Nutrient Enrichment on Coral Reefs: Is It a Major Cause of Coral Reef Decline?

Alina M. Szmant*

Department of Biological Science and Center for Marine Science, University of North Carolina at Wilmington, 5600 Marvin K. Moss Lane, Wilmington, North Carolina 28409

ABSTRACT: Coral reefs are degrading worldwide at an alarming rate. Nutrient over-enrichment is considered a major cause of this decline because degraded coral reefs generally exhibit a shift from high coral cover (low algal cover) to low coral cover with an accompanying high cover and biomass of fleshy algae. Support for such claims is equivocal at best. Critical examination of both experimental laboratory and field studies of nutrient effects on corals and coral reefs, including the Elevated Nutrient on Coral Reefs Experiment (ENCORE) enrichment experiment conducted on the Great Barrier Reef, does not support the idea that the levels of nutrient enrichment documented at anthropogenically-enriched sites can affect the physiology of corals in a harmful way, or for most cases, be the sole or major cause of shifts in coral-algal abundance. Factors other than nutrient enrichment can be significant causes of coral death and affect algal cover, and include decreased abundance of grazing fishes by fishing, and of grazing sea urchins to disease; grazing preferences of remaining grazers; temperature stress that kills coral (i.e., coral bleaching) and creates more open substrate for algal colonization; sedimentation stress that can weaken adult corals and prevent coral recruitment; coral diseases that may be secondary to coral bleaching; and outbreaks of coral predators and sea urchins that may be secondary effects of overfishing. Any factor that leads to coral death or reduces levels of herbivory will leave more substrate open for algal colonization or make the effects of even low-level enrichment more severe. Factors that contribute to an imbalance between production and consumption will result in community structure changes similar to those expected from over-enrichment. Over-enrichment can be and has been the cause of localized coral reef degradation, but the case for widespread effects is not substantiated.

Introduction

Coral reefs worldwide, and in particular in the Caribbean and southern Florida, are experiencing a recent period of decline. There has been a major loss of coral cover and diversity (Hoegh-Guldberg 1999; Wilkinson 2000) coupled in many areas with an increase in algal biomass and shift in algal community structure (McCook 1999). Coral reef algal communities are very productive (Hatcher 1988, 1990) but heavily grazed by herbivorous fishes and echinoids, and are made up mostly of low biomass red crustose coralline algae (CCA), mixed assemblages of short turfs, and calcified articulate forms (Steneck and Dethier 1994; Carpenter 1997; Hixon 1997). Fleshy corticated forms are usually limited to the back reef and refuges from herbivores. With minor exceptions reef-building corals dominate the substrate on healthy accreting reefs and algal biomass is low. On degraded reefs, algal biomass increases as the dead coral substrate and CCA become overgrown by thick turfs that trap sediment, and a variety of fleshy foliose and corticated foliose macrophytes become abundant. Because algae, like other plants, can respond to increased

nutrient availability with increased growth potential, any such shift in community structure from coral-CCA-short turf to fleshy macrophyte-tall turf is commonly attributed to anthropogenic nutrient inputs (e.g., Johannes 1975; Pastorok and Bilyard 1985; Bell 1992; Bell and Elimetri 1995; Lapointe 1997).

Community structure of coral and algal components is determined by more than just the growth potential of the algae. Sedimentation stress, storm damage, thermal stress, over-harvesting of grazers and predators, physical damage from ship groundings, coral mining, and destructive fishing practices are just a sample of important natural and anthropogenic stresses that are presently affecting community structure and reef health and contributing to present day coral reef decline (Johannes 1970; Hatcher et al. 1989; Glynn 1993; Dubinsky and Stambler 1996; McCook 1999). The question to be addressed here is how much coral reef decline is being caused by nutrient over-enrichment itself as opposed to the numerous other factors known to be currently affecting coral reefs (Fig. 1).

I evaluate reports based on the supporting evidence for nutrient enrichment and the other factors that could simultaneously affect coral reefs.

---

* Tele: 910/962-2362; fax 910/962-2410; e-mail: szmanta@uncwil.edu.

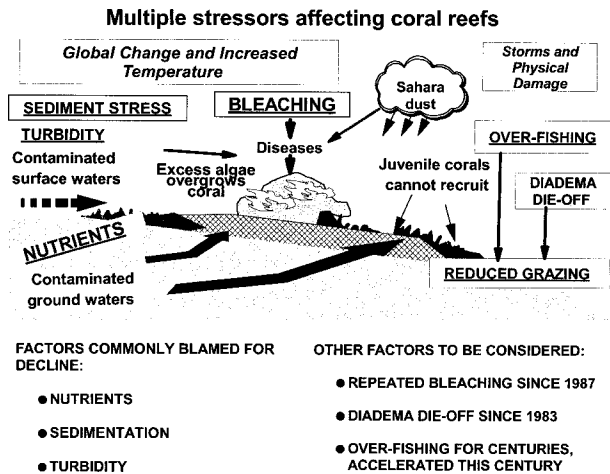**Multiple stressors affecting coral reefs**

Fig. 1. Diagrammatic representation of the many anthropogenic and natural stressors known to be affecting coral reef health and community structure.

Coral reefs prone to nutrient effects are usually exposed to other anthropogenic stressors that can make a reef more susceptible to nutrient effects or cause symptoms similar to those expected from nutrification. In this paper, nutrients refer to inorganic and organic forms of the elements nitrogen (N) and phosphorus (P). This includes nitrate, ammonium, and soluble reactive phosphate assimilated by plants, as well as dissolved organic forms of unknown composition (dissolved organic N, dissolved organic P), that can be remineralized to the inorganic forms available to plants. In many areas human activities have increased the flux of nutrients into coastal waters (= nutrification, as opposed to eutrophication, a term describing a more complex process involving organic production and accumulation and the nutritional status of a community; Nixon 1995), which alters the growth environment of coastal marine plant communities, and often leads to changes in community and ecosystem structure of the affected systems.

This paper is not a comprehensive review of coral reef decline, nor of all the facets of reef ecology involved in decline. The subject matter of nutrification is complex and hotly debated with regard to its effects on coral reefs, so any attempt to critically address this question will draw on a broad range of often contradictory studies. With coral reefs presently declining at a rapid rate, it is important to understand the complexity of these interactions, and to place the role of nutrients in perspective.

Nutrients as Determinants of Coral Reef Community Structure

Conceptual models are often used to summarize the broad role of nutrients in structuring coral
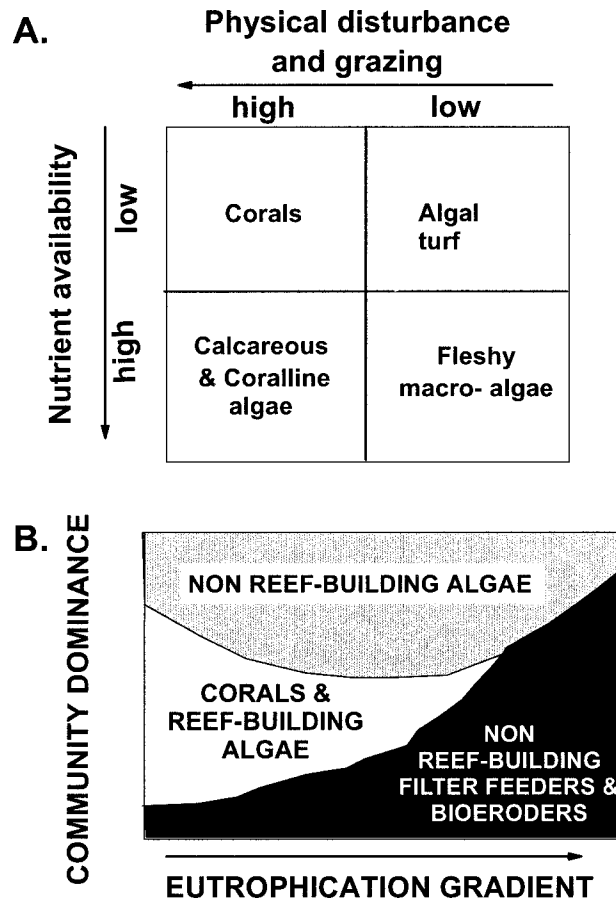

Fig. 2. Diagrammatic representations of two conceptual models relating nutrient levels to coral reef community structure. A) Relative dominance model proposed by Littler and Littler (1984). B) Eutrophication gradient model proposed by Birkeland (1988).

reefs and are invoked by those advocating the role of nutrification in coral reef decline. Littler and Littler (1984) proposed a relative dominance model for four photosynthetic functional groups that compete for reef substrate (corals, turfs, coralline algae, and macrophytes). In this model nutrients (bottom-up) and herbivory-physical disturbance (top-down) factors interact to determine community structure. Corals and turfs dominate under low nutrient conditions depending on whether herbivory levels are high or low, respectively. Dominance shifts towards fleshy macroalgae with increased nutrients and decreased herbivory (Fig. 2a). One shortcoming of this model is that there is an extensive literature showing CCA and short (highly grazed) turfs to be important components of pristine (low nutrient, high herbivory) coral reefs (Hatcher 1988, 1990). Predictions based on this model may lead to incorrect inferences about causes of community change (i.e., high CCA cover

and low coral cover could be interpreted to indicate nutrification).

Birkeland (1987) proposed another scheme in which at low nutrient fluxes and oligotrophic conditions, corals and reef-building algae co-exist with a limited number of non-reef building algae and filter feeders. The dominance of the latter two groups increases along an eutrophication gradient with filter feeders alone dominating under the most eutrophic conditions (Fig. 2b). Nutrient supply (a factor of both concentration and advective flow; Atkinson 1988) is an implicit part of his oligotrophic to eutrophic gradient. The role of herbivory in modulating shifts in community structure towards more eutrophic components with increased nutrient fluxes was recognized but not made an explicit part of the model.

Steneck and Dethier (1994) proposed a third model with similarities to the Littler and Littler model. They divide the algal community into seven functional forms (corals are not one of the forms) that differ in size, canopy height, longevity, and biomass-specific productivity. The relative abundance of the seven functional forms is determined by interactions between life-history characteristics, productivity potential and growth dynamics (which integrates their responses to nutrients, light, water flow, and other physical-chemical environmental characteristics), and the disturbance potential (which includes herbivory pressure).

Both the Littler and Littler and Birkeland models would predict that increasing nutrient flux would cause a loss of corals due to competition with algae, but their predictions differ otherwise. In the Littler and Littler model, fleshy algae would only dominate if herbivory also decreases, and coralline algae would prevail if herbivory remains high. In the Birkeland model, non-reef building algae would dominate over the corals and reef-building algal species (presumably fleshy algae become dominant over calcifying forms). The Steneck and Dethier model predicts that larger fleshy algal forms could dominate with reduced disturbance or herbivory even if there is no change in productivity potential and nutrient supply. This model does not make explicit predictions about the shift in coral and algal dominance, but if corals are grouped with the coralline functional groups, it would predict that fleshy algae would outcompete corals as nutrients increased or herbivory decreased.

Ignoring the differences between models, all three can be used to predict increased fleshy algal dominance with nutrient enrichment. This intuitive relationship between enrichment and increased algal growth is the primary factor behind the propensity to blame coral reef degradation on nutrient over-enrichment. As McCook (1999) asserted, this notion assumes that reef algae are normally growing under nutrient-limited conditions and that enrichment stimulates their growth. The evidence for this basic assumption is poor and based on three a priori assumptions. Coral reefs only occur under extremely low nutrient conditions (Bell 1992; Bell and Elimetri 1995; Lapointe 1997). This assumption is based on early studies of a few mid-oceanic atolls such as Eniwetak where ambient nutrient concentrations are low (Odum and Odum 1955; Johannes et al. 1972). It does not take into consideration a variety of recognized sources of nutrients to even remote reefs, such as various forms of upwelling, endo-upwelling, high advective flow, N fixation, bird guano, and atmospheric deposition. Nor does it consider that most reefs occur on island or continental shelves where some level of natural terrigenous inputs are to be expected (Sander 1981; Andrews and Gentien 1982; Smith 1983; Atkinson 1988; D'Elia 1988; D'Elia and Wiebe 1990; Lee et al. 1992, 1994; Rougerie and Wauthy 1993; Smith and Johnson 1995; Leichter et al. 1996). The high-latitude Houtman Abrolhos reef complex maintained vigorous reef growth throughout the Holocene in spite of naturally elevated nutrient conditions (Crossland et al. 1984; Collins et al. 1993). A second assumption is that algae on coral reefs are nutrient limited, evidence for which is sparse and contradictory (McCook 1999). Algae differ greatly in their response to nutrient supply. Nutrients may stimulate growth of some algae while that of others exhibit no change (Larned 1998; Schaffelke and Klump 1998; Schaffelke 1999; Stimson and Larned 2000; Thacker et al. 2001; Smith et al. 2001). A third assumption is that under normal circumstances algae are competitively dominant over corals, which has been recently challenged (McCook et al. 2001).

Evidence for Sensitivity of Coral Reefs to Nutrient Enrichment

Coral reefs are found wherever, over geological time scales, the combination of physical, chemical, and biological conditions favor the accretion of calcium carbonate secretions (limestone) in reef-building and calcareous algae dominated communities. Decreasing temperatures and herbivory pressure, the trend of increasing nutrient availability, and possibly decreasing aragonite saturation state with increasing latitude limit coral reefs to the tropics and subtropics (Wells 1957; Johannes et al. 1983; Miller 1998; Kleypas et al. 1999). Elevated nutrients can supposedly tip the competitive balance in favor of macroalgae, especially if herbivore densities are low. McCook et al. (2001)

TABLE 1. Nutrient concentrations at selected reef sites. Examples of ambient levels at naturally or anthropogenically elevated sites as well as major reef regions. For Canton, the values are from near the pass where coral cover was the highest. For older Kaneohe Bay data, values are lowest and highest for the five regions studied, plus the weighted bay mean. For the Great Barrier Reef (GBR), the Furnas et al. (1995) report includes a large number of data, and I selected means and SE for one representative lagoon station from their Cairns section. Values for nutrients are in μM, and for chlorophyll a (chl a) are in $\mu g\ l^{-1}$. nd = not detectable.

