, could have profound long-term consequences mediated through structural transformations and chemical modifications to reef systems and their herbivorous fish populations. In other words, excessive nutrient enrichment not only increases the productivity and biomass of weedy macroalgae via bottom-up controls that alter patterns of competitive dominance (Littler et al., 1993) but, over the long term, may lead to coral habitat degradation through (1) reduced spatial heterogeneity by overgrowth (Johannes, 1975; Pastorok and Bilyard, 1985; Szmant, 1997) and (2) nighttime anoxic conditions (tolerated by macroalgae, but not by coral competitors and herbivorous predators; Lapointe and Matzie, 1996) that could indirectly reduce top-down grazer effects. Furthermore, fleshy macroalgal blooms, irrespective of how they are induced, decrease the growth and reproductive capacity of the more structurally complex reef-building corals (Tanner, 1995; Miller and Hay, 1996; Bellwood et al., 2006; Hughes et al., 2007), as well as inhibit coral larval recruitment (Birke-land, 1977; Tomascik, 1991; Ward and Harrison, 1997) and survival (Lewis, 1986; Hughes et al., 1987; Hughes, 1989; Wittenberg and Hunte, 1992). Such complicated feedback loops following eutrophication (e.g., anoxia) are known to occur in seagrass meadows (Sand-Jensen and Borum, 1991; Duarte, 1995) and could also explain decreases in fish populations on coral reefs with long-term histories of eutrophication.

CORAL-REEF MANAGEMENT

The data relevant for long-term reef management consist of (1) many important short-term caging and feeding experiments (in the case of exceedingly well-documented top-down herbivory effects), (2) circumstantial evidence (Hallock et al., 1993), (3) correlative biogeographic surveys contrasting oligotrophic versus eutrophic systems (Littler et al., 1991; Verheij, 1993; Mora, 2008), (4) comparative experiments on systems containing natural nutrient gradients (Lapointe et al., 2004, 2005b; Vroom et al., 2005), (5) physiological assays (Littler and Littler, 1990; Lapointe et al., 1997), and (6) logistically complicated, in situ, long-term, experimental/causality studies, in the case of bottom-up nutrient controls (Smith et al., 2001; Littler et al., 2006a). Top-down control by abundant populations

of large mobile herbivores is particularly well studied for coral reefs, beginning nearly five decades ago with the caging study of Stephenson and Searles (1960). As examples, Sammarco et al. (1974), Ogden and Lobel (1978), Sammarco (1980), Carpenter (1986), Lewis (1986), Morrison (1988), and numerous other workers (see review by McCook et al., 2001) have demonstrated that lowering herbivory in low-nutrient habitats (usually assumed) often results in rapid increases in low-growing stages of fleshy macrophytes.

In the study of Lewis (1986) on the same reef flat studied by Littler et al. (2006a, 2006b), increases in a dominant vegetative algal turf form (*Vaughaniella* stage) with its upright fertile *Padina* blades, *not* blooms of mixed macroalgae, followed short-term (11 week) reductions of herbivorous fish grazing under conditions of low nutrient levels. Lewis' (1986) table 4 (although pseudoreplicated) shows statistically significant, but relatively small, increases (26%) in the above *Vaughaniella*-turf stage and its reproductive *Padina* blades; however, in contrast to several literature citations, no significant increases occurred in any of the abundant upright macroalgal dominants such as *Turbinaria turbinata* and *Halimeda* spp. Such low mats are unique in containing an abundance of nitrogen-fixing blue-green algae that can enrich other members within the low-growing algal community (Adey and Goertmiller, 1987; Adey, 1998). In presumably higher-nutrient environments, herbivore removals usually result in dramatic blooms of larger frondose macroalgae (Bellwood et al., 2006: fig. 4; Hughes et al., 2007).

