REVIEW

Assessment of coral reefs using herbivory/nutrient assays and indicator groups of benthic primary producers: a critical synthesis, proposed protocols, and critique of management strategies[†]

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ABSTRACT

1. Rapid assessment protocols for determining and monitoring the status of any given coral reef are provided and include measuring: (a) standing stocks of functional indicator groups, (b) herbivore populations, (c) water-column nutrient levels, (d) tissue C:N:P ratios, (e) algal physiological-response assays, and (f) herbivory assays. These measurements can reveal quantitative tipping-point levels beyond which resilience to undesirable phase shifts begins to become critically reduced. Universal tipping-point approximations are reviewed for inorganic nutrients, and posited for the first time for herbivory.

2. The relative roles of top-down and bottom-up controls in determining benthic community structure and the health of coral reefs are especially important management concerns. This paper specifically addresses the top-down effects of herbivory and bottom-up effects of nutrient enrichment on critical indicator groups, i.e. reef-building corals, crustose coralline algae, dense turf algae and frondose macroalgae.

3. A predominance of (a) massive corals and calcareous coralline algae relative to frondose macroalgae and algal turfs indicates a healthy spatially heterogeneous condition reflecting low nutrients and high herbivory. An abundance of (b) frondose macroalgae illustrates the least desirable condition of elevated nutrient levels and reduced herbivory, possibly reflecting pollution in concert with destructive herbivore fishing practices. High coverage of (c) coralline algae suggests healthy high herbivory levels, but problems with elevated nutrients that are inhibitory to some corals. Domination by (d) dense turf algae indicates desirably low nutrient levels, but an inadequate herbivory component.

4. The fast growth and turnover rates of fleshy algae compared to other reef organisms highlight their value as early warning indicators of reef degradation.

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5. From a management perspective, levels of herbivory and nutrients rank among the most useful quantitative indicators of coral reef resilience; whereas, the degree of degradation and mortality are inferred from the above functional indicator groups of benthic primary producers.
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INTRODUCTION

Because of the long history of environmental stability within tropical zones, coral reefs have evolved astounding levels of biological diversity. Turbulent water motion and the many uniquely specialized benthic algae and photosynthetic symbionts dominating tropical reefs are responsible for some of the most productive natural ecosystems known. Four major space-occupying groups of benthic primary producers combine to create the bulk of coral-reef primary production: cnidarian corals (containing symbiotic algae), crustose coralline algae, algal turfs (fleshy filamentous and prostrate forms <3 cm high), and frondose macroalgae. Of these, photosynthetic corals create much of the structural heterogeneity/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 understand 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 frequently cited tractable factors correlated with the marked global decline in tropical-reef communities over the past two decades (see reviews in Ginsburg (1994) and Birkeland (1997), and papers in Szmant (2001)). The concepts of 'top-down' and 'bottom-up' controls have been used (e.g. Atkinson and Grigg, 1984) to describe mechanisms where either the actions of predators or resource availability regulate the structure of coral-reef communities; such interacting concepts can be useful in understanding coral-reef ecosystems. These factors provide a valuable perspective to assess and manage the human activities that affect the interactive mechanisms controlling stable-states and phase-shifts (e.g. destructive overfishing, eutrophication) 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 overgrowing organisms. Given these conditions, the major tenets of the proposed management model 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, 1984b; Steneck and Dethier, 1994), primary producer abundances 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) of Littler and Littler (1984a; Figure 1), grazing (top-down) physically reduces biomass and nutrients (bottom-up) control production. The complex interactions between herbivory and nutrients are most dramatically impacted by large-scale catastrophic disturbances such as tropical storms (e.g. Done, 1992), warming events (e.g. Macintyre and Glynn, 1990; Lough, 1994), cold fronts (e.g. Precht and Miller, 2006), diseases (e.g. Santavy and Peters, 1997), and predator outbreaks (e.g. Cameron, 1977). These serve to catalyse or accelerate the ultimate long-term phase shifts postulated in the RDM. Such stochastic events
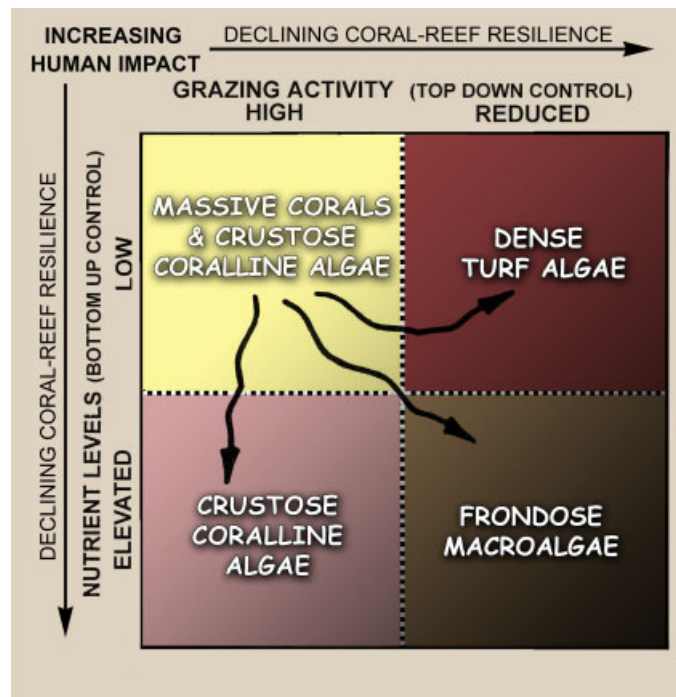
Figure 1. The competition-based Relative Dominance Model (modified from Littler and Littler, 1984a). All of the functional indicator groups occur under the conditions of every compartment of the model; however, the RDM predicts which group will most often **dominate**. Crustose coralline algae are posited to be competitively inferior and dominate mainly by default, i.e. where fleshy algae are removed by herbivores and some corals are inhibited by nutrients. The dotted lines approximate tipping points where declining herbivory and increasing nutrients reach critical levels that begin to reduce resilience to phase shifts. As a baseline for healthy coral-reef habitats, herbivore abundances and diversity should be high and palatable test plants should show at least a $> 50\%$ loss$\cdot 6\,h^{-1}$ (i.e. < 6-h half-life) during a replicated series of mid-day *in situ* exposures. Nutrient tipping points (i.e. thresholds,) have proven to be quite low and universal (i.e. $\sim 0.1\,\mu$M SRP, $\sim 1.0\,\mu$M DIN), as corroborated (Bell, 1992, 1995; Lapointe *et al.*, 1993) by laboratory growth experiments, case studies for macroalgal overgrowth of coral reef communities, and *in situ* experimental nutrient enrichment research. Light to dark shading indicates declining desirability of each functional group from a management perspective. One vector can partially offset the other (e.g. high herbivory can delay the impact of elevated nutrients, or low nutrients may offset the impact of reduced herbivory). We further posit that latent trajectories (reduced resiliencies to phase shifts) can be activated or accelerated by large-scale natural stochastic disturbances such as tropical storms, cold fronts, warming events, diseases, and predator outbreaks. These are events from which coral reefs have recovered for millions of years in the absence of humans, but when tipping points remain surpassed, less-desirable stable states can persist.