Station Type	$NO_3 + NO_2$	NH_4	PO_4	Chl a
Canton Lagoon, upwelling area; Smith and Jokiel 1978	2.5	1.5	0.6	—
Kaneohe Bay pre-sewage diversion; Smith et al. 1981	0.33 to 0.91	0.57 to 2.28	0.28 to 0.88	0.68 to 4.67
	bay $\bar{x} = 0.41$	bay $\bar{x} = 0.67$	bay $\bar{x} = 0.33$	bay $\bar{x} = 1.13$
Kaneohe Bay post-sewage diversion; Smith et al. 1981	0.27 to 0.66	0.38 to 0.57	0.09 to 0.18	0.55 to 1.33
	bay $\bar{x} = 0.37$	bay $\bar{x} = 0.43$	bay $\bar{x} = 0.11$	bay $\bar{x} = 0.78$
Kaneohe Bay, central bay 1998; Stimson et al. 2001	0.17 (0.39)	0.21 (0.20)	0.08 (0.03)	—
Mamala Bay, Baseline, bottom 1993–1994; Grigg 1995	0.04 (0.02)	0.05 (0.02)	0.13 (0.01)	0.17 (0.06)
Mamala Bay, High Wave, bottom 1993–1994; Grigg 1995	0.72 (0.02)	0.10 (0.06)	0.08 (0.01)	0.17 (0.06)
Mamala Bay, Rain Event, bottom 1993/1994; Grigg 1995	0.11 (0.13)	0.11 (0.04)	0.12 (0.02)	0.27 (0.20)
GBR, One Tree Reef; Hatcher and Hatcher 1981				
offshore	0.31 (0.03)	nd		
reef slope	0.31 (0.12)	0.76 (0.24)		
lagoon	0.95 (0.06)	2.86 (0.21)		
reef crest	1.54 (0.16)	5.52 (0.62)		
GBR, mid-lagoon Station 11; Furnas et al. 1995	0.05 (0.01)	0.46 (0.13)	0.08 (0.01)	0.35 (0.05)
Houtman Abrolhos Islands, Australia, Easter Group; Crossland et al. 1984				
front reef flat	1.02	0.21	0.22	
back reef flat	0.96	0.28	0.24	
lagoon	0.93	0.32	0.29	
Brazil, developed; Costa et al. 2000				
Wet	8.03	4.81	1.42	—
Dry	5.75	10.69	0.35	
Brazil, less developed; Costa et al. 2000				
Wet	1.68	3.59	0.18	—
Dry	0.41	0.86	0.13	

questioned the premise that corals are competitively inferior to algae, noting that many studies demonstrate the opposite (e.g., De Ruyter van Stevenninck et al. 1988; McCook 2001). Elevated nutrients may also affect physiological interactions between corals and their zooxanthellae by stimulating the cell division rates of the intracellular symbionts (see below). Elevated nutrients are also associated with higher levels of water column productivity and abundance of filter feeders and bioeroders (Birkeland 1977, 1987; reviewed by Glynn 1997). High rates of bioerosion will reduce rates of carbonate accretion and limit reef building (Hallock 1988). Tropical shallow platforms characterized by naturally nutrient-rich conditions due to high rates of upwelling or river discharge are generally devoid of coral reefs (Wells 1957; Hallock and Schlager 1986), but more moderate rates of upwelling allow for moderate to extensive reef building (Glynn 1977, 1993; Smith and Jokiel 1978; Andrews and Gentien 1982; Smith 1983). High islands surrounded by fringing and barrier reefs usually have breaks in their reefs where rivers discharge into their coastal zones, giving evidence that over reef-building time scales, inputs of terrestrial materials such as freshwater, nutrients, and sediments limit coral reef growth.

This broad general inverse relationship between naturally occurring, chronically elevated nutrient conditions and coral reef formation is the strongest evidence for a negative effect of high nutrient fluxes on coral reefs, and has given rise to the view that coral reefs are particularly susceptible to anthropogenic nutrient enrichment. The potential contributions of low temperature in upwelling situations and sediment-laden freshwater discharge to lower coral cover and growth rates confound a simple distribution-based interpretation of nutrient effects on coral reef health. There is very limited quantitative information on what constitutes high or low nutrient levels (concentrations or fluxes) that either limit coral reef formation or lead to their decline. From the scant data available it is apparent that coral reefs have formed under a broad range of natural nutrient regimes (Table 1), but there are few nutrient data for most reef areas to form a more complete view of this range (Crossland 1983; D'Elia 1988; Sorokin 1990; Szmant and Forrester 1996).

Anthropogenic nutrient enrichment is more

likely to affect coral reefs closer to shore, within lagoons or embayments (limited circulation and flushing), and reefs associated with larger land masses (high island and continental reefs), especially near significant human populations. Mid-ocean atolls and offshore barrier reefs, which are exposed to high ocean energy and much flushing, would not be expected to be as easily affected. Because the distribution of degraded reefs more or less fits this expectation (Wilkinson 1998), it is logical to suspect that local anthropogenic activities including nutrient enrichment are causing reef decline. Loss of coral often co-occurs with increased algal cover and biomass (Tomascik and Sander 1987; Wittenburg and Hunte 1992), especially of fleshy macroalgae that can overgrow corals, leading some to conclude that nutrient enrichment is the cause of the algal increases and that the algae themselves are directly responsible for the loss of coral. One example of a natural nutrient enrichment event that demonstrated such a cause-effect relationship was the sudden algal bloom caused by an unusual upwelling event in the Gulf of Eilat following the eruption of Mount Pinatubo in 1992 (Genin et al. 1995). Thick algal mats formed over the coral reef benthos except at a few locations where grazer abundance was noticed to be high. About 20% to 30% of the corals were smothered and killed by the algal mats that were clearly caused by upwelled nutrients, supporting the common tenet. Most published investigations that attribute high algal cover to nutrient enrichment do not include algal cover or nutrient time series, or experimental work demonstrating that the higher algal biomass was the cause of a decrease in coral cover.

The impact of eutrophication on coral reefs was dramatically brought to the world's attention in the late 1960s and 1970s when the water column of southern Kaneohe Bay, Hawaii, turned green with phytoplankton, its sediments turned anoxic, and its coral reefs were overgrown by the bubble alga, *Dictyosphaeria cavernosa* (summarized by Laws 1992). Attribution of the algal blooms to two major sewage outfalls was straight forward. After the sewage discharge was redirected to an ocean outfall, noticeable reef recovery was achieved within a decade. The phytoplankton blooms subsided within a few years, but it took longer for *D. cavernosa* to retreat because it was capable of drawing nutrients from the sediments over which it grew (rather than the water column; Larned and Stimson 1996), and the sediments had become enriched during the period of discharge within the bay (Fig. 3; Smith et al. 1981; Laws 1992). Largely because of Kaneohe Bay, nutrient enrichment and water quality decline are evoked as the primary cause for de-
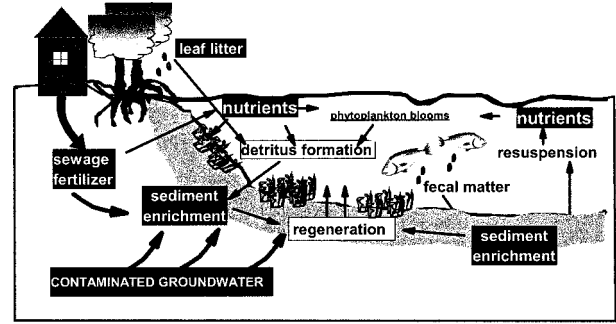

Fig. 3. Conceptual representation of processes by which nutrients enter coastal systems and are recycled and accumulate in sediments mediated by primary producers, detritus formation, and herbivores.

creased coral cover at other locations that is accompanied with increases in algal abundance.

Water quality degradation can be broader than just nutrification and also includes organic carbon enrichment, as well as metals and organic pollutants from numerous types of point and nonpoint sources, including agricultural and storm water discharges. Many areas with increased nutrient inputs also have increased sediment and pollutant loads entering the coastal zone from agricultural activities. Corals, as well as typical reef algae, are sensitive to sedimentation, especially by organic-rich, silt-sized sediments (Johannes 1970; Rogers 1990; Dubinsky and Stambler 1996; Fabricius and De'ath 2001). It may be difficult to distinguish between the effects of just nutrients and those caused by sediments rich in nutrients and organics.

Other Causes of Coral Reef Degradation

Any factor that kills coral, such as storms, bleaching, disease, and predation, opens up substrate for algal colonization and can lead to gradual and potentially permanent coral reef degradation if corals are not able to recruit or grow back (e.g., Ostrander et al. 2000). Bleaching is caused by periods of abnormally warm seawater temperatures and/or excess ultraviolet radiation. It has caused loss of coral cover on the order of 15% to 90% in the Indo-Pacific and Caribbean during the extremely warm years of 1997 and 1998 (Hoegh-Guldberg 1999; Wilkinson 2000). The increased incidence of coral diseases noted over the past decade may be related to corals being physiologically debilitated by repeated bleaching events (Harvell et al. 1999). Partial mortality is a common consequence of coral bleaching and disease, exposing coral skeletons to colonization by algae. Algal colonization success may be increased due to reduced herbivory resulting from overfishing (Ostrander et al. 2000). The increased algal cover leads to a greater susceptibil-
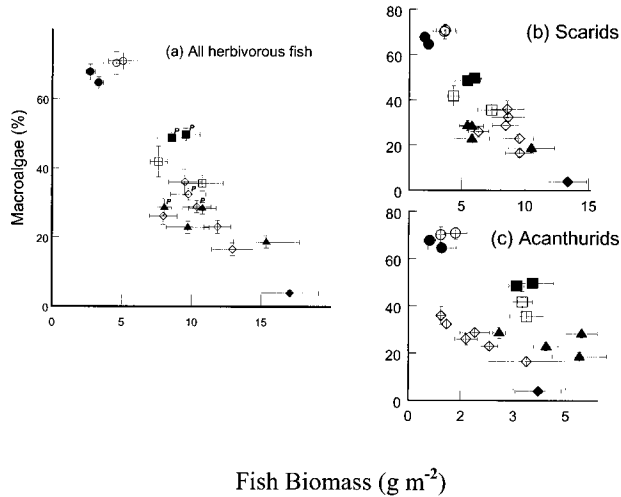
Fig. 4. Relationship between biomass of grazing fishes and algal cover on 19 reefs from seven geographic locations in the Caribbean (from Williams and Polunin 2001).

ity of the remaining part of the coral colony to algal overgrowth. A major shift in community structure can then occur without any change in nutrient conditions even though it may appear similar to what we would expect from a nutrient-induced effect.

Overfishing, by reducing grazing pressure, can affect the ability of reefs to recover from disturbance and lead to degradation. Fishing is a major human activity on coral reefs, and reefs worldwide are overfished, especially those close to human settlements (Roberts 1995; Wilkinson 2000; Jackson et al. 2001). The potential for overfishing to cause coral reef degradation is not generally recognized, but it is as serious a threat to coral reefs as that of water quality degradation (Szmant 1997). Loss of large predators and herbivores can result in trophic shifts because of decreased predation on reef organisms such as algae, sea urchins, and corallivores (McClanahan and Shafir 1990; McClanahan 1995; Roberts 1995). Williams and Polunin (2001) report an inverse relationship between herbivorous fish biomass and macroalgal cover over a broad range of Caribbean reefs (Fig. 4). Reefs with higher fish biomass were within no-fishing reserves where regulations were enforced. Reefs with more fish and less algae have greater potential to recover from storm impacts (Done 1992, 1999; Roberts 1995; Bythell et al. 2000). Algal blooms are common after major storms but usually dissipate soon thereafter. Coral cover is re-established by successful re-attachment of coral fragments or by coral sexual recruitment (Highsmith 1982; Harrison and Wallace 1990; Hughes et al. 1992). If grazers are reduced in abundance, the initial algal bloom can

be followed by a succession of more enduring algal types, and coral cover is not re-established. Such a successional sequence has been described as an alternative stable state of coral reef systems: an algal-dominated reef (Hatcher 1984; Hatcher et al. 1989).

Outbreaks of coral diseases and corallivores have both killed much coral exposing dead skeletons to algal colonization. Increases in algal cover on Pacific reefs followed outbreaks of the corallivorous seastar, *Acanthaster plancii,* beginning in the 1960s, and more recently, of the corallivorous snails *Drupella* spp. (Done 1999). Diseases have also contributed to reef degradation indirectly by killing off coral reef organisms that are ecologically important (Harvell et al. 1999). In the Caribbean, a disease epidemic in 1983 killed 95% of the sea urchin, *Diadema antillarum* (Lessios 1988), which was the major invertebrate herbivore controlling algal populations on reefs, especially where herbivorous fishes were overfished (Hay 1984). Within weeks, increases in algal cover followed the die-off, occurring before declines in coral cover were documented (e.g., Carpenter 1986; Lessios 1988; Hughes 1994; Steneck and Dethier 1994; Hughes et al. 1999).

It is widely accepted that climate change-related causes of coral reef decline have been extensive during the past two decades, and especially during the past three years (Hoegh-Guldberg 1999; Wilkinson 2000). Coral bleaching has affected even pristine reefs in remote areas where eutrophication is unlikely and overfishing less severe, but no single stress factor discussed is working alone. The challenge for scientists and environmental managers is to have sufficient understanding of local systems and the ability to discern among the potential causes of decline. The effects of local water quality degradation and overfishing can exacerbate global warming and bleaching. While much is known about the generalities of coral reef function, our understanding of major ecosystem processes and their interactions is rudimentary, and it may be difficult to pin-point the cause of a given reef's decline.

Experimental Evidence for Nutrient Effects on Coral Reefs

Nutrients can affect coral reef health through direct physiological effects on the corals, such as reduced growth or reproduction rates, or increased susceptibility to bleaching or disease mortality, mainly via effects on the coral-zooxanthellae symbiosis; indirect effects on coral reef community structure via stimulating growth of reef algae or promoting dominance by nutriphilic algae generally uncommon on coral reefs; and reducing car-

bonate accretion by promoting increased abundance of filter feeders, which are responsible for bioerosion (this topic will not be discussed further because a cause-and-effect relationship between rates of bioerosion and coral physiology or shifts in coral and algal dominance has not been demonstrated). Experimental evidence for effects of nutrients on the physiology and ecology of reef corals or coral reefs can be derived from either laboratory or field experimental work, or from studies of field systems exposed to either natural- or anthropogenically-elevated nutrient conditions.

PHYSIOLOGICAL EFFECTS

Laboratory

Most of the evidence for direct effect of nutrients on coral physiology is from laboratory studies in which corals were exposed to elevated nutrient concentrations in aquaria for periods of a few weeks to months. A limitation of such studies has been the high nutrient concentrations used in order to obtain effects during short experimental periods: e.g., 20 to 200 μM nitrate (Taylor 1978); 10 to 50 μM ammonium (Hoegh-Guldberg and Smith 1989; Jokiel et al. 1994); 10 μM phosphate (Dubinsky et al. 1990). Such concentrations are orders of magnitude higher than the highest levels measured on polluted coral reefs (Table 1), and it is difficult to extrapolate from them to effects at much lower elevated concentrations. Most of these experiments were designed to examine the hypothesis that zooxanthellae in hospite are nutrient limited. Their results must be interpreted cautiously when deducing negative effects of nutrients, since the experiments themselves were not designed for that purpose. The most common effects reported in enrichment experiments with ammonium were increases in zooxanthellae density and zooxanthellae chlorophyll content, often accompanied by elevated rates of photosynthesis. These responses to enrichment were interpreted to indicate that zooxanthellae in hospite are normally nutrient-limited, but the long-term effects of releasing the algae from such limitation remain unclear.