Throughout the past decade, many biologists and managers have not recognized the importance of chronic nutrient enrichment and associated eutrophication problems facing coral reefs. A recent study (Littler et al., 2006b) provided a detailed review and discussion of the misinterpretations, misunderstandings, and suboptimal experimental designs that pervade the literature in regard to nutrient enrichment and the health of coral reefs. Overgrown 0.5 L porous clay-pot diffusers ("mini-reefs," following a decade of recruitment, colonization, and competition) were utilized (Littler et al., 2006b) to evaluate protocols for studies of controlled nutrient enrichment on coral reefs. A commonly used nutrient source, Tree Food Stakes containing up to 6% chlorine, resulted in a significant 11-fold and 20-fold decrease of fleshy algae and calcareous coralline algae, respectively, relative to the control treatments, while blue-green algae (Cyanobacteria) became significantly (6 fold) more abundant. Osmocote-filled mini-reefs showed no significant differences from the controls for any of the indicator groups. By avoiding the

pitfalls of suboptimal study areas, insufficient duration of colonization/competition studies, inadequate nutrient detection limits, and inappropriate sources of enrichment in future research, the potential to provide new insights into the nutrient status of coral reefs will be greatly improved. Nutrient research is logistically difficult and, because the growth responses are relatively slow (i.e., chronic), requires more emphasis on multifaceted approaches carried out over sufficiently long time periods. Optimally, studies should include in situ enrichment experiments that test the long-term competitive interactions of functional indicator groups on healthy coral-dominated reefs, in addition to precisely monitoring water column nutrient levels, tissue C:N:P ratios, and algal physiological response assays.

Although nutrient data are typically lacking in coral-reef herbivory studies, natural background levels in conjunction with ample water motion are usually assumed to exceed levels that are limiting to macroalgal growth (Fong et al., 2003). As pointed out by Lewis (1986), large frondose macroalgae such as *Sargassum* and *Turbinaria* do occur in oligotrophic reef areas adjacent to coral colonies (see also Littler et al., 1986; McCook et al., 2001; Vroom et al., 2005); however, many of these frondose forms occupy microhabitats that generate increased current acceleration, such as the reef crest and tops of patch reef rocks, implicating higher nutrient fluxes (Atkinson et al., 2001). Also, large biomass/standing stocks of slow-growing perennial macroalgae (e.g., rockweeds) can develop over time under low inorganic nutrient concentrations; rainforests are good illustrations of this as well. Furthermore, *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999); therefore, in this particular situation, large plant biomasses of low diversity do not necessarily indicate detrimentally abundant dissolved nutrients. Tissue analyses of mid-shelf *Sargassum* transplants on the great barrier reef (McCook, 1999) revealed a C:N ratio of 32:1 and a C:P ratio of 1261:1, exceeding values for pelagic *Sargassum* in the nutrient-impovertised Sargasso Sea (C:P = 877:1; Lapointe, 1995), which are compelling for substantial N limitation and severe P limitation. A further consideration is the now-ubiquitous presence of significant anthropogenic nitrogen sources (from burning fossil fuels) in rainfall worldwide (Vitousek et al., 1997), making the term "pristine" relative, at best. The demise of copious coral cover (Pollock, 1928) and concomitant rise in frondose algae (Doty, 1971) and coralline algae (Littler, 1971) on the reef flat at Waikiki, Hawaii, was the first phase shift from coral to macroalgal domination that was postulated (Littler, 1973) as caused by increases in eutrophication (bottom-up control).

Eutrophication affects coral reefs to different degrees and on varying scales. Several studies (Atkinson et al., 1995; Grigg, 1995; Steven and Broadbent, 1997; McCook, 1999; Bongiorno et al., 2003) indicated no substantial adverse responses of coral species to elevated nutrients. However, other laboratory and field experiments (Pastorok and Bilyard, 1985; Tomascik and Sander, 1987; Muscatine et al., 1989; Stambler et al., 1991; Jokiel et al., 1994; Koop et al., 2001) have concluded that corals are negatively affected by increased levels of nutrients and that diversity suffers. Numerous in situ observations exemplify the types of shifts from coral dominance to algal dominance that suggest linkages with chronic nutrient loading, including case studies in Hawaii (Littler, 1973; Banner, 1974; Smith et al., 1981; Maragos et al., 1985; Grigg, 1995), Venezuela (Weiss and Goddard, 1977), the Red Sea (Mergener, 1981; Walker and Ormond, 1982), Barbados (Tomascik and Sander, 1985, 1987), American Samoa (Green et al., 1997), Reunion Island (Cuet et al., 1988; Naim, 1993), Bermuda (Lapointe and O'Connell, 1989), the Great Barrier Reef (Bell, 1992), the Florida Keys (Lapointe et al., 1994), Martinique (Littler et al., 1993), and Jamaica (Goreau et al., 1997; Lapointe et al., 1997).