selectively eliminate the longer-lived organisms in favour of faster growing fleshy macroalgae, which are often competitively superior.

On undisturbed oligotrophic coral-reef habitats, the effects of well-documented top-down physical controls via intense herbivory prevail; whereas, bottom-up stimulatory controls are minimal, owing to lack of nutrient availability and over-compensation by grazers. However, under persistent elevated nutrients (relative to low (undetectable) concentrations) consistent coral declines can occur, concomitant with algal increases that may lead to enduring states throughout all combinations of herbivory. 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 also 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 also lead to coral habitat degradation through: (1) reduced spatial heterogeneity by overgrowth (Johannes, 1975; Pastorok and Bilyard, 1985; Szmant, 1997), and (2) night-time 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), as well as inhibit coral larval recruitment (Birkeland, 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 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.

STATUS OF KNOWLEDGE

The data relevant for testing the RDM 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 (e.g. Hallock *et al.*, 1993), (3) correlative biogeography surveys contrasting oligotrophic versus eutrophic systems (e.g. Littler *et al.*, 1991; Verheij, 1993), (4) comparative experiments on systems containing natural nutrient gradients (e.g. Lapointe *et al.*, 2004, 2005b), (5) physiological assays (e.g. Littler and Littler, 1990; Lapointe *et al.*, 1997), and (6) logistically complicated *in situ* manipulative studies, in the case of bottom-up nutrient controls (e.g. Smith *et al.*, 2001; Littler *et al.*, 2006). Top-down control by abundant populations of large mobile herbivores is particularly well studied for coral reefs, beginning over four 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), Morrisson (1988), and numerous other workers (see review by McCook *et al.* (2001)) have demonstrated that lowering herbivory without changing nutrient inputs (usually assumed) mostly results in rapid increases in dense algal turfs (including diminutive stages of frondose macrophytes < 3 cm high). Such low mats are unique in containing an abundance of nitrogen-fixing blue-green algae that can enrich other members within the low-growing turf community (Adey and Goertmiller, 1987; Adey, 1998).

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 limiting to macroalgal growth (Fong *et al.*, 2003). As pointed out by Lewis (1986), large frondose macroalgae do occur in oligotrophic reef areas adjacent to coral colonies (see also Littler *et al.*, 1986a; McCook, 2001); however, many of these forms occupy micro-habitats 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 biomasses/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 co-exist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999a); therefore, in this particular situation, large plant biomasses do not necessarily indicate detrimentally abundant dissolved nutrients. A further consideration is the now-ubiquitous presence of substantial 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 as due to increases in eutrophication (bottom-up control) (Littler, 1973).