The most ecologically significant effect of elevated nutrients on coral physiology has been reduced calcification or skeletal extension rates, especially under P or P plus ammonium enrichment (Lamberts 1978; Stambler et al. 1991; Stimson and Kinzie 1991). Taylor (1978), however, reported an increase or no change in growth with ammonium or nitrate enrichment, respectively, and Stambler et al. (1991) found no change in growth with phosphate only. Of the more recent work designed to investigate effects of enrichment, McGuire (1997) found no measurable effect on a number of coral

and zooxanthellae parameters at sustained exposure to 2 μM ammonium for 8 wk but did find variable negative effects including decreased growth rates at 5 and 10 μM ammonium. Ferrier-Pages et al. (2000) also found reduced growth rates of coral nubbins exposed to 20 μM ammonium and 2 μM phosphate, separately and together, for 10 wk, and that recovery after return to normal nutrient levels was slow, especially for the corals exposed to phosphate. Marubini and Davies (1996) found a 25% to 50% decrease in growth rate for two species of coral exposed to as low as 1 μM nitrate (other treatments were 5 and 20 μM), but that the effect of 20 μM nitrate or ammonium enrichment were eliminated if 2 mM bicarbonate was added to the seawater medium (Marubini and Thake 1999). In work with a different species Marubini and Atkinson (1999) found no effect on growth at 5 μM nitrate but did find large reductions in calcification with decreased pH of seawater. Atkinson et al. (1995) reported higher long-term growth rates of corals exposed to elevated nutrients (5 μM nitrate, 2 μM ammonium, and 0.6 μM phosphate) in the Waikiki Aquarium where the sea water was low in pH and supersaturated in CO_2. There is increasing support for the hypothesis that reduced calcification rates, when they occur under nutrient-enriched conditions, may be due to competition for CO_2 and/or carbonate between the processes of photosynthesis and calcification.

Laboratory evidence shows that short-term exposure to significantly elevated nutrients, especially phosphate, can cause reductions in skeletal growth for some species. Inconsistent results between investigators may be due to different species used or experimental conditions and laboratory artifacts such as changes in the pH, carbonate equilibrium, and carbonate species concentrations, which were not often measured or controlled. Most of the studies only found significant changes in zooxanthellae density or coral growth rate when they used concentrations of nutrients significantly higher than those reported for heavily polluted reef areas or reef areas with intense upwelling (Table 1). As most of the laboratory studies lasted only 2 to 3 mo, there is also the possibility of long-term accommodation to elevated nutrients by the corals and their endosymbionts. Since decreased coral growth rates appear to be a consequence of increased zooxanthellae densities, eventually coral tissues could catch up and growth rates return to normal or even increase. The sustained high growth rates of the corals in the Waikiki Aquarium system (Atkinson et al. 1995) suggest that this is a realistic expectation.

TABLE 2. Subset of water quality characteristics reported by Tomascik and Sander (1985) for a series of stations along the west coast of Barbados characterized by the authors to represent a gradient of eutrophication due to sewage discharge. The two more polluted and two more pristine stations are ca. 15 km apart along an open coastline. Values for nutrients are in μM, for chlorophyll a (chl a) are in μg l^{-1}, and for suspended particulate matter (SPM) are mg l^{-1}.

Station Type	NO_3	NH_4	PO_4	Chl a	SPM
More polluted					
−1	0.82	0.98	0.10	0.90	7.11
−2	4.42	2.70	0.21	1.04	7.32
More pristine					
−1	0.36	0.54	0.06	0.42	5.21
−2	0.45	0.56	0.06	0.55	4.26

Field

Growth rates of corals from eutrophic localities along the coast of Barbados were lower than those of corals from nearby more pristine ones (Tomascik and Sander 1985). Average nutrient concentrations at the two most polluted and two most pristine stations are summarized in Table 2. Statistical analysis of their water quality data revealed that suspended particulate matter (SPM) had the strongest inverse correlation with coral growth rates, making it unclear that it is justifiable to attribute the decreased growth rates directly to nutrient effects. They also proposed that the corals exhibited the highest growth rates at intermediate levels of SPM, and suggested that the corals could be feeding on the suspended organic material. Lewis (1976) showed that corals can derive some nourishment from feeding on SPM, and recent reports confirm the potential importance of this food source to corals (Rosenfeld et al. 1999; Anthony 2000).

There are several reports of reduced growth rates of corals in upwelling areas where nutrient concentrations are elevated, but the low temperatures associated with upwelling conditions can also explain the reduced growth rates. Glynn (1977) reported a linear relationship between temperature and growth for *Pocillopora* sp. in the Gulf of Panamá with the lowest growth rates during the upwelling season, but growth rates increased steadily during the non-upwelling season reaching rates comparable to those of corals in the adjacent non-upwelling Gulf of Chiriquí. If elevated nutrients during the upwelling season were in part responsible for the lowered growth rates associated with the upwelling, their effect did not extend into later seasons when nutrient concentrations returned to normal. Wellington and Glynn (1983) subsequently compared growth and calcification rates of another eastern Pacific reef coral, *Pavona clavus,* and found that the corals from the Gulf of Panamá had both higher calcification and linear extension rates in spite of the upwelling than those from the Gulf of Chiriquí. This is surprising given the low temperatures under which the Gulf of Panamá corals grew during half the year, but indicates that elevated nutrients do not always have a negative effect on coral physiology. Wellington and Glynn (1983) suggested that increased food availability during the upwelling periods could stimulate both tissue and skeletal growth. They also reported an inverse correlation between extension rate and skeletal density, a general relationship that has been reported for other corals (e.g., Dodge et al. 1993; Lough and Barnes 2000).

ENCORE Field Experiment

The most ambitious field experiment to investigate the effects of nutrient enrichment, as narrowly defined here, on a number of coral reef processes, organisms, and coral physiology was the EN-CORE (Elevated Nutrient on Coral Reefs Experiment) project on the Great Barrier Reef (GBR). An important aspect of this experiment is that nutrient enrichment was done under what otherwise were considered pristine conditions, without confounding effects of increased sedimentation, high organic loading, or overfishing that co-occur at most anthropogenically disturbed reef sites. Twelve microatolls in the One Tree Island reef lagoon were divided into four treatments (control, +N, +P, +N+P) and dosed with nutrients daily for over 2 yr (Koop et al. 2001). Loading was increased from 10 μM ammonium and 2 μM phosphate to 20 μM ammonium and 4 μM phosphate in the second year because of the lack of clear effects by the original level of enrichment on many (most) of the systems studied. Nitrate and ammonium levels in this lagoon have been reported to be seasonally naturally elevated (Hatcher and Hatcher 1981).

It was apparent early in the experiment that the most expected result for a major shift in algal community structure, biomass, and productivity was not being demonstrated (Larkum and Koop 1997; Koop et al. 2001). There were also no effects on rhodolith growth, phytoplankton biomass or production, fish grazing and reproductive effort, or bioerosion (Koop et al. 2001; Kiene 1997). As expected, N-fixation increased with phosphate enrichment and denitrification increased with ammonium enrichment (Koop et al. 2001). Increased rates of denitrification may be one reason why nutrient concentrations did not build up during the 2-yr enrichment.

The only studies that claimed major significant effects of enrichment are those on the growth and

reproductive biology of various species of reef coral. It is important to examine critically this body of work because it is being cited as evidence that nutrients have effects on coral and reef health (e.g., Koop et al. 2001). It is apparent that in spite of the investigators' best efforts, the results are weak and contradictory. *Acropora palifera* grew 30% more in the +P and +N+P treatments, and 10% to 20% less in the +N treatment during the high level enrichment year (Steven and Broadbent 1997). *Stylophora pistillata* had 25% higher extension rates and calcification rates in the +N+P treatment, similar or higher extension rates in the +N and +P treatments and lower calcification rates for one of three growth intervals in the +P treatment compared to controls during the lower enrichment period but none of the results were statistically significant because of high variability between coral clones and between microatolls within treatment (Hoegh-Guldberg et al. 1997). A third set of investigators found no effect of ammonium enrichment on linear growth of *S. pistillata* or *A. aspera,* and variable effect on *A. longicyathus* depending on the season, but no net effect on an annual basis (Koop et al. 2001). No attempt is made in the summary paper (Koop et al. 2001) to reconcile or explain the inconsistencies in the results yet their overall conclusion is that nutrient enrichment reduces coral growth.

In the study of coral reproduction, colonies of *A. longicyathus* and *A. aspera* were transplanted into each microatoll and examined for various measures of reproductive effort (Ward and Harrison 2000). The authors also sampled colonies of the second species where they occurred naturally in nine of the microatolls and of the donor colonies in the lagoon from which the transplanted pieces were taken. The misused orthogonal statistical analyses reported in the paper and the text describing the results do not appear to agree with the bar graphs in which the data are presented. A direct comparison of *A. longicyathus* in the various treatments with their donor colonies (their Figs. 8–11) shows that the control, +N and +P corals had values similar to or higher than those of their donor colonies and that only the +N+P corals had lower values compared to donor colonies, casting doubt on the authors' interpretation of the biological significance of the experimental results. Naturally occurring colonies of *A. aspera* inside the microatolls did not exhibit the responses ascribed to the experimentally transplanted corals of the same species. Interannual variation for controls was as great or greater as was reported for treatment differences, and their reported statistically significant treatment effects were not reproducible from year to year. Some of the reported significant negative

effects were for November 1993 after only 2 mo of the lower level of enrichment with no difference for November 1994 after a whole year of enrichment, suggesting that the differences between corals in the various microatolls were not the result of the nutrient treatment. Inspection of the data does not lead me to conclude that the claimed nutrient effects on fecundity were real or ecologically significant. Most of the statistical significance was the result of underperformance of corals in the +N+P treatment.

An equally viable explanation is that the environmental conditions in the microatolls assigned to the +N+P treatment were unsuitable for the corals transplanted there. Two of these microatolls were located towards the rear of the lagoon and likely had different circulation and environmental conditions from the rest. That corals had to be transplanted into the microatolls for these experiments suggests that the microatolls were not a place where corals do well naturally (only 5% to 18% natural coral cover), and *A. longicyanthus* was not one of the species reported to occur in them (Koop et al. 2001). Studies comparing reproductive activity of two species of *Porites* and several species of Agariciidae in upwelling and non-upwelling zones off the coast of Panama found similar patterns of reproduction at the two types of sites (Glynn et al. 1994, 1996), showing that corals living naturally under recurring elevated nutrient conditions carry out normal gametogenic activity. Similar flaws exist in the work on nutrient effects on coral fertilization, larval settlement, and post-settlement survivorship reported in Ward and Harrison (1997).

The ENCORE results unfortunately do not constitute a solid basis from which to judge the role of nutrient enrichment on coral health or coral reef decline. There may have been confounding experimental factors such as a naturally high background level of nitrate, differences between microatolls in circulation due to their location within the One Tree Island lagoon (Larkum and Steven 1994; Kiene 1997) as well as large differences in the sizes and volumes of the microatolls used for each treatment (7× range in microatoll volume, and 6× range in microatoll area; Koop et al. 2001). I conclude that neither ENCORE or the other studies cited above demonstrated that there are major biologically or ecologically significant effects of nutrient enrichment on coral health at the levels of loading reported for reef areas suspected of nutrification. Direct effects of nutrient enrichment on coral physiology are unlikely to be a widespread contributor to coral reef decline.

Indirect Effects on Reef Community Structure

Caging or some other way of excluding herbivores is necessary to study nutrient effects on algal communities and coral-algal competition given that herbivory on reefs can be so intense that the effects of nutrient enrichment on algal growth may not be measurable unless grazing is reduced. The ENCORE experiment did not include experimental manipulation of grazing. Earlier enrichment experiments also did not use cages; results showed that community productivity increased (accompanied by a reduction in community calcification), but that no changes in algal or coral community structure were obvious after one year of daily enrichment (Kinsey and Domm 1974; Borowitzka et al. 1978; Kinsey and Davies 1979). The study by Hatcher and Larkum (1983) using a cage and enrichment design showed that for the outer slope, nutrients could influence algal turf biomass and productivity but only if herbivores were excluded, and that in the lagoon neither nutrient availability or herbivory rates explained seasonal patterns of algal abundance.

Miller et al. (1999) used cages and partial cages in the Florida Keys, with and without nutrient enrichment, to examine responses of the algal communities on artificial plates made of quarried limestone. The only effect of enrichment was a slightly higher percent cover by cyanobacteria (blue green algae), but only within the caged treatments. They found that the strongest experimental effect was due to excluding large herbivores, and that enrichment-herbivory interactions did not result in dominance by macroalgae or CCA as predicted by the Littler and Littler (1984) relative dominance model (Fig. 2a). Thacker et al. (2001) examined algal community structure on natural substrate on a Guamanian reef after 4 mo of caging and enrichment. They found an effect of enrichment on percent cover (but not biomass) of the brown alga *Dictyota* in caged and uncaged treatments (but not partial caged ones) as well as small non-significant increases in *Halimeda* biomass with enrichment in all treatments, but there was no effect of enrichment on total macroalgal cover or biomass. Their major result was a shift in species dominance from unpalatable species of cyanobacteria in uncaged treatments to palatable species of cyanobacteria and *Padina* in caged treatments. These results do not agree with the Littler and Littler model predictions either. The Littler and Littler model was generally upheld by the experimental results of another caging-enrichment factorial experiment conducted with artificial PVC substrates on a pristine Hawaiian reef located within a no-take marine preserve (Smith et al. 2001). These investigators found the greatest increase in total algal biomass, made up mostly of fleshy and calcareous forms, with combined enrichment and caging. Calcareous algae increased most with enrichment in the presence of herbivory (uncaged), suggesting that they were nutrient-limited on that reef under ambient nutrient conditions, and outcompeted by fleshy algae in the absence of herbivory. These experiments demonstrate that in the presence of normal grazing, moderate nutrient enrichment results in little change to algal community structure or biomass, but that when herbivory is reduced with or without nutrient enrichment, algal biomass may increase and there may be a shift to increased cover and biomass of fleshy algae. None of these experiments addressed the issue of coral-algal competition and how it is influenced by nutrient enrichment.

McCook (1999) provides a thoughtful review of the processes by which macroalgal growth could be stimulated by nutrient enrichment to outcompete corals, as well as several indirect ways in which the same outcome could occur. He concludes that there is at best limited evidence for direct nutrient-mediated shifts, but does not rule out that nutrients could be indirectly contributing to community structure shifts, especially when coupled with reduced herbivory, loss of topographic complexity by storms, or other disturbances such as increased sedimentation. Limitations to linking shifts in coral-algal dominance to nutrient enrichment include lack of good time series for the algal communities themselves (before and after enrichment), as well as experimental evidence that excludes other factors (McCook and Price 1997; McCook et al. 1997). Most studies that have examined coral-algal competition or reported algal overgrowth of corals have not included nutrient enrichment as a contributing factor. Coral overgrowth by algae was reported by Lewis (1986) who used large mesh corrals to exclude herbivorous fishes from an area of reef flat on Carrie Bow Cay, Belize, for a period of 8 wk. She found shifts in species composition, increases in macroalgae abundance, and some overgrowth of corals by algae, but also reported that the fishes grazed down the excess algae within hours of the cages being removed. There is no indication that nutrients were elevated on this reef that is about 30 km from land. In an experiment conducted on GBR reefs that differed in exposure to terrestrial nutrients, McCook (2001) manipulated coral-algal interactions by artificially wounding corals or removing turf algae. He found that corals competitively excluded the turf algae even on the reef closest to terrestrial influences, suggesting that the general belief that algae outcompete corals when exposed to elevated nutrients may not be

well founded. Both the functional type of alga (e.g., turf versus fleshy) and the coral species will determine the outcome of coral-algal interactions, and grazing pressure may be more important than nutrient enrichment in modulating these interactions. McCook et al. (2001) concluded that while there was ample evidence that corals and algae do compete, the direction of the outcome was highly dependent on the life-history characteristics of the specific corals and algae involved. Nutrients alone do not determine the outcome of the competitive interaction.

How Geographically Widespread is the Evidence for Nutrient Enrichment Effects on Coral Reefs?