In a number of cases, herbivory patterns alone (similar to nutrient levels) do not explain the distribution and abundance of benthic algae on coral reefs (Adey et al., 1977; Hay, 1981; Hatcher, 1983; Hatcher and Larkum, 1983; Carpenter, 1986). Several studies (Hatcher, 1981; Schmitt, 1997; Lirman and Biber, 2000) found no significant correlation between grazing intensity and algal biomass. A dramatic increase in algal biomass resulting from eutrophication, without any simultaneous reduction in herbivore populations, was reported (Fishelson, 1973). The importance of the very low nutrient levels involved in eutrophication (i.e., nutrient threshold hypothesis, NTH), either natural or anthropogenic, has only recently come to light (Bell, 1992; Lapointe et al., 1997; Small and Adey, 2001; Bell et al., 2007) regarding the potential for phase shifts from corals toward macroalgal dominance. These kinds of biotic phase shifts also have been attributed to overfishing of herbivore stocks (see Hughes, 1994 on Jamaican reef trends), in concert with cultural eutrophication (Goreau et al., 1997; Lapointe et al., 1997). It is now clear (Burkpile and Hay, 2006; Mora, 2008) that both herbivory and nutrient levels interact on large scales as major factors in maintaining or degrading coral-reef health.

We hasten to point out that individuals of all the functional indicator groups can and do occur under the conditions of every compartment of the RDM (see Figure 1);

however, the model predicts which group most often will *dominate* (as does the very similar fig. 2a in Bellwood et al., 2004). Such apparent presence/absence anomalies, on closer inspection, are often scientifically logical but have led to different perspectives. Following large coral bleaching events and die-offs in Belize, we have observed dramatic increases in chemically defended sponges (e.g., *Chondrilla*) and Cyanobacteria (blue-green algae) under high levels of grazing by sea urchins and fishes. Other observations that appear counterintuitive include some corals growing in high-nutrient habitats, some large fleshy macroalgae growing under low nutrients, certain turf algae exposed to high herbivory, and the frequent coexistence of crustose corallines and the other functional groups. We agree with these observations and have addressed such anomalies herein.

The general applicability as well as the limitations of the RDM can be demonstrated further in relationship to a number of recent studies. For example, nutrients and herbivory are not independent, and the positive effects of nutrients on marine plant productivity and growth can actually make plants more palatable and susceptible to grazers (McGlathery, 1995; Boyer et al., 2004). Furthermore, nutrient increases are sometimes associated with coral inhibition (Koop et al., 2001) as well as coral diseases (Harvell et al., 1999, 2002; Bruno et al., 2003), and algal blooms can serve as disease vectors (Nugues et al., 2004). The sophisticated enrichment study (ENCORE) on a large and carefully controlled scale (Larkum and Koop, 1997; Encore Group, 2001) did not produce supportive results because (1) ambient nutrient levels within the lagoon at One Tree Island are well above tipping-point concentrations that may be inhibitory to some corals, while being more than sufficient to support luxuriant frondose macroalgal growth (Bell, 1992; Larkum and Koop, 1997; Bell et al., 2007) and (2) the test organisms were isolated on raised grids to measure growth rates, precluding natural encroachment, overgrowth, or other competitive interactions crucial to testing the RDM. However, all increases in nutrient levels did adversely affect coral reproduction (Koop et al., 2001). Additionally, several short-term (<4 months) studies (Thacker et al., 2001; Belliveau and Paul, 2002; Miller et al., 1999; McClanahan et al., 2002) reported lack of algal stimulation following nutrient enrichment, further documenting the low ambient nutrient concentrations sustaining ample algal growth.