Eutrophication affects coral reefs to different degrees and on varying scales. Several studies (e.g. Atkinson *et al.*, 1995; Grigg, 1995; Steven and Broadbent, 1997; McCook, 1999; Bongiorni *et al.*, 2003) indicated no substantial adverse responses of coral species to elevated nutrients. However, other laboratory

and field experiments (e.g. 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 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, 1982; 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 (like nutrient levels) do not explain the distributions and abundances of benthic algae on coral reefs (Adey *et al.*, 1977; Hay, 1981; Hatcher, 1983; Hatcher and Larkum, 1983; Carpenter, 1986). Several studies (Hatcher, 1982; Schmitt, 1997; Lirman and Biber, 2000) found no significant correlation between grazing intensity and algal biomass. A dramatic increase in algal biomass due to eutrophication was reported (Fishelson, 1973) without any simultaneous reduction in herbivore populations. 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) regarding the phase-shifts from corals toward macroalgal dominance. These kinds of biotic phase shifts also have been attributed to overfishing of herbivore stocks (for example, see Hughes (1994) on Jamaican reef trends over the past 20 years), in concert with cultural eutrophication (Goreau *et al.*, 1997; Lapointe *et al.*, 1997).

The RDM is not infallible and exceptions are commonplace. One needs to realize that individuals of all of the functional indicator groups can occur under the conditions of every compartment of the model (Figure 1); however, the RDM predicts which group most often will **dominate** (as does the very similar Figure 2a in Bellwood *et al.* (2004)). These apparent presence/absence anomalies, on closer inspection, are often scientifically logical, but have led to different perspectives — which we hope will not cause readers who disagree with the RDM to, therefore, assume the proposed monitoring protocols are not useful. Observations that appear counter-intuitive 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 co-existence of crustose corallines and the other functional groups. We agree with these observations and address such concerns later in the section entitled 'Interpretation of functional indicator groups'.

The RDM's general applicability as well as its limitations can be demonstrated further in relation 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 with coral diseases (Harvell *et al.*, 1999, 2002; Bruno *et al.*, 2003), and algal blooms can serve as the 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 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) 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 (Miller *et al.*, 1999; Thacker *et al.*, 2001; Belliveau and Paul, 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* manipulative studies conducted over longer timescales in low-nutrient healthy coral-reef settings (Smith *et al.*, 2001; Littler *et al.*, 2006), in conjunction with natural successional/competitive interactions, provided the most relevant evidence demonstrating the importance of both nutrient and herbivory influences; the present study builds on these findings. 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) and Gardner *et al.* (2003)), particularly from coastal eutrophication (e.g. Bell, 1992; Windom, 1992; Nixon, 1995; Lapointe, 1997, 1999) and destructive overfishing (e.g. Hughes, 1994; Jackson *et al.*, 2001) makes this revitalized management perspective (Figure 1) valuable and opportune.

Although harmful macroalgal blooms on coral reefs have long been attributed to nutrient enrichment and eutrophication (e.g. 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 result primarily from natural stochastic events (Precht and Miller, 2006), overfishing of herbivorous fish stocks (Hughes, 1994; Pandolfi *et al.*, 2003; Lesser, 2004), and/or loss of keystone grazers, such as the long-spined sea urchin *Diadema antillarum* (Jackson *et al.*, 2001). These last conclusions are not supported by the majority of grazer reduction experiments in oligotrophic environments, most of which have reported an expansion of algal turfs (<3 cm high) rather than macroalgal blooms (as predicted in Figure 1; see Lapointe (1999)). Examples include studies in the Red Sea (Vine, 1974), Fiji (Littler and Littler, 1997), Belize (Lewis, 1986), the Great Barrier Reef (Sammarco, 1983), and St Croix (Carpenter, 1988).

As mentioned, the decline of keystone grazers has been attributed to be the leading cause of harmful macroalgal blooms on the reefs of south-east Florida and Jamaica (Hughes *et al.*, 1999; see also Jackson *et al.*, 2001; Pandolfi *et al.*, 2003). These workers did not recognize (see also Szmant and Forrester, 1996; Szmant, 2002; Precht and Miller, 2006) the compelling additional information (e.g. Lapointe *et al.*, 1990, 2004, 2005a, 2005b; Lapointe and Clark, 1993; Lapointe, 1997) suggesting the broad scale and escalating rate of anthropogenic nutrient pollution and its consequences to Florida's coral reefs. The timeline of Jackson *et al.* (2001) invoking keystone herbivore losses for the decline of coastal ecosystems, including the emergence of harmful macroalgal blooms, has been clarified in the rebuttal by Boesch *et al.* (2001; also see Lapointe *et al.*, 2005a, 2005b).