WESTERN PACIFIC AND SOUTHEAST ASIA

This region includes the center of biodiversity of Indo-Pacific coral reefs. Because many of the reefs in this region are fringing reefs or near major landmasses, they are at high risk of being affected by the whole gamut of human activities. There are few studies of nutrient conditions on reefs for this region. An issue of *Marine Pollution Bulletin* (1994:1) dedicated to problems faced by Pacific coral reefs provides some insight into the role of nutrients and eutrophication in the degradation of those reefs, but include few data on nutrients. While eutrophication was among the factors listed by several of the authors as being of localized concern, it was of far less importance to most reefs than overfishing and sedimentation.

Hutchings et al. (1994) expressed concern over sewage effluent from pig farms entering French Polynesian lagoons, but do not provide any nutrient data or evidence that it is causing a problem. They do cite several studies showing that sedimentation from runoff was affecting or killing nearshore reefs. The areas receiving increased sediments and nutrients are also areas experiencing high levels of overfishing. Increased algal growth in these areas could be due to nutrient inputs occurring together with sedimentation and overfishing stresses. Goldman (1994) attributes most of the coral reef problems on Yap to overfishing, and stated that water quality problems were limited to the main harbor of Colonia. Zann (1994) reviewed the problems on Western Samoa, Fiji, and Tonga. He noted overfishing and destructive fishing practices were a concern in all areas, as well as poor land-development policies including destruction of wetlands and mangroves. Sediments are filling in lagoons and killing nearshore reefs near major developments. Sediments and nutrients are causing expansion of mangroves and seagrass beds into areas formerly characterized by corals. Water quality in lagoons and major harbors has deteriorated, as evidenced by higher chlorophyll and turbidity. These effects appear to be limited to the more developed lagoons and harbors, and in the outer islands, eutrophication effects are limited to within 100–500 m of a village or resort. Over the past 30 yr, human population has doubled and fisheries production tripled, so any effect of just nutrients is difficult to separate from all the other anthropogenic activities.

The decline of Philippine coral reefs is also attributed to sedimentation stress from land development and destructive fishing practices, but natural events such as typhoons and volcanic eruptions have also taken their toll (Gomez et al. 1994). Sewage-associated nutrient effects appear to be limited to sheltered bays with restricted circulation. Gomez et al. state that the most significant causes of decline are coral extraction, dynamite and muro ami fishing, and Malthusian overfishing. On nearby Papua New Guinea (PNG), overfishing is less of a problem because local people do not depend on seafood as a major component of their diet, but destructive land practices for logging and agriculture are a serious problem since most PNG reefs are fringing reefs (Huber 1994). Huber states that while blast-fishing is considered by some as the most important threat to PNG reefs, in his opinion, sedimentation is the most extensive threat. He also states that eutrophication is only of local importance near urban centers and large villages.

A clear case can be made for eutrophication being one of several major causes for coral reef degradation in the Hong Kong area (Morton 1994). Coral mining was extensive before World War II and likely responsible for much loss of reef in the area. Coral mining stopped after the war, and reefs might have had a chance to recover, but extensive land development, dredging, and pollution of major Hong Kong harbors have prevented that. It is reasonable to expect that coral reefs near highly developed areas of the China mainland have suffered a similar fate, but no literature was found.

Sewage discharge into a well-flushed channel in Koror Harbor, Palau, had no harmful effect on coral cover or diversity when re-surveyed 10 years after the sewage pipe was installed (Birkeland et al. 1993).

Eutrophication (including nutrification) appears to be a problem around major human developments in the Indo-Pacific region, especially large harbors (reduced circulation) with large settlements, but nutrient enrichment does not appear to be a widespread problem for the reefs in the region, especially when compared with sedimentation, overfishing, and coral bleaching in recent years.

GREAT BARRIER REEF

Eutrophication is feared to be the cause of widespread decline of GBR coral reefs (Bell 1992; Bell and Elimetri 1995), and proponents of this view base it on the perception that water column chlorophyll levels and algal cover on coral reefs have increased especially in inshore areas. No data to document increases in algal cover or to show direct cause and effect are presented in papers making these claims (see McCook and Price 1997; McCook et al. 1997), and the concept of widespread decline has also been questioned (Done 1999). Furnas et al. (1995, 1997) have constructed nutrient budgets for major cross-shelf sections of the GBR, and estimate riverine and sewage discharges into the area as providing about 13% of the N demand and 20% of the P demand for water column primary production (requirements of benthic production are missing from their budget). Rates of N loss by denitrification are estimated to be comparable to those of riverine N input. Most of the nutrient demand appears to be supplied by resuspension and recycling. A major unknown in their budget is the exchange of nutrients at the oceanic end of the section (Furnas et al. 1997). If there is a net loss of nutrients from the system via lateral exchange of water at the shelf break (e.g., offshore flux during storms greater than onshore flux due to upwelling), then nutrients would not be building up enough on the GBR shelf to cause eutrophication. There is no evidence that GBR sediments are becoming enriched over time as happened in Kaneohe Bay prior to outfall diversion (Smith et al. 1981; Furnas et al. 1995; references cited in Furnas et al. 1997). Long-term studies of water column chlorophyll levels show much interannual variability, with consistently higher levels inshore, but no long-term trend of increase (Brodie et al. 1997). While there is considerable concern over the potential role nutrient enrichment and eutrophication could have in causing decline of nearshore GBR coral reefs, especially ones near river mouths, there is no evidence at this time to support any widespread nutrient effect.

HAWAII

The Kaneohe Bay case is a clear example of nutrient enrichment having caused coral reef decline, and it involved both increased water column chlorophyll concentrations and a large increase in benthic algal cover and overgrowth of corals by algae. After diversion of the sewage discharge to an offshore ocean outfall, the water column of the bay gradually regained its former chlorophyll levels and transparency, substrate cover by *Dictyosphaeria* decreased and coral cover increased (Laws 1992).

More recently, *Dictyosphaeria* cover has increased on some reefs in the bay, and there is concern about continued eutrophication. Stimson et al. (2001) found that abundance of this alga is low in the southern part of the bay where sewage was formerly discharged, and higher in the central reaches of the bay. Here, it is inversely correlated with the abundance of an introduced species of red alga that is a preferred food of herbivores. Where herbivores are scarce they graze on the reds and *Dictyosphaeria* is more abundant. Where herbivore abundance is high, they graze on both species, and algal cover is low. Growth rates of *Dictyosphaeria* appear at present to be unrelated to water column nutrient concentrations since this species appears to obtain most of it nutrients by intercepting diffusion from the substrate (Larned and Stimson 1996; Stimson and Larned 2000). A sewage outfall in Mamala Bay also caused loss of coral cover within 4 km of the outfall (from 60% elsewhere to < 10% near the outfall) until the sewage treatment was upgraded and the outfall relocated into deeper water in 1977 (Grigg 1995). Recovery proceeded after that, but coral cover in the entire bay was reduced to < 20% by two major typhoons in 1982 and 1992. Nutrient levels in the bay measured 15 years after diversion are generally low (Table 1) except during rainy and high-wave events, but even where they were elevated near Pearl Harbor they are within the range of concentrations at which corals grew well in the Waikiki Aquarium (Atkinson et al. 1995; Grigg 1995).

INDIAN OCEAN AND RED SEA

Kenyan coral reefs have been extensively studied (McClanahan and Muthiga 1988; McClanahan and Obura 1995, 1997; McClanahan et al. 2001). The reefs are heavily affected by overfishing except where protected by marine parks, and they have been recently affected by bleaching (McClanahan et al. 2001). Sediments coming down the rivers affect coral community composition but not necessarily diversity (McClanahan and Obura 1997). Overgrazing of the substrate by sea urchins limits coral recruitment on many reefs; sea urchins are overabundant because of reduced predation. McClanahan states that sediments and eutrophication are not currently major threats compared to overfishing. In nearby Tanzania, a study of nutrients in Zanzibar Town harbor reported very high levels of phosphate (up to 10 μM close to the sewage discharge) with nutrient-enriched water being transported to nearby reefs by tidal flushing (1 to 4 μM phosphate maxima; with means of about 0.1 to 0.2 μM) (Bjork et al. 1995). These researchers reported a 60% decrease in CCA cover with proximity to sewage source and by phosphate con-

centrations above 0.2 μM. They also conducted laboratory and field experiments that showed that CCA growth rates declined by 50% at concentrations above 1.5 μM, but found no effect on growth when CCA were exposed to elevated nitrate or ammonium. They gave no information on coral or macroalgal cover nor status of the areas' coral reefs.

Nitrate-enriched groundwater is likely contributing to the maintenance of a major shift from coral-dominated to algal-dominated community structure that was precipitated by an extreme low tide in 1982 that killed reef flat corals on Reunion Island, Indian Ocean (Cuet et al. 1988; Naim 1993). While the groundwater seepage was not the cause of the coral death, and was present before the die-off, the researchers think it is contributing to the persistence of the algal-dominated state. The potential relationship between grazer abundance and algal dominance is only briefly discussed (Naim 1993), but she states that herbivorous fishes are more abundant and sea urchins less abundant on the degraded reef compared to nearby non-degraded reefs. No information is given about the spatial extent of the degraded reef, but from the maps in the papers it appears the effect of the contaminated ground water in this case is localized. Nitrate-rich groundwater discharge into reef areas has also been reported for Mayotte Island, in the Comoro Archipelago, and the lagoon has among the highest levels of nitrate, ammonium, and phosphate reported for high-island lagoons (Vacelet et al. 1999). The status of the coral reef communities is not discussed, and it is not clear whether these elevated nutrient fluxes have affected reef condition. Coral reefs in the Indian Ocean suffered very high coral mortality (ca. 90%) during the 1997–1998 bleaching events (Wilkinson 1998; McClanahan 2000; Edwards et al. 2001; Lindahl et al. 2001; McClanahan et al. 2001), and bleaching-killed coral is quickly colonized by algae (e.g., Lindahl et al. 2001; McClanahan et al. 2001). There is reason for concern that high nutrient inputs from contaminated groundwater seepage could interfere with reef recovery here as it has in Reunion.

Nutrient pollution of Aqaba, in the Red Sea, comes from sewage and apatite dust from loading fertilizer onto cargo ships. These are released into a fringing reef resulting in elevated levels of phosphate in reef waters (Walker and Ormond 1982). The affected area has low coral and high algal cover compared to reference reefs 10 km away. Walker and Ormond concluded that poor water quality contributed to higher rates of coral death in the polluted area, but that algae were not the direct cause of coral mortality. Rather, algae colonized the exposed coral skeletons quickly after death, and sediment trapping by the algae both prevented coral recovery and contributed to further coral tissue loss.

CARIBBEAN AND TROPICAL AMERICAS

The coral reefs at Discovery Bay, Jamaica are among the most studied in the Caribbean, and the time-course of their degradation has been recorded. Jamaican reefs were characterized by high coral cover and diversity before a 1980 hurricane struck and was followed by the 1983 *Diadema* die-off (Hughes 1994). Several investigators were able to carefully document the changes in algal cover and biomass as grazing pressure was reduced (e.g., Hughes et al. 1987; Liddell and Ohlhorst 1986; Morrison 1988; Hughes 1994). The devastating storm damage to branching reef corals prior to the *Diadema* die-off was a critical initial event in the degradation sequence, coupled with pre-existing overfishing of herbivorous fishes (Hughes 1994; Aronson and Precht 2000). The potential role of nutrient enrichment in this phase shift was not given much consideration until Lapointe (1997) argued that the mostly top-down cause of reef decline reported by Hughes and others for Discovery Bay reefs ignored the bottom-up contribution of eutrophication. He provided data on nutrient analyses for a day in July 1989 compared to an earlier nutrient study in 1980 (D'Elia et al. 1981). He also presented C:N:P tissue ratios for reef and grotto algal species and nutrient-enhanced P-I curves that he interpreted as evidence that nitrate enrichment from groundwater seepage was the major cause of increased algal abundance. Lapointe's paper was critiqued by Hughes et al. (1999), who pointed out that the temporal patterns of shifts in coral-algal composition were more consistent with reduced herbivory than with sudden enrichment, and that the temporal patterns of reef decline in Jamaica were similar to those observed elsewhere where nutrient enrichment was not suspect (e.g., St. Croix, U.S. Virgin Islands, Carpenter 1986; San Blas, Panama, Shulman and Robertson 1996). This critique was followed by a rebuttal in which Lapointe (1999) re-affirmed his position but added that he did not discount a role for reduced herbivory in the story. This debate was followed by several papers that have shown recent large decreases in algal cover on Discovery Bay reefs coincident with the return of *Diadema* to densities comparable to those before the die-off (Woodley 1999; Aronson and Precht 2000; Edmunds and Carpenter 2001). Reef zones where *Diadema* have returned have lost algal cover and appear to be regaining coral cover, while those where *Diadema* have not returned still have high algal cover and

fewer coral recruits (Edmunds and Carpenter 2001). This evidence of recovery has occurred without any measurable change in grazing fish abundance nor reason to expect reduced anthropogenic nutrient inputs (no decreases in human population, no improvement to wastewater treatment, no change in rainfall; Aronson and Precht 2000). While Lapointe may be correct with regard to the fact that anthropogenic nutrients are entering the Discovery Bay coastal zone, the weight of evidence does not suggest that those nutrients had a major role in the phase shift and decline of Discovery Bay reefs, since the recovery now evidently underway is happening without any effort to reduce nutrient loading.

Reef degradation at other Caribbean reef sites has been documented over a similar time-frame as the Discovery Bay reefs, but the role of hurricanes in initiating the decline did not occur at those sites. On San Blas reefs, bleaching in the early 1980s followed by the *Diadema* die-off are thought to be the major causes, although the authors expressed concern about the possible role of sedimentation and nutrients due to increased deforestation of coastal mountains (Shulman and Robertson 1996).

Reefs on the Belize barrier reef suffered a major decline in coral cover between 1986 and 1990, primarily due to loss of the staghorn coral *Acropora cervicornis*, presumably to white band disease (Aronson and Precht 2000), although the sampling time-frame provided in the paper cannot rule out that bleaching played a part in the loss. These authors propose that the phase shift from coral to algal domination widely observed throughout the Caribbean, requires a loss of coral to open up substrate for algal colonization, and that this has occurred through major loss of the acroporid corals to disease, bleaching, and storm damage. They also express a concern about a potential role of eutrophication, but provide no evidence for its occurrence. The lagoon of the remote atoll, Glovers Reef, located 30 km offshore of the Belize barrier reef, also suffered a major decline in coral cover (about 75%) sometime between 1971 and 1996, primarily due to loss of acroporids, but all species of corals declined while the cover by fleshy erect brown algae increased (McClanahan and Muthiga 1998). While there is little possibility of local anthropogenic eutrophication being the cause of this particular phase shift, many of the species of brown algae found in the Glovers lagoon were the same ones claimed by Lapointe (1997) to be indicators of nutrification in Discovery Bay.