In contrast, two in situ experimental studies conducted over longer time scales in healthy coral-reef settings (Smith et al., 2001; Littler et al., 2006a), in conjunction with natural successional and competitive interactions,

provided the most relevant causality data demonstrating the importance of both nutrient and herbivory influences; the present review builds on these findings. The paper by Lapointe (1997) was the first to put forth a convincing case for the effectiveness of the RDM in addressing harmful algal bloom issues on coral reefs. Additionally, highly diverse living model systems of coral-reef communities (i.e., mesocosms), operated for decades (Small and Adey, 2001), clearly have demonstrated that minute increases in nitrogen and phosphorus reduce coral growth (sometimes causing substantial die-backs). Such self-contained systems require continuous removal of nutrients by algal-turf scrubbers or protein skimmers in combination with an abundance of fish and invertebrate grazers to maintain a high coral and algal diversity. The burgeoning awareness of coral-reef degradation worldwide (see Ginsburg, 1994; chapters in Birkeland, 1997; Gardner et al., 2003), particularly from coastal eutrophication (Bell, 1992; Windom, 1992; Nixon, 1995; Lapointe, 1997, 1999) and destructive overfishing (Hughes, 1994; Jackson et al., 2001), makes this management perspective relevant and opportune (see Figure 1).

Although harmful macroalgal blooms on coral reefs have long been attributed to nutrient enrichment and eutrophication (Littler, 1973; Banner, 1974; Johannes, 1975; Smith et al., 1981; Lapointe, 1997; Lapointe et al., 2005a, 2005b), some reef biologists have countered that such changes in benthic community structure routinely result primarily from natural stochastic events (Precht et al., 2005), overfishing of herbivorous fish stocks (Hughes, 1994; Pandolfi et al., 2003; Lesser, 2004), or loss of keystone grazers, such as the long-spined sea urchin *Diadema antillarum* (Jackson et al., 2001). Although generally supported, these last observations are not typical of the majority of grazer reduction experiments in extreme oligotrophic environments (see Lapointe, 1999), most of which have reported an expansion of small low-growing algal forms rather than macroalgal blooms (as predicted in Figure 1). It is encouraging that the critical role of excess nutrients on coral reefs has begun to receive attention in recent review papers (Scheffer et al., 2001; Hughes et al. 2003; Bellwood et al., 2004; Pandolfi et al., 2005; Burkepile and Hay, 2006; Mora, 2008). Some scientists (e.g., Precht et al., 2005) downplay declining resilience issues, instead emphasizing fundamental stochastic factors such as upwellings, hurricanes, and cold fronts (see caption, Figure 1). These occurrences represent unmanageable events from which coral reefs have recovered for millions of years, but not in the presence of modern human influences such as destructive overfishing and nutrient pollution (see Mora,

2008). There are strong interactions between catastrophic stochastic factors and the roles of herbivores and nutrients that strongly impact reefs. For example, coral mortality following hurricanes and coral bleaching events opens up large amounts of new two-dimensional space readily colonized by fast-growing algae. Such increases in productivity and the area available for grazing hypothetically satiate the herbivore pressure over large areas, assuming that natural herbivore populations have an upper limit in the amount of reef area that they can graze effectively (Williams et al., 2001; Mumby, 2006). This diluted grazing pressure and reduction in suitable shelter could in turn lead to further increases in algal cover and a decline in the recovery capacity (i.e., resilience) of coral communities. Thus, stochastic processes are unquestionably important factors in determining the trajectories of reef health and interact with the processes discussed herein.

To establish the baseline conditions and detect subsequent changes, a combination of environmental, survey, inventory, and bioassay data are essential to characterize and monitor the ambient nutrient and herbivory environments and antecedent nutrient history of a given management area. Valid and reliable data are the cornerstone needed to prioritize among different management strategies and motivate the local populace and politicians/lawmakers to support and implement the goals necessary for responsible management. The RDM provides a clear visual depiction that is easily understood and, therefore, can serve as a convincing illustrative aid. It is essential that assessment and monitoring methods should be both simple and rapid to use. Chlorophyll *a* concentration (determined by fluorometric or spectrophotometric methods; see Bell and Elmetri, 1995) is an especially useful ancillary indicator of water column enrichment because phytoplankton blooms can rapidly attenuate critical light energy while buffering inorganic nutrient pulses. Along with nutrient levels, chlorophyll *a* serves as a valuable tipping-point indicator, where levels in excess of 0.2–0.3 $\mu\text{g L}^{-1}$ indicate approaching overabundances of nutrients (Bell et al., 2007).