However, it is encouraging that the critical role of excess nutrients on coral reefs has begun to receive appropriate recognition in recent review papers (Scheffer *et al.*, 2001; Hughes *et al.*, 2003; Bellwood *et al.*, 2004; Pandolfi *et al.*, 2005). Although, some scientists (e.g. Precht and Miller, 2006) continue to downplay declining resilience issues, instead invoking fundamental, but unmanageable, stochastic factors such as upwellings, hurricanes, and cold fronts (see Figure 1 caption); events from which coral reefs have recovered for millions of years in the absence of human influences. However, nutrient/herbivory models are now beginning to receive considerable attention (cf. Figure 7 of Littler and Littler (1984a) with the very similar Figure 2a in Bellwood *et al.* (2004)). The coral-reef scientific community needs a broader theoretical perspective (e.g. Scheffer *et al.*, 2001; Bellwood *et al.*, 2004; Pandolfi *et al.*, 2005) to further the recognition of the role played by chronic nutrient enrichment in the coral-reef health/resilience paradigm. Hopefully, the well-founded plea (Pandolfi *et al.*, 2005) for scientists to 'stop arguing about the relative importance of different causes of coral reef decline', will encourage much-needed insightful research on the role of nutrients.

ASSESSMENT AND MONITORING PROCEDURES

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/herbivory environments and antecedent nutrient history of a given management area. The purpose here is to decide which of nutrients and/or herbivores to manage (usually both merit as much effort as possible), and valid/reliable data are the cornerstone needed to prioritize among different management strategies and to convince 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 (also the very similar Figure 2a in Bellwood *et al.* (2004)) and, therefore, can serve as an influential illustrative aid. It is essential that assessment/monitoring methods should be both simple and rapid to use. Some of the following protocols are well known and require minimal elaboration; whereas, several are new and, therefore, must be described in more detail. The frequency of monitoring is entirely dependent on the system in question, but should document the time and scale of significant changes.

Environmental data

Secchi disc depths should be determined weekly at noon in order to physically characterize water quality (light penetration). Salinity is also easily measured by hand-held refractometer. Water temperature must be monitored as frequently as possible (we recommend programmable data loggers) because of the devastating impact of elevated temperatures on reef-building corals. Chlorophyll *a* concentration (determined by fluorometric or spectrophotometric methods; see Bell and Elmetri (1995) is an especially useful indicator of water-column enrichment because phytoplankton blooms can rapidly buffer inorganic nutrient pulses. It serves as a valuable tipping-point indicator, where levels in excess of 0.25–$0.5\,\mu g.L^{-1}$ universally indicate detrimental over-abundances of nutrients (Bell and Elmetri, 1995).

Analysis of macroalgal tissue nutrient levels (C:N:P ratios)

Collections of dominant macroalgae should be analysed monthly for tissue C, N and P contents. These data are useful to assess the long-term nutrient history within any given environment, since antecedent nutrient events will have been recorded via uptake by the plants themselves. Tissue samples are usually sent to laboratories that contract for analytical services. At present, C:N and C:P ratios can be calibrated to the range of values reported (e.g. Lapointe *et al.*, 1992, 1994, 1997, 2005a) for a wide variety of taxa throughout a spectrum of systems, ranging from oligotrophic to eutrophic. In the future, the range of tissue nutrient ratios should be calibrated to the growth rates of cosmopolitan indicator algae for even greater precision (for example, see values reviewed in Larned (1998)).

Water column nutrient levels

To further characterize the nutrient environment, replicate water samples should be collected monthly, filtered, and quick-frozen from each target site. Dissolved inorganic nitrogen ($DIN = NH_4^+ + NO_3^- + NO_2^-$) and soluble reactive phosphorus ($SRP = PO_4^{3-}$) analyses usually are contracted with laboratories that provide these services. To interpret water-column nutrient data, it must be emphasized that both delivery rates and concentrations are important (Atkinson *et al.*, 2001), but concentrations are paramount. Once diffusion gradients are eliminated by the levels of water motion typically present on most coral reefs, concentration becomes the issue. Also, 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 a coral reef. Consequently, a nutrient threshold model based on nutrient concentrations (rather than on nutrient fluxes) is not only valid, but is probably the best index of nutrient status.

Because tipping points are an essential, but still controversial, component of the proposed assessment strategy, we critique them in considerable detail. Low-nutrient tipping points, where increasing nutrients reach critical levels that begin to reduce resilience to phase shifts (i.e. $\sim 1.0\,\mu M$ DIN, $\sim 0.10\,\mu M$ SRP), have been broadly corroborated (as the Nutrient Threshold Hypothesis (NTH)), (Bell, 1992; Lapointe *et al.*, 1993) for macroalgal overgrowth of seagrass and coral reef communities at Kaneohe Bay in Hawaii, fringing reefs of Barbados, inshore reefs within the Great Barrier Reef lagoon, and the reefs of the Houtman Abrolhos Islands, Western Australia (Crossland *et al.*, 1984). The physiological/kinetic basis for such low-nutrient tipping points is the well-known Michaelis – Menten model, which is also supported by controlled, high-flux, continuous-culture, laboratory experiments (Caperon *et al.*, 1971; DeBoer *et al.*, 1978; Lapointe and Tenore, 1981).