Hallock et al. (1993) have suggested that Caribbean-wide coral reef decline is associated with basin-wide eutrophication from destructive land-use practices, increased deforestation, and contaminated runoff into the semi-enclosed Caribbean Sea. If so, local enrichment could be less of a factor than chronic basinwide elevated nutrient concentrations. Williams and Polunin (2001) found a strong inverse correlation between macroalgal cover and herbivorous fish biomass when they surveyed 19 reefs within seven broadly distributed sites within the Caribbean (Fig. 4), which together with experimental work on grazing effects reviewed above, suggests that local herbivory rates are an important determinant of macroalgal cover. They also found a positive correlation between herbivore biomass and cropped turf area. They noted that coral cover was generally below 25% at most of their sites, likely from coral loss due to bleaching during recent years, thus making most of the substrate available for algal colonization. They suggest that even where reefs are not overfished, and herbivorous fishes are abundant, that fishes can only keep 60% of the substrate cropped. As corals lose ground from bleaching and disease mortality, more surface area is made available for algal colonization than fishes alone can graze. *Diadema* abundance was very low (less than 0.01 m^2) at their sites. The macroalgae that dominated at high algal cover sites were those known to be chemically or structurally defended against fish grazing (*Dictyota, Halimeda, Lobophora*), but algae that *Diadema* readily consume in laboratory and field experiments (Szmant unpublished; Szmant and Miller unpublished).

Costa et al. (2000) provide a comparison on nutrient concentrations and reef community structure for two Brazilian reefs that differ in the amount of human development. Fishing pressure is similar and both are unprotected. Nutrient concentrations at the more developed site were extremely high compared to those reported for other anthropogenically influenced sites (Table 1). Macroalgal cover was twice as high at the developed site, coral cover was low at both, and the amount of bare substrate, dead coral, and sediment cover was twice as high at the less developed site. While nutrient enrichment undoubtedly is a major cause of higher macroalgal cover at the developed site as the authors suggest, nutrient levels at the less developed site are also high, and it seems likely that there are factors other than nutrient enrichment, such as sedimentation and grazing, that are contributing to the differences in algal cover.

Florida Keys

Coral reefs in the Florida Keys, like those in the Caribbean region as a whole, have lost much coral cover in the past few decades (Dustan 1977; Dustan and Halas 1987; Porter and Meier 1992), and especially since 1987 when coral bleaching became

an almost annual event. Because of the rapid urban and agricultural development of South Florida since the 1960s, many have been quick to blame water quality degradation and nutrient enrichment for the loss of coral, implicating algal overgrowth of the corals as the cause of coral loss (e.g., Ward 1990; Torrance 1991; Hallock et al. 1993; Lapointe and Clark 1992; Lapointe and Matzie 1996). The U.S. Environmental Protection Agency (1992) has catalogued the various types and sources of anthropogenic nutrient inputs to the Florida Keys. There is no doubt that the porous limestone of the Florida Keys allows sewage nutrients from septic tanks, cesspools, and shallow injection wells to seep into canal waters, and several studies have reported higher nutrient concentrations and other indicators of pollution in canal and inshore waters (Lapointe and Clark 1992; Paul et al. 1995; Lapointe and Matzie 1996; Szmant and Forrester 1996). Florida reefs are separated from inshore waters by Hawk Channel, a deeper channel that runs the length of the Florida reef tract 1–3 km from shore. It serves as a partial hydrographic barrier between inshore and offshore waters of the Florida reef tract lagoon (Pitts 1994; Smith 1994), and Szmant and Forrester (1996) found that offshore waters had significantly lower nutrient concentrations than inshore waters. The question is whether anthropogenic nutrients are reaching Florida reefs at rates that can alter reef community structure. One approach to addressing this question is to examine patterns of nutrients in the sediments, since sediment nutrient pools reflect long-term nutrient dynamics, especially the balance between input and export (Laws 1992; Fig. 3). Sediments in basins and lagoonal areas become nutrient-enriched when nutrient additions are sustained as was observed in Kaneohe Bay.

Szmant and Forrester (1996) found inshore sediments to be relatively enriched in N compared to more offshore sediments, but that both inshore and reef sediments had lower N concentrations than sediments from other reef sites considered pristine. Offshore sediments tended to be more enriched with P than inshore sediments but still low in comparison with reefs sediments from the Bahamas and St. Croix, U.S. Virgin Islands. Repeated sampling of the Florida transects in 1996 and again in 1998 after Hurricane Mitch found no change in nutrients from the levels measured in 1990 and 1991 (Fig. 5; Szmant unpublished data). Hanisak and Siemon (2000) examined the C:N:P ratios of a large number of macroalgal samples collected from 12 inshore-offshore transects throughout the Florida Keys as an indicator of nutrient availability to the plants. They found no pockets of nutrient enrichment, but found a similar trend of
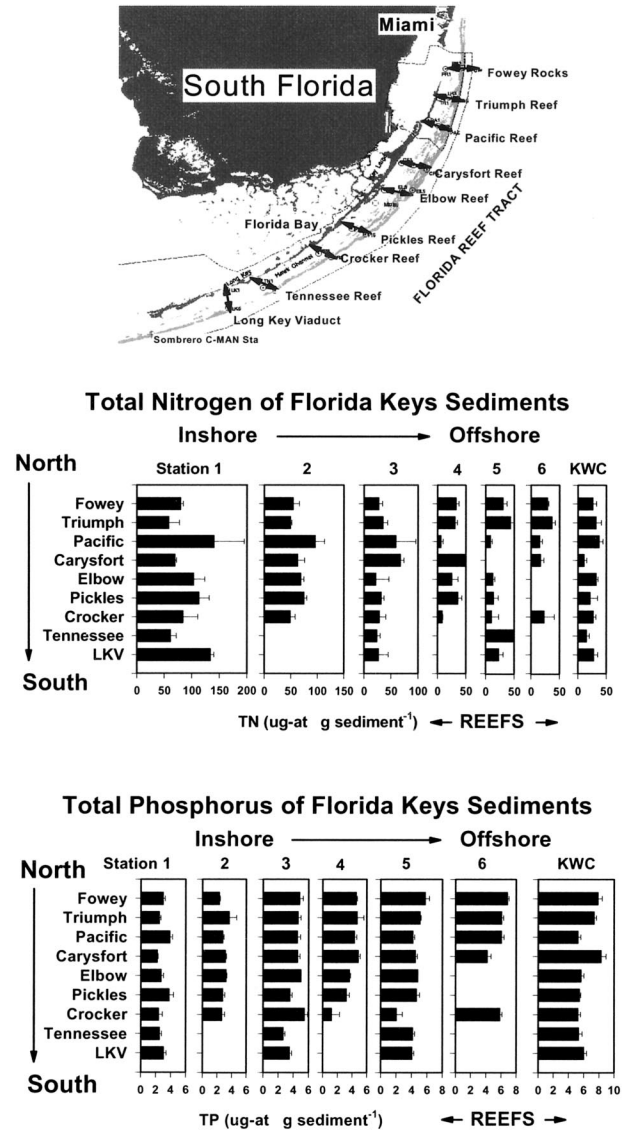

Fig. 5. Sediment nitrogen and phosphorus concentrations along nine inshore to offshore transects in the northern and middle regions of the Florida Keys, sampled in spring–summer 1996. Upper panel) Map of South Florida and Florida Reef Tract showing the locations of the nine transects. The transects are designated by the names of major charted offshore towers or navigation markers on offshore bank reefs, except for LKV which is named after the Long Key Viaduct in the Middle Keys. Middle panel) Total nitrogen content of sediment samples. Lower panel) Total phosphorus content of sediment samples. Two to five sediment cores or grab samples were collected from each station. Stations 1 to 3 along each transect were inshore of Hawks Channel; stations 4 and 5 were on patch reefs on White Banks; station 6 was from the shallow fore reefs (10 m depth) of the offshore bank reefs; KWC (Keys Wide Cruise) samples were from the deeper fore reefs (20 m depth) of the offshore bank reefs. See Szmant and Forrester (1996) for details of sample collection and analysis.

higher tissue N/lower P content in algae collected from inshore sites compared to offshore ones as Szmant and Forrester (1996) found in their sediment samples. Szmant and Forrester (1996) suggested that upwelling could be an important source of nutrients, especially of phosphate, to offshore Florida reefs, since major upwelling events have been documented for the Florida Keys (Smith 1982; Lee et al. 1992, 1994). Leichter and Miller (1999) have shown upwelling events to be more frequent during the summer, when Florida reef algae achieve higher cover and biomass (Lirman and Biber 2000; Szmant unpublished data).

There are no published historical data on algal cover and biomass on Florida reefs to document temporal trends in algal abundance, and none of the studies reporting coral loss include data on algal cover, or show that increased algal cover preceded coral loss or caused the loss of coral. Porter and Meier (1992) report a high algal cover of 13.8% at a station where *Diadema* abundance was zero, and only 4.2% at the same station when *Diadema* abundance increased to 0.4 m^{-2}. These values are low compared to other surveys that show algal cover to be generally much higher (70% to 80% cover) on Florida reefs (Chiappone 1996). Chiappone (1996) found the highest algal cover and the lowest coral cover on offshore reefs compared to more nearshore patch reefs, and this is contrary to the pattern one would predict if land-based nutrients were responsible for promoting algal abundance, but it could indicate that upwelling-supplied P is contributing to greater algal cover offshore. Miller et al. (2000) found lower adult coral cover and coral recruitment on offshore reefs of the northern reef tract than on patch reefs, in spite of higher temperature stress, nutrient concentrations and sediment resuspension closer to shore. Ginsburg et al. (2002) surveyed coral cover on shallow patch reefs throughout the Keys and found no correlation between recent partial mortality and proximity to urban centers. There are no data that show a clear direct correlation between present day water quality conditions and coral health that would explain general patterns of decline for Florida reefs. The general patterns of decline are more consistent with being due to regional bleaching stress.

An Integrated Conceptual Model for Productivity, Nutrient Dynamics, and Trophic Dynamics

INTERACTIONS ON CORAL REEFS

It is clear that nutrients are one of many factors affecting coral reef community structure and function. While there is evidence that nutrient enrichment can and has affected coral reefs, this effect appears to have been mostly localized. An understanding of how and when nutrient enrichment will contribute to coral reef decline requires consideration of all of the mechanisms involved in nutrient dynamics within coral reef ecosystems. If nutrient enrichment is going to affect coral reef community structure, it will most likely occur by altering the productivity of certain algal groups. The patterns of productivity and normal fate of primary production on coral reefs must be considered.

Coral reefs are often described as productive, diverse, and complex ecosystems because of their high rates of gross production as well as the large numbers and diverse types of animals that dwell on them, yet at the same time recognized to have values of net excess production close to zero (Odum and Odum 1955; Lewis 1977; Kinsey 1985; Crossland et al. 1991; Hatcher 1997). In other words, reef heterotrophs consume most of the algal primary production on a daily basis (ratio of 24 h photosynthesis to 24 h respiration $\approx$ 1; Lewis 1977; Smith 1983; Kinsey 1985). It is impossible to measure community metabolism for entire coral reefs because of their large size, and hydrographic and spatial complexity, and most measurements have been made on either reef flats or lagoons, where water flow is more constrained. It is recognized that some reef zones are more productive than others because of their biotic composition or environmental conditions. Investigators have taken this into account in generating ecosystem-wide estimates of metabolism (Kinsey 1985; Johnson et al. 1995), based on the premise that coral reefs are functionally integrated ecosystems with physical or biological transport and exchange of materials among the various reef zones (Szmant-Froelich 1983; Hatcher 1997). Kinsey (1985) proposed that coral reef flats have a modal standard performance of gross production of 7 ± 1 g C m^{-2} d^{-1}, and P/R of 1.0 ± 0.1 that is independent of species composition. Pichon (1997) refuted this based on data from a diverse set of reefs from seven geographic regions. Interestingly, the reported values of community gross production vary 20-fold over a range from about 1 to 19 g C m^{-2} d^{-1} (Lewis 1977; Rogers 1979; Smith 1983; Kinsey 1985; Gattuso et al. 1993 and references therein; Kraines et al. 1996; Pichon 1997; Gattuso et al. 1998). This broad range in area-specific gross production can be explained by the amount of substrate area available for autotrophs to grow on, which is a factor of both the proportion of the substrate occupied by non-photosynthetic organisms, and the amount of structural complexity per planar area: the higher the complexity the more surface area for algae to grow on (Pichon 1997; Szmant 1997); the sizes and types of dominant primary producers and their

biomass-specific rates of production (Hatcher 1988, 1990; Steneck and Dethier 1994); physical-chemical conditions (e.g., nutrient fluxes, circulation and turbulence, light) that affect biomass specific rates of production; or a combination of the above, since they are not mutually exclusive.

For the P/R of coral reefs to remain close to one regardless of absolute level of gross production, reefs with higher production must have a greater respiratory demand, i.e., a greater biomass of respiring organisms per unit area. As long as heterotrophs consume most of the algal production and pass it up the food web (e.g., grazers feeding on algae, microbes using mucus excreted by autotrophic corals, detrital food webs based on algal fragments; Szmant 1997), algal biomass cannot increase on a reef.

When a reef has a high algal standing crop, it can be inferred that at some point in time, algal production has exceeded the capacity of the heterotrophic community to consume it. This can happen if the rates of production of existing algal groups increases (i.e., same species of algae, but greater productivity due to more nutrients if nutrient limited, more turbulence breaks down diffusion barriers, less turbid/more light); if more productive algal groups replace less productive ones (shifts in algal species composition: see Steneck and Dethier 1994); if more surface area becomes available for algae to occupy (after storms, bleaching events or coral disease, exposed coral skeleton becomes available for algal colonization); if loss of grazers and other consumers (overfishing, *Diadema* die-off); or if shifts in algal composition towards species that are not palatable. These alternatives are not mutually exclusive and can be synergistic.

The question now is what potential role does nutrient availability play in determining the gross ecosystem production of a coral reef via any of the above or other mechanisms? Nutrient recycling is accepted as being the source of most of the nutrient demand for gross production (Smith 1983; Szmant-Froelich 1983; D'Elia 1988; Furnas et al. 1995) but if all reef ecosystems are equally efficient at recycling, recycling cannot explain the large range of gross production among reefs. The reef systems with the highest reported rates of gross and net production are either those in upwelling areas (Smith 1983; Pauley 1997) or near high islands (Pichon 1997; Gattuso et al. 1998). Mioche and Cuet (1999) report that a nutrified reef had higher levels of gross production and consumption than a nearby unpolluted reef. Based on first principles and sparse data, it is reasonable to suggest that higher nutrient fluxes will allow for greater rates of gross production on coral reefs.