Water column nutrient concentrations represent the net sum of internal cycling, algal assimilation, and external inputs, relative to macroalgal growth demands (Lapointe, 1997), and therefore offer the most direct method to assess nutrient excesses on any given coral reef. Consequently, a nutrient threshold model based on nutrient concentrations (rather than on nutrient fluxes) is not only valid but is likely the best index of nutrient status. Low-nutrient tipping points, where increasing nutrients reach hypothetically critical levels that begin to reduce recoverability from phase shifts (i.e., $\sim 1.0 \mu\text{M}$ dissolved inorganic nitrogen

[DIN] = nitrogen: 0.014 ppm N or 0.040 ppm NO₃ and ~0.10 μM soluble reactive phosphorus [SRP] = phosphorus: 0.003 ppm P or 0.007 ppm PO₄), have been broadly corroborated (in developing the nutrient threshold hypothesis [NTH]; Bell, 1992; Lapointe et al., 1993; Bell et al., 2007) for sustaining macroalgal overgrowth of seagrass beds and coral reefs. The physiological/kinetic basis for such low-nutrient tipping points is the hyperbolic Monod relation (Droop, 1985; Bell et al., 2007), which is also supported by controlled, high-flux, continuous-culture laboratory experiments (Caperon et al., 1971; DeBoer et al., 1978; Lapointe and Tenore, 1981). In our experience, if modern analytical instruments can detect measurable nutrient levels, so can growth-limited macroalgae.

Additionally, a wealth of in situ coral-reef studies carried out in areas characterized by nutrient levels only moderately above the putative 0.1 μM SRP and 1.0 μM DIN tipping points (Larkum and Koop, 1997; Miller et al., 1999; Thacker et al., 2001) have reported minimal algal stimulation following experimental nutrient enrichment, further documenting the low natural nutrient concentrations required for ample algal growth and their widespread applicability. Some corals can tolerate high levels of DIN and SRP; however, nutrient tipping points not much above the present analytical limits of detection represent levels of resource availability at which resilience begins to be reduced (Scheffer et al., 2001), such that stochastic or other disturbances and stresses can trigger coral-reef ecosystem shifts toward sustained dominance by macroalgal stable states. Moreover, the macroalgal overgrowth experimentally stimulated (Smith et al., 2001; Littler et al., 2006b) in reduced-grazing/elevated-nutrient treatments demonstrates that ambient nutrient concentrations inhibitory to growth under the natural turbulence levels found on coral reefs are similar to those reported above for other tropical marine algae. It should be noted that the remote reef in the northwestern Hawaiian Islands studied by Smith et al. (2001) had nutrient levels at or above the hypothetical levels needed to sustain macroalgal growth (i.e., 1.1 μM DIN and 0.2 μM SRP). This system, with its present lack of macroalgae and dominance by unbroken thickets of three branching and one massive coral species, may be the result of overcompensation by intense grazing and, consequently, could be susceptible to a future relative dominance reversal.

Littler et al. (2006a: tbl. 1) give typical baseline herbivorous fish assay and population density data contrasting natural Belize Barrier Reef sites of low and high herbivory. Based on similar experiments conducted worldwide on coral reefs by a range of workers (Hay, 1984;

Lewis and Wainwright, 1985; Paul et al., 1987; Sluka and Miller, 2001; Littler et al., 2006a), Littler and Littler (2006) posited that less than a six hour half-life (>50% mean loss per 6 h for palatable algae) during a series of in situ, midday, assay periods is indicative of a healthy level of herbivory for the particular habitat(s) tested. Herbivore abundances also should be enumerated by counting numbers of individuals (by species), from midmorning to midafternoon throughout a typical day for weather (Littler et al., 2006a, see their table 1), at fixed distances on either side of random replicates of standardized transect lines. Video transects are quick; enumeration can be done later in the laboratory, and the videos provide a permanent record of the target species (Littler et al., 1986).