Additionally, a wealth of *in situ* coral-reef studies carried out in areas characterized by nutrient levels only moderately above the $0.1\,\mu M$ SRP and $1.0\,\mu M$ DIN tipping points (Larkum and Koop, 1997; Miller *et al.*, 1999; Thacker *et al.*, 2001), reported minimal algal stimulation following experimental nutrient enrichment — further documenting the low natural nutrient concentrations required for ample algal growth and their widespread applicability. Moreover, the macroalgal overgrowth experimentally stimulated (Smith *et al.*, 2001; Littler *et al.*, 2006) in reduced-grazing/elevated-nutrient treatments demonstrates that ambient nutrient concentrations inhibitory to growth under the natural turbulence levels found on coral reefs are extremely low, but universally similar to those reported above for other tropical marine algae.

Some corals can tolerate high levels of DIN and SRP; however, nutrient tipping points not much above present analytical limits of detectability represent a universal level of resource availability at which resilience begins to be reduced (Scheffer *et al.*, 2001), such that stochastic or other disturbances/stresses can shift coral-reef ecosystems towards dominance by macroalgal stable states. Managers need to realize that orthophosphate can inhibit (Simkiss, 1964) carbonate formation at concentrations above $0.01\,\mu M$ and also block deposition of external skeletal materials in some marine animals. Ammonium enrichment can also negatively impact reef-building corals (Muller-Parker *et al.*, 1994).

Nutrient enrichment assays

The photosynthetic responses to DIN and SRP enrichment (O_2 method detailed in Lapointe (1987), Littler and Littler (1990) and Schaffelke (1999b)) are useful as an index to the long-term integration of ambient nutrient concentrations. Lack of significant increases of P_{max} following enrichment of DIN and/or SRP indicates problematically high antecedent nutrient histories. Supporting data such as tissue and seawater nutrient concentrations in conjunction with physiological responses, such as respiration and photosynthetic rates, following realistic nutrient pulses (Schaffelke, 1999b), are not only useful to determine whether management areas have had oligotrophic or eutrophic histories, but can also identify the problem nutrients.

Herbivory tipping point assays

Because this concept is novel, the methods involved require a relatively detailed presentation. The tipping point for herbivory, where decreasing grazing reaches a critical level that begins to reduce resilience to phase shifts, should be assayed using a highly palatable cosmopolitan test alga such as *Acanthophora spicifera*. This ubiquitously abundant red alga is a preferred food item of both parrotfishes and surgeonfishes (Lewis and Wainwright, 1985), as well as of sea urchins (Littler *et al.*, 1983b). The alga is cut into measured segments (e.g. 7.0 cm lengths) and attached to dead coral-rubble fragments by thin rubber bands. Replicates are placed haphazardly in each reef zone of interest for up to 6 h at midday, collected, and again measured (i.e. length, area or wet weight).

At first, herbivore activity is generally lower but increases with each early trial, so assays should be repeated until narrow confidence limits are achieved. Also, trials should be closely monitored and terminated when about 50% of the test plants have been consumed. Additionally, blades of the palatable

Table 1. Herbivorous fish densities and grazing intensities for typical Belize Barrier Reef (Carrie Bow Cay, CA) back-reef flat zones of low-herbivory and high-herbivory (see Littler *et al.* (2006) for details). The high herbivory site was characterized as having an average of 145-fold more surgeonfish and 148-fold more parrotfish than the low herbivory site. In agreement, the healthy high herbivory site averaged 80% *Acanthophora spicifera* loss $\cdot$ 6 h^{-1} and 100% *Thalassia testudinum* loss $\cdot$ 3.2 h^{-1}; compared with 5% (16-fold lower) and 3% (62-fold lower) losses, respectively, for the low-herbivory site. All *in situ* percentage loss values ($N = 15$) between the two study sites are significantly different ($P < 0.01$, Kruskal–Wallis)

Study and taxa	Low-herbivory site		High-herbivory site	
	$N \cdot m^{-2}$	% loss $\cdot$ h^{-1}	$N \cdot m^{-2}$	% loss $\cdot$ h^{-1}
Littler *et al.*, (2006)				
Acanthophora spicifera assay	—	1.0	—	16.5
Scaridae	0.001	—	0.180	—
Acanthuridae	0.001	—	0.164	—
Lewis and Wainwright (1985)				
Acanthophora spicifera assay	—	0.7	—	10.2
Scaridae	0.001	—	0.115	—
Acanthuridae	0.001	—	0.126	—
Hay (1981)				
Thalassia testudinum assay	—	0.5	—	30.9

red alga *Gracilaria* spp., the brown alga *Padina* spp. (Lapointe *et al.*, 2004), or the seagrass *Thalassia testudinum* (Hay, 1981) can be substituted in the above assay or used to further augment the data. This technique avoids novelty effects (i.e. artifactual conspicuousness) that could bias grazing patterns and rates. Gaudy markers, or materials such as coloured rope and surveyor's tape, alarm herbivorous fishes in areas where they are intensively harvested and, conversely, attract them in protected (no-fishing) reserves (personal observations). The percentage eaten is determined by re-measuring the algal segments. Herbivore abundances also should be enumerated by counting numbers of individuals (by species), from mid-morning to mid-afternoon throughout a typical day for weather, 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 they provide a permanent record of the target species (Littler *et al.*, 1986b).