The simple conceptual model proposed here is based on this assumption, that upper limits of gross production and levels of net production depend at least in part on nutrient flux, and that there is an idealized linear relationship between primary production and nutrient supply rate. If we accept that on pristine reefs the ratio of production-to-consumption will hover around one over a broad range of rates of gross production as has been more or less empirically observed, then the amount of gross production transferred to the coral reef food web via herbivory will also increase linearly with nutrient supply, up to a point determined by the grazing capacity of the consumers, after which algae can overgrow the substrate (and corals) and coral reef degradation begins (Fig. 6a). If the starting point is one of low algal biomass (the general vision of a pristine coral reef), as long as most of daily algal production is consumed, macroalgae will remain in low cover and biomass, and corals, coralline algae, and highly grazed turfs will dominate the substrate if conditions are otherwise suitable for these organisms (e.g., substrate type and depth, temperature, light, circulation). This situation is represented in the left half of Fig. 6a. At some level of nutrient flux ($= N_k$) the amount of production will be greater than what the herbivore and detritivore communities can consume because their populations and biomass will ultimately be limited by factors other than food availability, such as predation, shelter, or recruitment dynamics. Above this nutrient flux, algal biomass and cover will gradually increase and coral cover decrease by interactions as discussed previously (right side of Fig. 6a). The amount of productivity transferred to the food web may decrease if non-palatable species begin to dominate over palatable species. The nutrient flux at which shifts in coral reef community structure become evident, N_k, will be highly dependent on the grazer community's ability to consume the production supported by the level of nutrient flux. The level of nutrient flux at which coral reef decline begins can be viewed as a threshold level. Several investigators have proposed levels of nutrients (in units of concentration, not flux) above which coral reefs become degraded (1 μM ammonium plus nitrate, 0.1 μM phosphate; Bell 1992; Lapointe 1997), but the conceptual threshold proposed here is not a fixed concentration. Rather it is a range of fluxes that vary depending on the ability of the reef heterotrophs to consume the production. If conditions change such that greater grazing pressure can be accommodated (heavy recruitment of herbivores, increased shelter for reef dwellers), then the nutrient flux needed to cause degradation would shift upwards and corals will thrive at higher nutrient

A. Normal herbivory on a pristine unfished reef

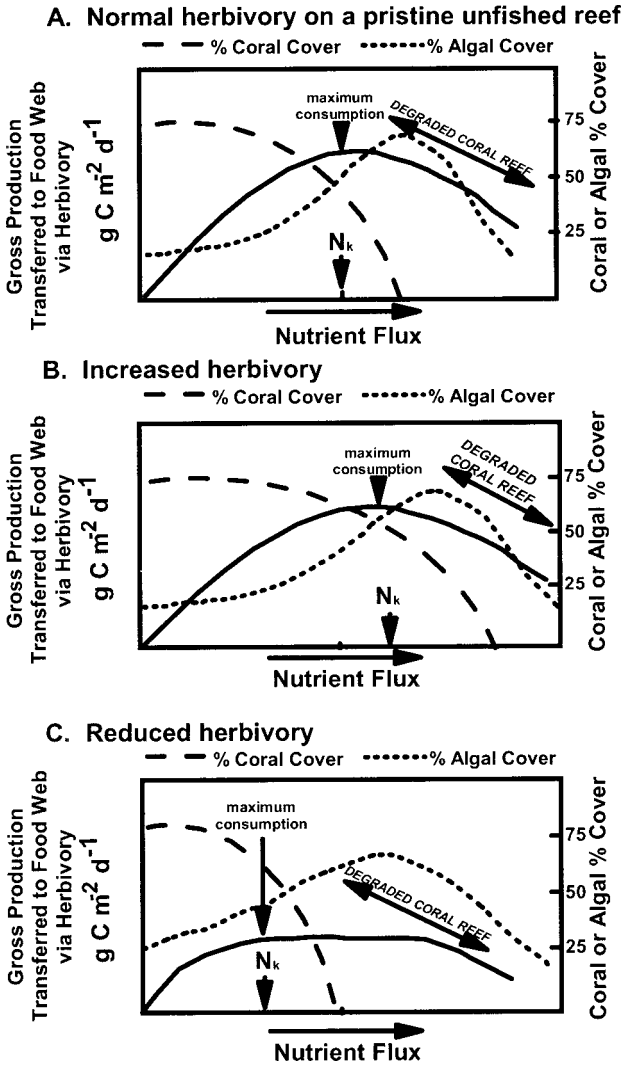## B. Increased herbivory

C. Reduced herbivory

Fig. 6.   Conceptual model of nutrient effects on coral reef community structure mediated through interactions between gross production and total community consumption including herbivory. A) Representation of relative nutrient tolerance of unfished, pristine coral reefs. This scenario represents the range of nutrient fluxes under which coral reefs would be able to form. N_k is the natural nutrient flux at which primary production would exceed the capacity of a healthy coral reef community to use the production, leading to a build-up of excess production in the form of algal biomass. Past that relative level of nutrient flux, coral cover would decrease, algal cover increase, and at some level reef-building would cease. This model is conceptually similar to that of Birkeland (1988) shown in Fig. 2b. Such a model can explain changes in reef productivity and structure associated with increasing latitude or upwelling zones where nutrient supplies are higher. B) Representation of how nutrient tolerance and productivity of a reef could increase with increased consumption, in this case increased herbivory. Note that N_k moves to the right. Factors that could lead to increased N_k include increased substrate for primary producers coupled with increased shelter for herbivores and other reef consumers. Increasing topographic complexity over time could lead to both such changes. C) Model scenario for how coral reef response to nutrient flux can be affected by loss of herbivory. This will result in less production being passed on to the coral reef food web, and a shift from coral to algal dominance even at low nutrient fluxes. Notice N_k moves to the left.

When the ratio of [% algal cover] to [grazing pressure] increases, algal species shift towards calcified or chemically defended algae
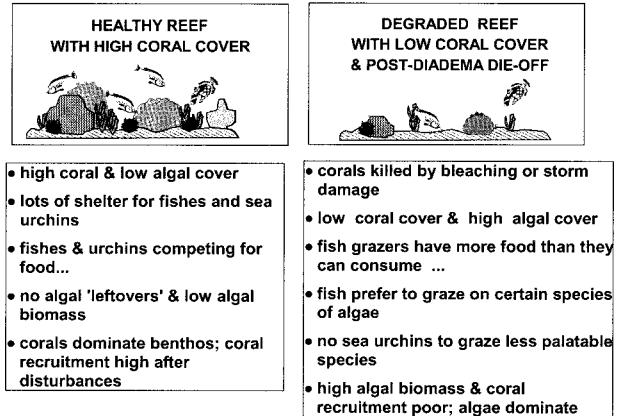

Fig. 7.   Diagrammatic summary of sequence of events that begin with loss of coral cover and reef structural complexity due to events such as bleaching or storm damage, with or without loss of herbivory, and can result in eventual dominance of the substrate by chemically or structurally defended macroalgae. Key to the community structure change in the right panel is that grazing pressure per unit area of reef is lower because of more surface area available for algal growth, while there is less habitat available for herbivore shelter; in the Caribbean, there is also the loss of an invertebrate herbivore that was less responsive to algal defenses than herbivorous fishes.

levels than before (Fig. 6b). If grazing pressure decreases or if substrate available for primary producers increases faster than the size of the grazer community (e.g., overfishing of herbivores or *Diadema* die-off for the former; coral killed by bleaching, disease or storms for the latter), then shifts from coral to algal dominance will occur even at low nutrient fluxes (Fig. 6c). This last scenario can explain the observed shifts in coral-algal abundance that have been observed so widely in the Caribbean even in remote areas where nutrient enrichment is highly unlikely.

Two scenarios of the conceptual model that are not visually represented in Fig. 6 are the loss of live coral due to extraneous causes, and effects of relative algal palatability on shifts in algal community structure (Fig. 7). Williams et al. (2001) experimentally showed the positive relationship between coral cover and grazing pressure per area, and how a reduction in the percent substrate available to algae caused a reduction in algal cover on the remaining substrate. Many reef algae are chemically or structurally defended against fish grazers (Hay 1997), and the species of macroalgae now dominating many Caribbean reefs belong to those groups (*Halimeda, Dictyota, Lobophora*). Many fishes will graze on very small plants of these species (when they are in minute turf form) before they have a chance to build up chemical or structural defenses, but not once they get bigger. When sub-

strate available to algae is low (i.e., when coral cover is high), high grazing pressure on limited substrate keeps these species from growing to a defended size. As substrate for algal colonization increases when corals die from storm damage or bleaching, or as grazing pressure decreases due to overfishing or herbivore die-off, grazing pressure per area is lower (Williams et al. 2001), and some of the non-palatable plants will reach a larger, nongrazed size. The non-palatable species can gradually take over a significant portion of the reef, and the corals cannot recruit into areas dominated by these larger fleshy forms. Because they are not grazed, the productivity of these species can only enter the coral reef food chain through a detrital pathway as the algae senesce and are ripped off the substrate by storms. These changes in carbon pathways can lead to changes in reef community structure (Johnson et al. 1995). Such a sequence of events can explain how, without invoking widespread nutrification, repeated severe bleaching of Caribbean corals since the late 1980s has contributed to a dramatic regional change from low algal cover and greater than 50% coral cover in the 1970s to less than 25% coral cover and over 50% algal cover at present. It is also consistent with observations reported by Hughes (1994), Shulman and Robertson (1996), McClanahan and Muthiga (1998), Williams and Polunin (2001), and others.

Conclusions

Anthropogenic nutrient over-enrichment has affected the integrity of freshwater and coastal marine ecosystems worldwide, especially systems such as estuaries that can serve as nutrient traps (National Research Council 2000). It is only logical to expect that tropical ecosystems such as coral reefs, which occur in relatively oligotrophic waters, would be highly susceptible to nutrient enrichment, and for investigators to invoke this as a major cause for recent coral reef decline wherever such decline is associated with large increases in macroalgal abundance. The evidence that nutrient enrichment has widely impacted corals reefs is poor, and there are mitigating reasons why coral reefs may have largely escaped this fate. Coral reefs generally require high water flow and turbulence, and only reefs in embayments with restricted circulation are likely to experience nutrient build-up. Reefs in more exposed locations experience frequent storms so that nutrients in sediments and detrital materials are either flushed out to sea or transported to the back reef areas where nutrients normally accumulate and support algal communities and grassbeds. Many coral reefs are associated with smaller land masses that support smaller human populations and watersheds relative to those

of temperate coastal ecosystems, and sewage production is likely less per area of reef than might be expected. The two major activities that humans conduct locally that contribute to coral reef degradation are land-clearing for logging, agriculture, and urbanization, which cause large increases in sediment loading to tropical coastal areas where reefs grow, and fishing which removes large numbers of mobile grazers and predators from the reefs. Global warming as a result of fossil fuel burning and generation of other greenhouse gases has devastated coral reefs worldwide by causing coral bleaching and subsequent coral death; the resulting coral-algal abundance shifts likely have pre-disposed reefs to becoming sensitive to even normal levels of nutrient flux. While nutrient enrichment may be the major factor in the decline of a few reefs, it appears to mostly play a secondary role compared to those of sedimentation, overfishing, and global warming.

Literature Cited

Andrews, J. C. and P. Gentien. 1982. Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: A solution to Darwin's question? *Marine Ecology Progress Series* 8:257–269.

Anthony, K. R. N. 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* 19:59–67.

Aronson, R. B. and W. F. Precht. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnology and Oceanography* 45:251–255.

Atkinson, M. J. 1988. Are coral reefs nutrient limited? *In* J. H. Choat (ed.), Proceedings of the 6th International Coral Reef Symposium 1:157–166. James Cook University Press, Townsville, Australia.

Atkinson, M. J., B. Carlson, and G. L. Crow. 1995. Coral growth in high-nutrient, low-pH seawater: A case study of corals cultured at Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs* 14:215–223.

Bell, P. R. F. 1992. Eutrophication and coral reefs—Some examples in the Great Barrier Reef lagoon. *Water Research* 26:553–568.

Bell, P. R. F. and I. Elimetri. 1995. Ecological indicators of large-scale eutrophication in the Great Barrier Reef lagoon. *Ambio* 24:208–215.

Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *In* R. N. Ginsburg and D. L. Taylor (eds.), Proceedings of the 3rd International Coral Reef

Symposium 1:15–21. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida.

BIRKELAND, C. 1987. Nutrient availability as a major determination of differences among coastal hard-substratum communities in different regions of the tropics, p. 1–26. *In* C. Birkeland (ed.), Comparison between Atlantic and Pacific Tropical Coastal Systems, United Nations Educational, Scientific, and Cultural Organization Reports in Marine Science 46. UNESCO Division of Marine Science, Paris, France.

BIRKELAND, C. 1988. Geographic comparisons of coral-reef community processes. *In* J. H. Choat (ed.), Proceedings of the 6th International Coral Reef Symposium 1:211–220. James Cook University Press, Townsville, Australia.

BIRKELAND, C., S. S. AMESBURY, AND R. H. RANDALL. 1993. Koror wastewater facility biological survey. University of Guam Technical Report. University of Guam, Mangiloa, Guam.

BJÖRK, M., S. M. MOHAMMED, M. BJÖRKLUND, AND A. SEMESI. 1995. Coralline algae, important coral-reef builders threatened by pollution. *Ambio* 24:502–505.

BOROWITZKA, M. A., A. W. D. LARKUM, AND L. J. BOROWITZKA. 1978. A preliminary study of algal turf communities of shallow coral reef lagoon using an artificial substratum. *Aquatic Botany* 5:365–381.

BRODIE, J. E., M. J. FURNAS, A. D. L. STEVEN, L. A. TROTT, F. PANTUS, AND M. WRIGHT. 1997. Monitoring chlorophyll in the Great Barrier Reef lagoon: Trends and variability. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:797–802. Smithsonian Tropical Research Institute, Balboa, Panama.

BYTHELL, J. C., Z. M. HILLIS-STARR, AND C. S. ROGERS. 2000. Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series* 204:93–100.

CARPENTER, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56:345–356.

CARPENTER, R. C. 1997. Invertebrate predators and grazers, p. 198–229. *In* C. Birkeland (ed.), Life and Death of Coral Reefs. Chapman and Hall, New York.

CHIAPPONE, M. 1996. Coral Watch program summary. A report on volunteer and scientific efforts to document the status of reefs in the Florida Keys National Marine Sanctuary. The Nature Conservancy, Summerland Key, Florida.

COLLINS, L. B., Z. R. ZHU, K.-H. WYRWOLL, B. G. HATCHER, P. E. PLAYFORD, J. H. CHEN, A. EISENHAUER, AND G. J. WASSERBURG. 1993. Late Quaternary evolution of coral reefs on a cool-water carbonate margin: The Abrolhos Carbonate Platforms, southwest Australia. *Marine Geology* 110:203–212.

COSTA, JR., O. S., Z. M. A. N. LEÃO, M. NIMMO, AND M. J. ATTRILL. 2000. Nutrification impacts on coral reefs from northern Bahia, Brazil. *Hydrobiologia* 440:370–315.

CROSSLAND, C. J. 1983. Dissolved nutrients in coral reef waters, p. 56–68. *In* D. J. Barnes (ed.), Perspectives in Coral Reefs. Published for the Australian Institute of Marine Science, Brian Clouston Publishers, Manuka, Australia.

CROSSLAND, C. J., B. G. HATCHER, M. J. ATKINSON, AND S. V. SMITH. 1984. Dissolved nutrients of a high-latitude coral reef, Houtman Abrolhos Islands, Western Australia. *Marine Ecology Progress Series* 14:159–163.

CROSSLAND, C. J., B. G. HATCHER, AND S. V. SMITH. 1991. Role of coral reefs in global ocean production. *Coral Reefs* 10:55–64.

CUET, P., O. NAIM, G. FAURE, AND J. Y. CONAN. 1988. Nutrient-rich groundwater impact on benthic communities of La Saline fringing reef (Réunion Island, Indian Ocean): Preliminary results. *In* J. H. Choat (ed.), Proceedings of the 6th International Coral Reef Symposium 2:207–212. James Cook University Press, Townsville, Australia.

D'ELIA, C. F. 1988. The cycling of essential elements in coral reefs, p. 196–245. *In* L. R. Pomeroy and J. J. Alberts (eds.), Concepts of Ecosystem Ecology: A Comparative View. Springer, New York.