FUNCTIONAL INDICATOR GROUPS

The fast growth and turnover rates of fleshy algae compared to other reef organisms suggest their value as early-warning indicators of reef degradation. Representatives of ubiquitous algal form/function groups (from Littler and Littler, 2006) are increasingly encountered as dominants on reefs, particularly those subjected to human activities (see Littler and Littler, 2006: fig. 2).

REEF-BUILDING CORALS (CNIDARIA)

A predominance of diverse corals and calcareous coralline algae are universally accepted as the most desirable components of biotic reefs because of (1) their three-dimensional architecture, which provides habitats for a myriad of other reef organisms (largely responsible for much of the heterogeneity/high biodiversity), (2) their roles in producing the massive carbonate structure of reefs, and (3) their aesthetic qualities. The vertical structure and horizontal canopies of branching forms allow abundant populations of shade-dwelling crustose coralline algae to co-occur. Reef-building corals, while preyed upon by a few omnivorous fishes and specialist invertebrates (e.g., crown-of-thorns sea star), generally achieve dominance under the top-down control of intense herbivory (Lewis, 1986; Lirman, 2001) and extremely low nutrient concentrations (Bell, 1992; Lapointe et al., 1993). Massive corals are resistant to grazing at the higher levels of herbivory (Littler et al., 1989). Hard mound-shaped forms show relatively little colony mortality under high grazing pressure, even though occasionally rasped by parrotfishes. Contrastingly, some delicately branched corals such as *Porites porites* are quite palatable and readily eaten by

parrotfishes (e.g., *Sparisoma viride*; Littler et al., 1989; Miller and Hay, 1998). Nutrient increases are sometimes associated with coral diseases (Harvell et al., 1999, 2002; Bruno et al., 2003). As mentioned earlier, numerous corals tolerate elevated nutrient levels (Atkinson et al., 1995; Steven and Broadbent, 1997; Bongiorno et al., 2003), but their diversity suffers. Conversely, others are physiologically inhibited by increases in nitrate (e.g., *Montastrea annularis* and *Porites porites*: Marubini and Davies, 1996), ammonium (e.g., *Pocillopora damicornis*: Stambler et al., 1991; Muller-Parker et al., 1994), and orthophosphate (e.g., *Porites compressa*: Townsley, cited in Doty, 1969; *P. damicornis* and *Stylophora pistillata*: Høegh-Guldberg et al., 1997). Nutrient inhibition of coral larval settlement also has been shown for *Acropora longicyathis* (Ward and Harrison, 1997). During the extensive ENCORE program on Heron Island, all increases in nutrient levels adversely affected coral reproduction (Koop et al., 2001).

MACROALGAE

With an increase in nutrients, the growth of harmful fleshy algae is favored over that of the slower-growing but highly desirable corals (Genin et al., 1995; Miller and Hay, 1996; Lapointe et al., 1997), and the latter become inhibited by competition for space and light, increased diseases, and physiological inhibition. On healthy oligotrophic coral reefs, even very low nutrient increases may exceed critical levels that can shift relative dominances by stimulating macroalgal production while inhibiting corals. As indicated earlier, large biomass, or standing stocks, of slow-growing perennial macroalgae (e.g., rockweeds) can develop over time under low inorganic nutrient concentrations (McCook, 1999), and *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999). Therefore, in this particular situation, large plant biomasses do not necessarily indicate detrimentally abundant dissolved nutrients. Filamentous and frondose algae can outcompete corals (Birkeland, 1977; but see McCook et al., 2001), many of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies, 1996). Fast-growing algae are not just opportunists that depend on disturbances to release space resources from established longer-lived populations but become the superior competitors (Birkeland, 1977) when provided with sufficient nutrients. As a result, frondose macroalgae as a group are now generally recognized as harmful to the longevity of coral reefs because of the linkage between excessive blooms and coastal eutrophication (ECO HAB, 1997). Potential competitive

dominance of fast-growing macroalgae is inferred from their overshadowing canopy heights, as well as from inverse correlations in abundances between algae and the other benthic producer groups (Lewis, 1986), particularly at elevated nutrient concentrations (Littler et al., 1993; Lapointe et al., 1997). Macroalgae, such as *Halimeda* spp., also gain competitive advantage by serving as carriers of coral diseases (Nugues et al., 2004). The fleshy macroalgal form-group has proven to be particularly attractive to herbivores (see Hay, 1981; Littler et al., 1983a, 1983b) and only becomes abundant where grazing is decreased or swamped by excessive algal growth (chemically defended forms, e.g., Cyanobacteria, are exceptions). Such overcompensation by herbivory may explain some of the reported cases (Crossland et al., 1984; Szmant, 1997; Smith et al., 2001) of specific corals surviving high-nutrient reef environments.