In reef systems having healthy levels of herbivory, grazer abundances and diversity should be high and palatable test plants will show the kinds of losses posited below. Table 1 gives typical baseline herbivorous fish assay and 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 (e.g. Hay, 1984; Lewis and Wainwright, 1985; Paul *et al.*, 1987; Sluka and Miller, 2001; Littler *et al.*, 2006), we posit that less than a 6-h half life ($> 50\%$ mean loss per 6 h) during a series of *in situ*, mid-day, assay periods is indicative of a healthy level of herbivory for the particular habitat(s) tested.

Biotic indicator patterns

Multiple, photographic (digital images or video), randomly located transects on compass headings 90° to biotic zonational patterns should be taken perpendicular to the substrate (Littler *et al.*, 1986b). Simultaneously, voucher specimens of dominant macrophytes and turf algae are required for taxonomic purposes. In the laboratory, the digital images are randomly selected and scored for percentage cover (see Littler and Littler, 1985). To describe the natural species assemblages along transects in an unbiased manner, the cover data of each species for all quadrats are subjected to hierarchical cluster analysis (flexible sorting, unweighted pair-group method) using the Bray and Curtis (1957) coefficient of similarity. The resultant dendrogram of similar quadrat groupings, based on the dominant biota and environmental

affinities, is used to characterize zones (see Littler *et al.*, 2006). An abundance of palatable algae indicates declining natural populations of herbivorous reef fishes. Corals and members of the calcified-crustose and jointed-calcareous algal forms have evolved anti-herbivore defences (e.g. toughness, structural inhibition, low calorific content, or low palatability), and show the greatest resistance to herbivory by generalist fish grazers with a gradient of increasing palatability from the more fleshy thick-leathery forms toward the coarsely branched, sheet-like and filamentous algal forms (see Littler *et al.* (1983a) for functional/ morphological characterization).

INTERPRETATION OF 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 are increasingly encountered as dominants on reefs, particularly those subjected to human activities. Considering Figure 1: (1) a predominance of diverse corals and calcareous coralline algae relative to frondose macroalgae and algal turfs would indicate a desirable healthy state reflecting low nutrients and high herbivory. An abundance of (2) frondose macroalgae most often indicates the least desirable condition of elevated nutrient levels and reduced herbivory, possibly reflecting pollution in concert with destructive (i.e. trapping, netting, poisoning, blasting) herbivore fishing practices. High coverage of (3) coralline algae could indicate problems with elevated nutrients, but healthy high-herbivory levels. Domination by (4) turf algae suggests desirably low nutrient levels, but an inadequate herbivory component. However, as with any environmental indicator group, knowledge of ecology and natural history is needed to justify the application. To provide such information the four functional indicator groups are characterized in detail below.

Reef-building corals (Cnidaria)

Corals (Figure 2(A)) 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 (Figure 2(A)) 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 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); however, numerous corals tolerate elevated nutrients (e.g. Atkinson *et al.*, 1995; Grigg, 1995; Steven and Broadbent, 1997; Bongiorni *et al.*, 2003), but 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; and *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 programme on Heron Island, all increases in nutrient levels adversely affected coral reproduction (Koop *et al.*, 2001).
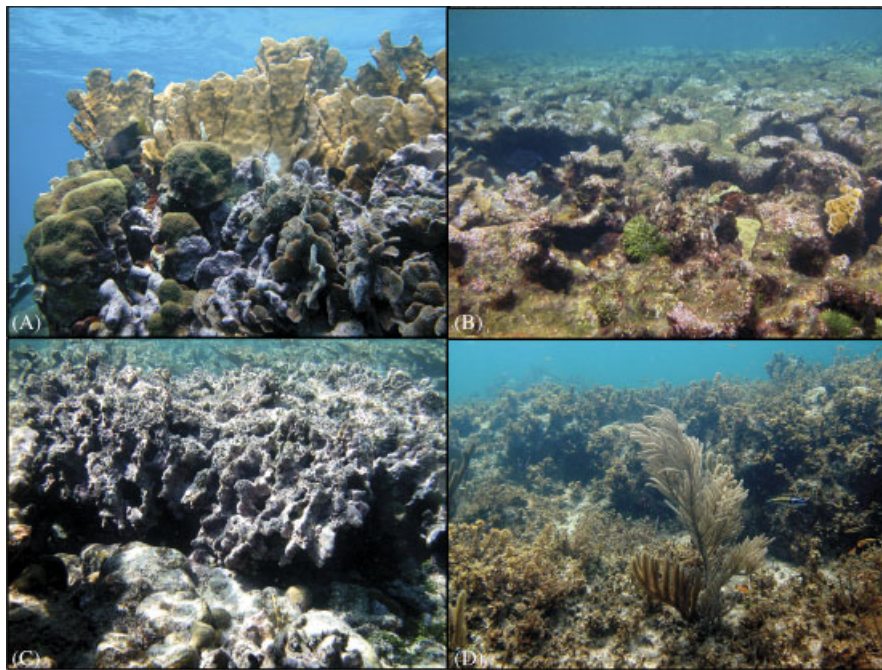
Figure 2. Examples of the four functional indicator-groups of benthic primary producers, i.e. (A) reef-building corals (+ crustose coralline algae), (B) dense turf algae, (C) crustose coralline algae and (D) frondose macroalgae. Photographs are from Bahamian reefs.