D'ELIA, C. F., K. L. WEBB, AND J. W. PORTER. 1981. Nitrate-rich groundwater inputs to Discovery Bay, Jamaica: A significant source of N to local reefs? *Bulletin of Marine Science* 31:903–910.

D'ELIA, C. F. AND W. J. WIEBE. 1990. Biogeochemical nutrient cycles in coral reef ecosystems, p. 49–74. *In* Z. Dubinsky (ed.), Ecosystems of the World, Volume 25. Coral Reefs. Elsevier Press, New York.

DE RUYTER VAN STEVENINCK, E. D., L. L. VAN MULEKON, AND A. M. BREENAN. 1988. Growth inhibition of *Lobophora variegata* (Lamouroux) Womersley by scleracterian corals. *Journal of Experimental Marine Biology and Ecology* 115:169–178.

DODGE, R. E., A. M. SZMANT, R. GARCIA, AND P. K. SWART. 1993. Skeletal structural basis of density banding in the reef coral *Montastrea annularis*. *In* R. H. Richmond (ed.), Proceedings of the 7th International Coral Reef Symposium 186–195. University of Guam Press, Mangilao, Guam.

DONE, T. J. 1992. Constancy and change in some Great Barrier Reef coral communities: 1980–1990. *American Zoologist* 32:655–662.

DONE, T. J. 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist* 39:66–79.

DUBINSKY, Z. AND N. STAMBLER. 1996. Marine pollution on coral reefs. *Global Change Biology* 2:511–526.

DUBINSKY, Z., N. STAMBLER, M. BEN-ZION, L. R. MCCLOSKY, L. MUSCATINE, AND P. G. FALKOWSKI. 1990. The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. *Proceedings of the Royal Society London Series B* 239:231–246.

DUSTAN, P. 1977. Vitality of reef coral populations off Key Largo, Florida: Recruitment and mortality. *Environmental Geology* 2:51–58.

DUSTAN, P. AND J. C. HALAS. 1987. Changes in reef-coral community of Carysfort Reef, Key Largo, Florida. *Coral Reefs* 6:91–106.

EDMUNDS, P. J. AND R. C. CARPENTER. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences of the USA* 98:5067–5071.

EDWARDS, A. J., S. CLARK, H. ZAHIR, A. RAJASURIYA, A. NASEER, AND J. RUBENS. 2001. Coral bleaching and mortality on artificial and natural reefs in Maldives in 1998, sea surface temperature anomalies and initial recovery. *Marine Pollution Bulletin* 42:7–15.

FABRICIUS, K. AND G. DE'EATH. 2001. Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19:303–309.

FERRIER-PAGES, C., J. P. GATTUSO, S. DALLOT, AND J. JAUBERT. 2000. Effect of nutrient enrichment on growth and photosynthesis of zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19:103–113.

FURNAS, M. A., W. MITCHELL, AND M. SKUZA. 1995. Nitrogen and phosphorus budgets for the central Great Barrier Reef shelf. Research Publication Number 36. Great Barrier Reef Marine Park Authority, Townsville, Australia.

FURNAS, M. A., A. MITCHELL, AND M. SKUZA. 1997. Shelf-scale nitrogen and phosphorus budgets for the central Great Barrier Reef (16–19°S). *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium, Panama City, Panama 1:809–814. Smithsonian Tropical Research Institute, Balboa, Panama.

GATTUSO, J. P., M. FRANKIGNOULLE, AND R. WOLLAST. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* 29:405–434.

GATTUSO, J. P., M. PICHON, B. DELESALLE, AND M. FRANKIGNOULLE. 1993. Community metabolism and air-sea CO_2 fluxes in a

coral reef ecosystem (Moorea, French Polynesia). *Marine Ecology Progress Series* 96:259–267.

GENIN, A., B. LAZAR, AND S. BRENNER. 1995. Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature* 337:507–510.

GINSBURG, R. N., E. GISCHLER, AND W. E. KIENE. 2002. Partial mortality of massive reef-building corals: An index of patch reef condition, Florida Reef Tract. *Bulletin of Marine Science* 69:1149–1173.

GLYNN, P. W. 1977. Coral upgrowth in upwelling and nonupwelling areas off the Pacific coast of Panama. *Journal of Marine Research* 35:567–585.

GLYNN, P. W. 1993. Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. *Atoll Research Bulletin* 379:1–66.

GLYNN, P. W. 1997. Bioerosion and coral reef growth: A dynamic balance, p. 68–95. *In* C. Birkeland (ed.), Life and Death of Coral Reefs. Chapman and Hall, New York.

GLYNN, P. W., S. B. COLLEY, C. M. EAKIN, D. B. SMITH, J. CORTES, N. J. GASSMAN, H. M. GUZMAN, J. B. DEL ROSARIO, AND J. S. FEINGOLD. 1994. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). 2. Poritidae. *Marine Biology* 118:191–208.

GLYNN, P. W., S. B. COLLEY, N. J. GASSMAN, K. BLACK, J. CORTES, AND J. L. MATE. 1996. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, And Galapagos Islands (Ecuador). 3. Agariidea (*Pavona gigantea* and *Gardineroseris planulata*). *Marine Biology* 125:579–601.

GOLDMAN, B. 1994. Environmental management in Yap, Caroline Islands: Can the dream be realized? *Marine Pollution Bulletin* 29:42–51.

GOMEZ, E. D., P. M. ALIÑO, AND W. Y. LICUANAN. 1994. A review of the status of Philippine reefs. *Marine Pollution Bulletin* 29: 62–68.

GRIGG, R. W. 1995. Coral reefs in an urban embayment in Hawaii: A complex case history controlled by natural and anthropogenic stress. *Coral Reefs* 14:253–266.

HALLOCK, P. 1988. The role of nutrient availability in bioerosion: Consequences to carbonate build-ups. *Paleogeography, Paleoclimatology, Paleoecology* 62:275–291.

HALLOCK, P., F. E. MULLER-KARGER, AND J. C. HALAS. 1993. Coral reef decline. *National Geographic Research and Exploration* 9: 358–378.

HALLOCK, P. AND W. SCHLAGER. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios* 1:389–398.

HANISAK, M. D. AND L. W. SIEMON. 2000. Macroalgal tissue nutrients as indicators of nitrogen and phosphorus status in the Florida Keys. *Journal of Phycology* 36:28.

HARRISON, P. L. AND C. C. WALLACE. 1990. Reproduction, dispersal and recruitment of scleractinian corals, p. 133–208. *In* Z. Dubinsky (ed.), Ecosystems of the World Volume 25: Coral Reefs. Elsevier, New York.

HARVELL, C. D., K. KIM, J. M. BURKHOLDER, R. R. COLWELL, P. R. EPSTIEN, D. J. GRIMES, E. E. HOFMANN, E. K. LIPP, A. D. M. E. OSTERHAUS, R. M. OVERSTREET, J. W. PORTER, G. W. SMITH, AND G. R. VASTA. 1999. Emerging marine diseases—Climate links and anthropogenic factors. *Science* 285:1505–1510.

HATCHER, A. I. AND B. G. HATCHER. 1981. Seasonal and spatial variation in dissolved inorganic nitrogen in One Tree Reef lagoon. *In* E. D. Gomez et al. (eds.), Proceedings of the 4th International Coral Reef Symposium 1:419–424. Marine Sciences Center, University of Philippines, Quezon City, Philippines.

HATCHER, B. G. 1984. A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. *Coral Reefs* 3:199–204.

HATCHER, B. G. 1988. Coral reef primary productivity: A beggar's banquet. *Trends in Ecology and Evolution* 3:106–111.

HATCHER, B. G. 1990. Coral reef primary productivity: A hierarchy of pattern and process. *Trends in Ecology and Evolution* 5:149–155.

HATCHER, B. G. 1997. Coral reef ecosystems: How much greater is the whole than the sum of the parts? *Coral Reefs* 16:S77–S91.

HATCHER, B. G., R. E. JOHANNES, AND A. I. ROBERTSON. 1989. Review of research relevant to the conservation of shallow tropical marine ecosystems. *Oceanography and Marine Biology: An Annual Review* 27:337–414.

HATCHER, B. G. AND A. W. D. LARKUM. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *Journal of Experimental Marine Biology and Ecology* 69:61–84.

HAY, M. E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? *Ecology* 65:446–454.

HAY, M. E. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs* 16:S67–S76.

HIGHSMITH, R. C. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7:207–226.

HIXON, M. A. 1997. Effects of reef fishes on corals and algae, p. 230–248. *In* C. Birkeland (ed.), Life and Death of Coral Reefs. Chapman and Hall, New York.

HOEGH-GULDBERG, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine Freshwater Research* 50:839–866.

HOEGH-GULDBERG, O. AND G. J. SMITH. 1989. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *Journal of Experimental Marine Biology* 129:279–303.

HOEGH-GULDBERG, O., M. TABAYASHI, AND G. MORENO. 1997. The impact of long-term nutrient enrichment on coral calcification and growth. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium, Panama City, Panama 1:861–866. Smithsonian Tropical Research Institute, Balboa, Panama.

HUBER, M. E. 1994. An assessment of the status of the coral reefs of Papua, New Guinea. *Marine Pollution Bulletin* 29:69–73.

HUGHES, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.

HUGHES, T. P., D. AYRE, AND J. C. CONNELL. 1992. The evolutionary ecology of corals. *Trends in Evolution and Ecology* 7:292–295.

HUGHES, T. P., D. C. REED, AND M. J. BOYLE. 1987. Herbivory on coral reefs: Community structure following mass mortalities of sea urchins. *Journal of Experimental Marine Biology and Ecology* 113:39–59.

HUGHES, T., A. M. SZMANT, R. STENECK, R. CARPENTER, AND S. MILLER. 1999. Algal blooms on coral reefs: What are the causes? *Limnology and Oceanography* 44:1583–1586.

HUTCHINGS, P., C. PAYRI, AND C. GABRIÉ. 1994. The current status of coral reef management in French Polynesia. *Marine Pollution Bulletin* 29:26–33.

JACKSON, J. B. C., M. X. KIRBY, W. H. BERGER, K. A. BJORNDAL, L. W. BOTSFORD, B. J. BOURQUE, R. H. BRADBURY, R. COOKE, J. ERLANDSON, J. A. ESTES, T. P. HUGHES, S. KIDWELL, C. B. LANGE, H. S. LENIHAN, J. M. PANDOLFI, C. H. PETERSON, R. S. STENECK, M. J. TEGNER, AND R. R. WARNER. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.

JOHANNES, R. E. 1970. How to kill a coral reef—I. *Marine Pollution Bulletin* 1:186–187.

JOHANNES, R. E. 1975. Pollution and degradation of coral reef communities, p. 13–51. *In* E. J. F. Wood and R. E. Johannes

(eds.), Tropical Marine Pollution. Elsevier Oceanography Series 12. Elsevier, Amsterdam, The Netherlands.

JOHANNES, R. E., J. ALBERTS, C. F. D'ELIA, R. A. KINZIE, L. R. POMEROY, W. SOTTILE, W. WIEBE, J. A. MARSH, P. HELFRICH, J. MARAGOS, J. MEYER, S. SMITH, D. CRABTREE, A. ROTH, L. R. McCLOSKEY, S. BETZER, N. MARSHALL, M. E. Q. PILSON, G. TELEK, R. I. CLUTTER, W. D. DuPAUL, K. L. WEBB, AND J. M. WELLS. 1972. The metabolism of some coral reef communities: A team study of nutrient and energy flux at Eniwetok. *BioScience* 22:541–543.

JOHANNES, R. E., W. J. WIEBE, C. J. CROSSLAND, D. W. RIMMER, AND S. V. SMITH. 1983. Latitudinal limits to coral reef growth. *Marine Ecology Progress Series* 11:105–111.

JOHNSON, C., D. KLUMPP, J. FIELD, AND R. BRADBURY. 1995. Carbon flux on coral reefs: Effects of large shifts in community structure. *Marine Ecology Progress Series* 126:123–143.

JOKIEL, P. L., Z. DUBINSKY, AND N. STAMBLER. 1994. Results of the United States-Israel workshop, ''Nutrient limitation in the symbiotic association between zooxanthellae and reef-building corals.'' *Pacific Science* 48:215–218.

KIENE, W. E. 1997. Enriched nutrients and their impact on bioerosion. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:897–902. Smithsonian Tropical Research Institute, Balboa, Panama.

KINSEY, D. W. 1985. Metabolism, calcification and carbon production. I. Systems level studies. *In* B. Salvat (ed.), Proceedings of the 5th International Coral Reef Symposium 4:505–526. Antenne Museum-Ephe, Moorea, French Polynesia.

KINSEY, D. W. AND P. J. DAVIES. 1979. Effects of elevated nitrogen and phosphorus on coral reef growth. *Limnology and Oceanography* 24:935–939.

KINSEY, D. W. AND A. DOMM. 1974. Effects of fertilization on a coral reef environment—Primary production studies. *In* A. M. Cameron, B. M. Campbell, A. B. Cribb, R. Endean, J. S. Jell, O. A. Jones, P. Mather, and F. H. Talbot (eds.), Proceedings of the 2nd Internatational Coral Reef Symposium. Great Barrier Reef Committee, Brisbane, Australia 1:49–66.

KLEYPAS, J. A., R. W. BUDDEMEIER, D. ARCHER, J.-P. GATTUSO, C. LANGDON, AND B. N. OPDYKE. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118–120.

KOOP, K., D. BOOTH, A. BROADBENT, J. BRODIE, D. BUCHER, D. CAPONE, J. COLL, W. DENNISON, M. ERDMANN, P. HARRISON, O. HOEGH-GULDBERG, P. HUTCHINGS, G. B. JONES, A. W. D. LARKIM, J. O'NEILL, A. STEVEN, E. TENTORI, S. WARD, J. WILLIAMSON, AND D. YELLOWLEES. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Marine Pollution Bulletin* 42:91–120.

KRAINES, S., Y. SUZUKI, K. YAMADA, AND H. KOMIYAMA. 1996. Separating biological and physical changes in dissolved oxygen concentration in a coral reef. *Limnology and Oceanography* 41:1790–1799.

LAMBERTS, A. E. 1978. Coral growth: Alizarin method, p. 523–527. *In* D. R. Stoddart and R. E. Johannes (eds.), Coral Reefs: Research Methods. UNESCO Monograph Oceanographic Method, Volume 5. United Nations Educational, Scientific, and Cultural Organization, Paris, France.

LAPOINTE, B. 1997. Nutrient thresholds for eutrophication and macroalgal overgrowth of coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119–1131.

LAPOINTE, B. 1999. Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. *Limnology and Oceanography* 44:1586–1592.

LAPOINTE, B. E. AND M. W. CLARK. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries* 15:465–476.

LAPOINTE, B. E. AND W. R. MATZIE. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. *Estuaries* 19:422–435.

LARKUM, A. W. D. AND K. KOOP. 1997. ENCORE, algal productivity and possible paradigm shifts. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:881–884. Smithsonian Tropical Research Institute, Balboa, Panama.

LARKUM, A. W. D. AND A. D. L. STEVEN. 1994. ENCORE: The effect of nutrient enrichment on coral reefs: 1. Experimental design and research programme. *Marine Pollution Bulletin* 29:112–120.