CRUSTOSE CORALLINE ALGAE

The predominant members of this indicator group, the coralline algae, tend to be slow-growing, competitively inferior taxa abundant in most reef systems (Littler, 1972). However, they span a spectrum of morphotypes from thin sheet-like crusts to thick massive pavements to upright branched and columnar coral-like heads that contribute to both cementation and bulk. This functional group is highly resilient and is able to recover or restore the coral-reef system relatively more quickly, given that some crustose coralline algae chemically attract and facilitate the survival of coral larvae (Harrington et al., 2004) whereas the other two algal functional groups inhibit larval settlement. Because crustose corallines continually slough upper surface layers, they play a key role, as do filter-feeding corals, in physically preventing the settlement and colonization of many undesirable fleshy fouling organisms on coral reefs (Littler and Littler, 1997). Crustose corallines, because of their slow growth rates, tolerate low nutrient levels and generally are conspicuous, but not dominant, under low concentrations of nutrients and high levels of herbivory (Littler et al., 1991). Accordingly, they do well under both low and elevated nutrients; that is, most are not inhibited by nutrient stress and many are maintained competitor free by surface cell layer shedding (Johnson and Mann, 1986), even at lower levels of grazing (Littler and Littler, 1997). Therefore, crustose coralline algae do not require elevated nutrients, as might be inferred from the RDM (Figure 1); instead, their rise to dominance is largely controlled indirectly by the factors influencing the abundances of the other groups, primarily corals and

fleshy macroalgae. The key point is that crustose corallines predominate mainly by default (i.e., under conditions of minimal competition), where either corals are inhibited by elevated nutrients or fleshy algae are removed by intense herbivory. In independent corroboration of the herbivory portion of the RDM, a gradient of frondose- to turf- to coralline algal groups was closely correlated with escalating herbivory on coral reefs (Steneck, 1989).

LOW-GROWING AND TURF ALGAE

The turf algae are mostly dense filamentous and low-growing frondose members of all four algal phyla and tend to become dominant under minimal inhibitory top-down and stimulatory bottom-up controls. Domination by low-growing algae suggests desirably low nutrient levels but an inadequate herbivory component. Their relatively small size and rapid perennation results in moderate losses to herbivory at low grazing pressures. They have opportunistic life history characteristics, including the ability to maintain substantial nutrient uptake and growth rates under low-nutrient conditions (Rosenberg and Ramus, 1984), and also contain an abundance of nitrogen-fixing Cyanobacteria (Adey and Goertemiller, 1987; Adey, 1998) that can enrich other low-growing members of the dense turf community. Algal turfs have been shown to be favored under reduced nutrient-loading rates (Fong et al., 1987) or infrequent nutrient pulses (Fujita et al., 1988) and can form extensive horizontal mats.

DISCUSSION

This paper directly addresses the goals of an imperative research agenda (ECO HAB, 1997) by providing a management perspective and assessment strategies for the mechanisms that initiate and sustain harmful blooms of algae that degrade coral-reef ecosystems. The complex interactions of herbivory and nutrients can change gradually with no apparent effects to induce subtle declines in resiliency and recoverability of coral/coralline-dominated reef systems (Scheffer et al., 2001). As mentioned, these systems then become vulnerable to catastrophic impacts by large-scale stochastic disturbances that typically trigger or accelerate such low-resilience reef systems (Scheffer et al., 2001; Bellwood et al., 2004). Most importantly, recovery to coral domination cannot occur unless tipping points are returned to healthy levels, and even then alternative stable states may persist. For example, when catastrophic events selectively eliminate the longer-lived organisms in favor of

early-successional fleshy algae (Littler and Littler, 1984), the settlement of coral planulae is prevented and the algae persist as competitively superior states (Birkeland, 1977; Lewis, 1986). For completeness, we also point out the obvious devastating effects of toxic spills, carbonate mining, land-fill, and sediment inundation, some of which also are associated with nutrient pollution and algal blooms.