Crustose coralline algae

The predominant members of this indicator group (Figure 2(C)) 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/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), while 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 (Figure 2(A); Littler et al., 1991). Accordingly, they do well under both low and elevated nutrients (i.e. 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 (Figures 1 and 2(C)); 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 become 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).

Turf algae

These are mostly dense filamentous members of all four algal phyla (Figure 2(B)) and tend to become dominant under minimal inhibitory top-down and stimulatory bottom-up controls. 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 favoured under reduced nutrient-loading rates (Fong et al., 1987) or episodic nutrient pulses (Fujita et al., 1988) and can form extensive horizontal mats. Numerous studies have shown the expansion of mostly dense algal turfs, and to a lesser extent macroalgae, resulting from the removal of fish or echinoid grazers on a wide variety of oligotrophic reefs worldwide, including the Red Sea (Vine, 1974), Fiji (Littler and Littler, 1997), Belize (Lewis, 1986), the Great Barrier Reef (Hatcher and Larkum, 1983; Sammarco, 1983; Klumpp et al., 1987), and Saint Croix (Carpenter, 1988).

Macroalgae

With an increase in nutrients, the growth of harmful fleshy algae (Figure 2(D)) is favoured over 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. 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 (Figure 2(D)) are now generally recognized as harmful to the longevity of coral reefs due to the linkage between excessive blooms and coastal eutrophication (ECOHAB, 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 (e.g. 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 (Figure 2(D)) has proven to be particularly attractive to herbivores (see Hay, 1981; Littler et al., 1983a, 1983b) and only becomes abundant where grazing is lowered or swamped by excessive algal growth. Such overcompensation by herbivory may explain some of the reported cases (e.g. Crossland et al., 1984; Szmant, 1997) of specific corals surviving high-nutrient reef environments.

DISCUSSION

Significance

The issues addressed in this paper concerning the roles of top-down and bottom-up controls in determining benthic community structure of coral reefs are vital management concerns (NRC, 1995, 2000). The following are six key points: (1) The critical interactions of productivity (bottom-up) and those of disturbance (top-down) must be known in order to manage the mechanisms that mediate the competitive interactions determining the health of a particular coral-reef habitat. (2) 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/enhancing and herbivory controls with the local physical/spatial

variability, such that a mosaic of environmental conditions typically occur in close proximity. (3) Although the RDM appears straightforwardly simple, because of the nature of direct/indirect and stimulating/limiting interacting factors 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. (4) 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. pre-emption of substrate). High herbivory (via physical removal) also acts indirectly on fleshy algae through reduced competitive abilities; whereas, lowered herbivory and elevated nutrients also indirectly inhibit/control corals and coralline algae by fleshy-algal competition. (5) Other ecologically important bottom-up factors, such as reduced light, abrasion, allelopathy, disease vectoring, and sediment smothering, also can be indirect side effects of fleshy algal competition. These tend to selectively eliminate the longer-lived organisms in favour of fast-growing species, thereby reducing desirable complexity and biodiversity. (6) The most practical indicators of coral-reef degradation and mortality, from a management perspective, are functional groups of dominant benthic primary producers (i.e. corals, coralline algae, dense algal turfs, frondose macroalgae; Figure 2) and their herbivore associates.

This paper directly addresses the goals of an imperative research agenda (ECOHAB, 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 resiliencies 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). 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 favour of early successional fleshy algae (Littler and Littler, 1984b), 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 sediment inundation (land-based and dredging), toxic spills, carbonate mining, and landfill, some of which also are associated with nutrient pollution.

Because of global-scale degradation of coral-reef ecosystems (e.g. Ginsburg, 1994; Wilkinson, 1999), it is important to obtain relevant information on tipping points for both top-down herbivory and bottom-up nutrient controls, both of which are re-emphasized. As the first approximation, we propose that on a healthy reef system, herbivore abundances and diversity should be high (Table 1), and palatable test plants show at least a 50% mean loss per 6-h (i.e. <6-h half-life) during a series of mid-day $in\ situ$ assays. Table 1 summarizes baseline assay and fish count data of this sort for two natural coral-reef zones of low and high herbivory.