LARNED, S. 1998. Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology* 132:409–421.

LARNED, S. AND J. STIMSON. 1996. Nitrogen-limited growth in the coral reef chlorophyte *Dictyosphaeria cavernosa* and the effect of exposure to sediment-derived nitrogen on growth. *Marine Ecology Progress Series* 145:95–108.

LAWS, E. A. 1992. Aquatic Pollution. John Wiley and Sons, New York.

LEE, T. N., M. E. CLARKE, E. WILLIAMS, A. M. SZMANT, AND T. BERGER. 1994. Evolution of the Tortugas gyre and its influence on recruitment in the Florida Keys. *Bulletin of Marine Science* 54:621–646.

LEE, T. N., C. ROOTH, E. WILLIAMS, M. McGOWAN, A. M. SZMANT, AND M. E. CLARKE. 1992. Influence of Florida current, gyres and wind-driven circulation on larval transport and recruitment in the Florida Keys coral reefs. *Continental Shelf Research* 12:971–1002.

LEICHTER, J. J. AND S. L. MILLER. 1999. Predicting high-frequency upwelling: Spatial and temporal patterns of temperature anomalies on a Florida coral reef. *Continental Shelf Research* 19:911–928.

LEICHTER, J. J., S. R. WING, S. L. MILLER, AND M. W. DENNY. 1996. Pulsed delivery of sub-thermocline water to Conch Reef, Florida Keys by internal tidal bores. *Limnology and Oceanography* 41:1490–1501.

LESSIOS, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* 19:371–393.

LEWIS, J. B. 1976. Experimental tests of suspension feeding in Atlantic reef corals. *Marine Biology* 36:147–150.

LEWIS, J. B. 1977. Processes of organic production on coral reefs. *Biological Reviews* 52:305–347.

LEWIS, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:183–200.

LIDDELL, W. D. AND S. L. OHLHORST. 1986. Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *Journal of Experimental Marine Biology* 95:271–278.

LINDAHL, U., M. C. OHMAN, AND C. K. SCHELTENS. 2001. The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin* 42:127–131.

LIRMAN, D. AND P. BIBER. 2000. Seasonal dynamics of macroalgal communities of the northern Florida reef tract. *Botanica Marina* 43:305–314.

LITTLER, M. M. AND D. S. LITTLER. 1984. Models of tropical reef biogenesis: The contribution of algae. *Progress in Phycological Research* 3:323–364.

LOUGH, J. M. AND D. J. BARNES. 2000. Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* 245:225–243.

MARUBINI, F. AND M. J. ATKINSON. 1999. Effects of lowered pH and elevated nitrate on coral calcification. *Marine Ecology Progress Series* 188:117–121.

MARUBINI, F. AND P. S. DAVIES. 1996. Nitrate increases zooxanthellae population density and reduces skeletonogenesis in corals. *Marine Biology* 127:319–328.

MARUBINI, F. AND B. THAKE. 1999. Bicarbonate addition promotes coral growth. *Limnology and Oceanography* 44:716–720.

McClanahan, T. R. 1995. A coral reef ecosystem-fisheries model: Impacts of fishing intensity and catch selection on reef structure and processes. *Ecological Modelling* 80:1–19.

McClanahan, T. R. 2000. Bleaching damage and recovery potential of Maldivian coral reefs. *Marine Pollution Bulletin* 40: 587–597.

McClanahan, T. R. and N. A. Muthiga. 1988. Changes in Kenyan coral reef community structure and function due to exploitation. *Hydrobiologia* 166:269–276.

McClanahan, T. R. and N. A. Muthiga. 1998. An ecological shift in a remote coral reef atoll of Belize over 25 years. *Environmental Conservation* 25:122–130.

McClanahan, T. R., N. A. Muthiga, and S. Mangi. 2001. Coral and algal changes after the 1998 coral bleaching: Interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380–391.

McClanahan, T. R. and D. Obura. 1995. Status of Kenyan coral reefs. *Coastal Management* 23:57–76.

McClanahan, T. R. and D. Obura. 1997. Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209:103–122.

McClanahan, T. R. and S. H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83:362–370.

McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:1–11.

McCook, L. J. 2001. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. *Coral Reefs* 19:419–425.

McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* 19:400–417.

McCook, L. J. and I. R. Price. 1997. Macroalgal distributions on the Great Barrier Reef: A review of patterns and causes, Volume 2:37–46. Proceedings of the Great Barrier Reef Conference, November 1996, James Cook University Press, Townsville, Australia.

McCook, L. J., I. R. Price, and D. W. Klump. 1997. Macroalgae on the Great Barrier Reef: Causes or consequences, indicators or models of reef degradation? *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 2:1851–1856. Smithsonian Tropical Research Institute, Balboa, Panama.

McGuire, M. P. 1997. The biology of the coral *Porites astreoides*: Reproduction, larval settlement behavior and responses to ammonium enrichment. Ph.D. Dissertation, University of Miami, Miami, Florida.

Miller, M. W. 1998. Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanography and Marine Biology: An Annual Review* 36: 65–96.

Miller, M. W., M. E. Hay, S. L. Miller, D. Malone, E. E. Sotka, and A. M. Szmant. 1999. Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. *Limnology and Oceanography* 44:1847–1861.

Miller, M. W., E. Weil, and A. M. Szmant. 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* 19:115–123.

Mioche, D. and P. Cuet. 1999. Métabolisme du carbone, des carbonates et des sels nutritifs en saison chaide, sur un récif frangeant soumis à une pression anthropique (île de la Réunion, océan Indien). *Compté Rendu Académie Sciences de Paris, Sciences de la Terre et des Planètes* 329:53–59.

Morrison, D. 1988. Comparing fish and urchin grazing in deep and shallow coral reef algal communities. *Ecology* 69:1367–1382.

Morton, B. 1994. Hong Kong's coral communities: Status, threats and management plans. *Marine Pollution Bulletin* 29: 74–83.

Naim, O. 1993. Seasonal responses of a fringing reef community to eutrophication (Reunion Island, Western Indian Ocean). *Marine Ecology Progress Series* 99:137–151.

National Research Council. 2000. Clean Coastal Waters. Understanding and Reducing the Effects of Nutrient Pollution. National Academy Press, Washington, D.C.

Nixon, S. W. 1995. Coastal marine eutrophication: A definition, social causes and future concerns. *Ophelia* 41:199–219.

Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs* 25:291–320.

Ostrander, G. K., K. M. Armstrong, E. T. Knobbe, D. Gerace, and E. P. Scully. 2000. Rapid transition in the structure of a coral reef community: The effects of coral bleaching and physical disturbance. *Proceedings of the National Academy of Sciences, U.S.A.* 97:597–5302.

Pastorok, R. A. and G. R. Bilyard. 1985. Effects of sewage pollution on coral reef communities. *Marine Ecology Progress Series* 21:175–189.

Paul, J. H., J. B. Rose, J. Brown, E. A. Shinn, S. Miller, and S. Farrah. 1995. Viral tracer studies indicate contamination of marine waters by sewage disposal practices in Key Largo, Florida. *Applied and Environmental Microbiology* 61:2230–2234.

Pauley, G. 1997. Productivity plays a major role in determining atoll life and form: Tarawa, Kiribati. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:483–488. Smithsonian Tropical Research Institute, Balboa, Panama.

Pichon, M. 1997. Coral reef metabolism in the Indo-Pacific: The broader picture. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:977–980. Smithsonian Tropical Research Institute, Balboa, Panama.

Pitts, P. A. 1994. An investigation of near-bottom flow patterns along and across Hawk Channel, Florida Keys. *Bulletin of Marine Science* 54:610–620.

Porter, J. W. and O. W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. *American Zoologist* 32:625–640.

Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* 9:988–995.

Rogers, C. S. 1979. The productivity of San Cristobal Reef, Puerto Rico. *Limnology and Oceanography* 24:342–349.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185–202.

Rosenfeld, M., V. Bresler, and A. Abelson. 1999. Sediments as a possible source of food for corals. *Ecology Letters* 2:345–348.

Rougerie, F. and B. Wauthy. 1993. The endo-upwelling concept: From geothermal convection to reef construction. *Coral Reef* 12:19–30.

Sander, F. 1981. A preliminary assessment of the main causative mechanisms of the ''island mass'' effect of Barbados. *Marine Biology* 64:199–205.

Schaffelke, B. 1999. Short-term nutrient pulses as tools to assess responses of coral reef macroalgae to enhanced nutrient availability. *Marine Ecology Progress Series* 182:305–310.

Schaffelke, B. and D. W. Klump. 1998. Short-term nutrient pulses enhance growth and photosynthesis of the coral reef macroalga *Sargassum baccularia*. *Marine Ecology Progress Series* 170:95–105.

Shulman, M. J. and D. R. Robertson. 1996. Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. *Coral Reefs* 15:231–236.

Smith, J. S. and C. R. Johnson. 1995. Nutrient inputs from seabirds and humans on a populated coral cay. *Marine Ecology Progress Series* 124:189–200.

SMITH, J. E., C. M. SMITH, AND C. L. HUNTER. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332–342.

SMITH, N. P. 1982. Upwelling in Atlantic shelf water off South Florida. *Florida Scientist* 45:125–138.

SMITH, N. P. 1994. Long-term Gulf-to-Atlantic transport through tidal channels in the Florida Keys. *Bulletin of Marine Science* 54:602–609.

SMITH, S. V. 1983. Net production of coral reef ecosystems, p. 127–131. *In* M. L. Reaka (ed.), The Ecology of Deep and Shallow Coral Reefs, Symposium Series Undersea Research. National Oceanic and Atmospheric Administration Undersea Research Program, Rockville, Maryland.

SMITH, S. V. AND P. L. JOKIEL. 1978. Water composition and biogeochemical gradients in the Canton Atoll lagoon. *Atoll Research Bulletin* 221:15–53.

SMITH, S. V., W. J. KIMMERER, E. A. LAWS, R. E. BROCK, AND T. W. WALSH. 1981. Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35:279–385.

SOROKIN, Y. I. 1990. Plankton in reef systems, p. 291–327. *In* Z. Dubinsky (ed.), Ecosystems of the World, Volume 25. Elsevier Science Publishing, New York.

STAMBLER, N., N. POPPER, Z. DUBINSKY, AND J. STIMSON. 1991. Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. *Pacific Science* 45:299–307.

STENECK, R. S. AND M. N. DETHIER. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498.

STEVEN, A. D. L. AND A. D. BROADBENT. 1997. Growth and metabolic responses of *Acropora palifera* to long term nutrient enrichment. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:867–872. Smithsonian Tropical Research Institute, Balboa, Panama.

STIMSON, J. AND R. A. KINZIE. 1991. The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *Journal of Experimental Marine Biology and Ecology* 153:63–74.

STIMSON, J. AND S. T. LARNED. 2000. Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. *Journal of Experimental Marine Biology and Ecology* 252:159–180.

STIMSON, J., S. T. LARNED, AND E. CONKLIN. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19:343–357.

SZMANT, A. M. 1997. Nutrient effects on coral reefs: The importance of topographic and trophic complexity on nutrient dynamics. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 2:1527–1532. Smithsonian Tropical Research Institute, Balboa, Panama.

SZMANT, A. M. AND A. FORRESTER. 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs* 15:21–41.

SZMANT-FROELICH, A. 1983. Functional aspects of nutrient cycles on coral reefs, 1:133–139. *In* M. L. Reaka (ed.), The Ecology of Deep and Shallow Coral Reefs, Symposium Series Undersea Research. National Oceanic and Atmospheric Administration Undersea Research Program, Rockville, Maryland.

TAYLOR, D. L. 1978. Nutrition of algal-invertebrate symbiosis. II. Effects of exogenous nitrogen sources on growth, photosynthesis and the rate of excretion by algal symbionts in vivo and in vitro. *Proceedings of the Royal Society of London* 201:401–412.

THACKER, R. W., D. W. GINSBURG, AND V. J. PAUL. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* 19:318–329.

TOMASCIK, T. AND F. SANDER. 1985. Effects of eutrophication on reef building corals. I. Growth rate of the reef-building coral *Montastrea annularis*. *Marine Biology* 87:143–155.

TOMASCIK, T. AND F. SANDER. 1987. Effects of eutrophication on reef building corals: II. Structure of scleractinian coral communities on fringing reefs, Barbados, W.I. *Marine Biology* 94:53–75.

TORRANCE, D. C. 1991. Deep ecology: Rescuing Florida's coral reefs. *Nature Conservancy* July–August:9–17.

U.S. ENVIRONMENTAL PROTECTION AGENCY. 1992. Water quality protection program for the Florida Keys National Marine Sanctuary. Phase I Report. Prepared for U.S. Environmental Protection Agency, Office of Wetlands, Oceans and Watersheds by Continental Shelf Associates, Jupiter, Florida.

VACELET, E., A. ARNOUX, B. A. THOMASSIN, AND M. TRAVERS. 1999. Influence of freshwater and terrigenous material on nutrients, bacteria and phytoplankton in a high island lagoon: Mayotte, Comoro Archipelago, Indian Ocean. *Hydrobiologia* 380:165–178.

WALKER, D. I. AND R. F. G. ORMOND. 1982. Coral death from sewage and phosphate pollution at Aqaba, Red Sea. *Marine Pollution Bulletin* 13:21–25.

WARD, F. 1990. Florida's coral reefs are imperiled. *National Geographic* 178:114–132.

WARD, S. AND P. HARRISON. 1997. The effects of elevated nutrient levels on settlement of coral larvae during the ENCORE experiment; Great Barrier Reef, Australia. *In* H. A. Lessios and I. G. MacIntyre (eds.), Proceedings of the 8th International Coral Reef Symposium 1:891–896. Smithsonian Tropical Research Institute, Balboa, Panama.

WARD, S. AND P. HARRISON. 2000. Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. *Journal of Experimental Marine Biology and Ecology* 246:179–221.

WELLINGTON, G. M. AND P. W. GLYNN. 1983. Environmental influences on skeletal banding in eastern Pacific (Panama) corals. *Coral Reefs* 1:215–222.

WELLS, J. 1957. Coral reefs. *Memoirs of the Geological Society of America* 67:609–631.

WILKINSON, C. 1998. The 1997–1998 mass bleaching event around the world, p. 15–38. *In* C. Wilkinson (ed.), Status of Coral Reefs of the World 1998. Australian Institute of Marine Science, Townsville, Australia.

WILKINSON, C. 2000. Status of Coral Reefs of the World: 2000. Australian Institute of Marine Science, Townsville, Australia.

WILLIAMS, I. D. AND N. V. C. POLUNIN. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19:358–366.

WILLIAMS, I. D., N. V. C. POLUNIN, AND V. J. HENDRICK. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187–196.

WITTENBURG, M. AND W. HUNTE. 1992. Effects of eutrophication and sedimentation on juvenile corals. I. Abundance, mortality, and community structure. *Marine Biology* 112:131–138.

WOODLEY, J. D. 1999. Sea urchins exert top-down control of macroalgae on Jamaican coral reefs (1). *Coral Reefs* 18:192.

ZANN, L. P. 1994. The status of coral reefs in south western Pacific islands. *Marine Pollution Bulletin* 29:52–61.

SOURCE OF UNPUBLISHED MATERIALS

MILLER, M. W. Unpublished Data. NOAA Fisheries, Southeast Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.