Because of global-scale degradation of coral-reef ecosystems (Ginsburg, 1994; Wilkinson, 1999), it is important to obtain relevant information on tipping points for both top-down herbivory (relatively fast acting, acute) and bottom-up nutrient controls (slower acting, chronic), both of which are reemphasized. As the first approximation, we posit that on a healthy reef system, herbivore abundances and diversity should be high, and palatable test plants should show at least a 50% mean loss per six hours (i.e., <6 h half-life) during a series of midday in situ assays. Table 1 in Littler and Littler (2006) summarizes baseline assay and critical fish population data of this sort for two natural coral-reef zones of low and high herbivory.

Nutrient threshold points (where increasing water column nutrients reach critical resilience levels such that they reduce recovery from phase shifts) have been widely postulated (as $\sim 1.0 \mu\text{M}$ DIN and $\sim 0.10 \mu\text{M}$ SRP [NTH]; Bell, 1992; Lapointe et al., 1993; Bell and Elmetri, 1995) for potential macroalgal overgrowth of coral-reef communities. As mentioned earlier, a further useful tipping-point indicator is water column chlorophyll *a*, where levels in excess of $0.2\text{--}0.3 \mu\text{g L}^{-1}$ also indicate detrimental overabundances of nutrients (Bell and Elmetri, 1995).

CONCLUSIONS

Assessment protocols for determining and monitoring the status of any given coral reef are suggested: these include (a) herbivore population assessments, (b) herbivory assays, (c) water column nutrient levels, and (d) standing stocks of functional indicator groups. These measurements can reveal quantitative tipping-point levels beyond which resilience to and recovery from undesirable phase shifts begin to become critically reduced. Tipping-point approximations are reviewed and posited both for inorganic nutrients and for herbivory.

This review specifically addresses the relatively acute top-down effects of herbivory and the more chronic bottom-up effects of nutrient enrichment on critical indicator groups of benthic primary producers: reef-building corals, crustose coralline algae, dense turf algae, frondose macroalgae, and herbivore associates.

A predominance of massive corals and calcareous coralline algae relative to frondose macroalgae and low-growing algae indicates a healthy spatially heterogeneous condition reflecting low nutrients and high herbivory. With a few exceptions, an abundance of frondose macroalgae illustrates the least desirable condition of elevated nutrient levels and reduced herbivory, possibly reflecting eutrophication in concert with destructive herbivore fishing practices. A high coverage of coralline algae suggests healthy high herbivory levels but also suggests problems with elevated nutrients that may be inhibitory to some corals. Domination by dense low-growing and turf algae indicates desirably low nutrient levels but also suggests an inadequate herbivory component.

From a management perspective, levels of herbivory and herbivore populations and of nutrients rank among the most useful quantitative indicators of coral-reef resilience and recoverability, whereas the degree of health, degradation, and mortality are inferred by the relative abundances of functional indicator groups.

The bioassay and indicator group monitoring approaches provide powerful perspectives and essential measurement criteria to enable resource managers to protect coral reefs and similar coastal systems from eutrophication, destructive overfishing, and initiation of harmful algal blooms. Human population growth has always been accompanied by changes in land and sea use and by increased exploitation of natural resources, attitudes that continue to cause broad alterations in the structure of coral-reef communities. Unless curbed, anthropogenically induced phase shifts will expand geographically at an accelerated pace. However, solutions are available, which include the use of Marine Protected Areas, banning of destructive fishing practices (e.g., trapping, poisoning, blasting, netting), and regulations protecting keystone herbivorous fish species (e.g., parrotfish, surgeonfish) from market exploitation. Fisheries controls must be backed up by strategies to regulate the effects of pollution along with an international commitment to reduce the emission of greenhouse gases and, finally, the implementation of long-term strategies to reduce or stabilize the ultimate cause of all these stressors, the world's human population growth.

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