Universal nutrient tipping points (where increasing water-column nutrients reach critical levels such that they reduce resilience to phase shifts) have been widely verified (as $\sim 1.0\,\mu M$ DIN and $\sim 0.10\,\mu M$ 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 0.25–0.5 $\mu g.L^{-1}$ also universally indicate detrimental over-abundances of nutrients (Bell and Elmetri, 1995).

Conclusions

Only a handful of studies have tested the RDM. Three broad-based correlative papers (Littler $et\ al.$, 1991; Verheij, 1993; Lapointe $et\ al.$, 2004) provided large-scale support. Several other attempts were conducted in

enriched systems that had already exceeded nutrient tipping-point concentrations conducive to unlimited algal growth. For example, relatively short-term (4-month) fertilization studies in the Florida Keys (Miller *et al.*, 1999) and Guam (Thacker *et al.*, 2001) were both carried out in DIN-sufficient ($\sim 1 \mu M$) study areas characterized by minimal coral cover and excessive algal overgrowth. However, these *in situ* experimental findings, regarding the absence of short-term bottom-up effects, are important and serve to emphasize the low ambient nutrient-replete concentrations involved and their broad applicability, as well as documenting interesting colonization patterns (see also Belliveau and Paul (2002) 5-week study). Two investigations, conducted in appropriately healthy coral-reef systems over time periods sufficiently long for revealing competitive dominances (Smith *et al.*, 2001; Littler *et al.*, 2006), have provided the strongest experimental support for all tenants of the model.

Bottom-up research is logistically difficult and requires more emphasis on multifaceted approaches carried out over sufficiently long time periods. These should include examining (by *in situ* enrichment experiments) the competitive dominances of indicator groups on oligotrophic coral-dominated reefs (Smith *et al.*, 2001; Littler *et al.*, 2006), in addition to monitoring water-column nutrient levels, tissue C:N:P ratios, and assays of algal physiological responses. We encourage both biologists and managers to consider more broadly the complex role that escalating nutrient enrichment plays in the regulation of harmful macroalgal blooms on coral-reef ecosystems.

Over half a decade ago, Risk (see 'Paradise lost . . .', 1999) pointed out how both science and management are failing coral-reef conservation, and we concur. The RDM was published over two decades earlier, but has not been widely adopted by resource managers as a management tool. The same can be said for the argument of top-down control (Hughes, 1994; McCook, 1999; Lesser, 2004) as the primary cause of phase shifts to macroalgal blooms, which also has not been embraced by coral-reef managers. The reasons for this apparent disconnect between science and management are many, but scientific confusion over the relative roles of herbivory versus eutrophication versus salinity versus stochastic events has only frustrated both managers and scientists. Also, as astutely pointed out in the paper by Pandolfi *et al.* (2005), managers burdened by bureaucratic constraints have focused on piecemeal actions such as getting management plans in place, reducing immediate impacts, or conserving parts of systems, rather than targeting the more-relevant goals of restoring low nutrient/high herbivory conditions that support desirable functional groups on vigorous coral reefs. This is not to say that all reef managers are unaware or not making progress. For example, on the Great Barrier Reef, the Australian Government is working very hard to: (1) address water quality issues (despite the ongoing and seemingly endless scientific squabbles about what effect it does or does not have, and very strong criticism by some sectors of the public), and (2) prevent overfishing, through a substantial increase in no-take zones and fishery management plans (Laurence McCook, pers. comm.). In the equally challenging case of the Florida Keys coral reefs, managers are also working to address a broad range of threats, including, in recent years, nutrient pollution (Causey and Andrews, 2005; Kruczynski, 2005).

Owing to the growing problems associated with coastal eutrophication and destructive overfishing along tropical and subtropical shorelines, the ecological responses of coral reefs and macroalgae to both nutrient enrichment and reduction in herbivory have been repeatedly cited (ECOHAB, 1997) as priority areas in need of intense management. 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. Thus, this synthesis is crucial in proposing realistic assessment/monitoring guidelines and pragmatic goals for the authoritative understanding and decisive management of critical coral reef ecosystems.

Unfortunately, the recurrent role of modern humankind on coral reefs will continue to be the elevation of nutrients via sewage and agricultural eutrophication (i.e. increasing bottom-up controls, Littler *et al.*, 1991, 1993; Goreau *et al.*, 1997; Lapointe *et al.*, 1997, 2005a, 2005b), while simultaneously decreasing herbivorous fish populations (Littler *et al.*, 1991, 1993; Hughes, 1994) through destructive overharvesting techniques

(i.e. reducing top-down controls). The reviews of Høegh-Guldberg (1999) and Adey *et al.* (2000) project a dim outlook for an unprecedented ongoing kill-off of the world's coral reefs. Unless curbed, such anthropogenically induced shifts (long predicted (Figure 7 in Littler and Littler, 1984a) – see also Figure 2a in Bellwood *et al.* (2004)) will expand geographically at an accelerated pace.

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