

**NUTRIENT EFFECTS ON CORAL REEFS: A HYPOTHESIS ON THE IMPORTANCE OF TOPOGRAPHIC
AND TROPHIC COMPLEXITY TO REEF NUTRIENT DYNAMICS**

A. M. Szmant

Rosenstiel School of Marine and Atmospheric Science, University of Miami
4600 Rickenbacker Cswy., Miami FL 33149

ABSTRACT

Quantitative aspects of nutrient dynamics on coral reefs are poorly understood. Gaining such understanding is critical since eutrophication is a main anthropogenic threat to reef health. In some areas, nutrient sources impacting reefs are obvious, but for others we lack information on natural nutrient sources and processes, and confounding factors such as over-fishing or grazer die-offs make attribution much more difficult. We are in need of a more integrative understanding of factors that regulate and affect nutrient dynamics on coral reefs. This paper presents a hypothesis regarding the importance of (1) habitat complexity and (2) intact trophic pathways to the nutrient flux rates tolerated by coral reef ecosystems without major shifts in dominance from corals to algae. It predicts that coral reef communities have the ability to utilize and benefit from higher fluxes of nutrients than are generally recognized, without changing to algal-dominated systems, if (a) there is sufficient habitat complexity to provide shelter for large numbers of grazers and a diversity of consumers, and (b) the major trophic groups of fishes and invertebrates have not been impacted by fishing, disease or other disturbance. It further predicts that alterations in community and trophic structure that result from overfishing can result in generalized coral reef deterioration, that at times may be indistinguishable from increased nutrient supply.

INTRODUCTION

Despite decades of interest and effort by coral reef scientists, functional level nutrient dynamics on coral reefs remain poorly studied. Gaining a better quantitative understanding of such aspects at this time is critical since eutrophication is widely considered one of the main anthropogenic threats to reef health (Pastorok and Bilyard 1985; Birkeland 1988a,b; Wells and Roberts 1993). The dramatic case of Kaneohe Bay, Hawaii, in the late 1960's through 1970's, where sewage discharge resulted in the algal overgrowth and death of most of the coral reefs in the southern bay (Smith et al. 1981), alerted scientists and managers to the severe impact humans can have on coral reefs via increased nutrient inputs. In the aftermath of Kaneohe Bay, recent observations of widespread algal overgrowth of corals and algal diseases are also being attributed to anthropogenic eutrophication (e.g. Lapointe 1989; Shinn 1989; Hallock et al. 1993), even where significant local nutrient sources have not been demonstrated and natural nutrient sources and other processes, such as grazing dynamics, are unknown. Many of these reports ignore or fail to recognize the significance of confounding factors such as over-fishing or grazer die-offs (e.g. *Diadema*; Hughes 1994). The general concern over anthropogenic nutrients gave rise to project ENCORE on the Great Barrier Reef, a multi-disciplinary study of the effects of nutrient enrichment on coral reefs (Steven and Larkum 1993). However, after one year of daily nutrient addition to 10 times ambient concentrations, ENCORE researchers were hard-put to measure any significant response by enriched algal communities (Larkum and Steven, personal communications). Thus, we are in need of a more integrative understanding of factors that regulate and affect nutrient and algal dynamics on coral reefs.

Coral reefs are generally found in waters with much lower nutrient concentrations than those of temperate coastal systems, and have many features that we interpret as adaptations to low nutrient conditions (D'Elia 1988; Smith 1988; D'Elia and Wiebe 1990). Increasing nutrient concentrations with higher latitude have been invoked as a major factor limiting the latitudinal distribution of coral reefs (Johannes et al. 1983), and persistent upwelling as a factor limiting the development of coral reefs in otherwise suitable areas (Hallock and Schlager 1986). While there is no doubt that persistent high concentrations and fluxes of nutrients will favor dominance by algae over corals, the literature reveals that coral reefs have both formed and thrived under much higher nutrient conditions than generally recognized (Table 1; also see summary for Houtman

Abrolhos by Hatcher and Collins 1993). The question is, then: What are the factors that have allowed those reefs to form under what some present investigators consider nutrient-polluted water quality conditions (Tomascik and Sander 1985; Bell 1992)? I suggest that the answer to this question is the presence of both (a) sufficient habitat for consumers (high topographic complexity), and (b) intact, complex food webs. I present here a synthetic hypothesis on the functional aspects of nutrient processing by coral reef communities, that hopefully will foster more integrated studies of nutrients on coral reefs. Given the space limitations of the proceedings, I've unfortunately had to limit the number of literature citations; the ideas I present here are synthesized from a large number of published works by a large number of investigators; my contribution, I hope, is the integration across disciplines.

Table 1: Examples of areas with elevated nutrients that formed Holocene reefs. The threshold limits for eutrophication proposed by Bell (1992) are included at the bottom. DIN= dissolved inorganic N. Concentrations in μM

AREA	NO ₃	NH ₄	DON	PO ₄
Palau	0.2-1.0			0.1-0.2
Lizard Island	0.7	0.2-0.3	4-5	0.3- 0.6
N GBR	2			
Canton	2.6	1		0.6
Tarawa	2-3	0.3	9.4	0.4
Yap	0.2-0.35	1.2-1.4	4.5	0.1- 0.2
Gulf of Panama				0.5->2
St. Croix	0.5	0.76	6.6	
Bell(1992)	≥ 1.0 DIN			0.1

PRESENT PARADIGM

One of the generally held popular paradigms regarding coral-reef nutrient dynamics is that coral reefs are adapted to "low" nutrient conditions, and that ANY increase in nutrient flux (or concentration) will result in coral reef deterioration (e.g. Hallock et al. 1993; newspaper and magazine articles too numerous to cite). One problem that surfaces in management issues is to define the upper limits of this LOW concentration range, and Bell (1992) has proposed that these are 1 μM dissolved inorganic N (DIN) and 0.1 μM soluble reactive phosphate. The origin of this popular view derives from studies of coral reef gross and net productivity, mostly from work on reef flats and lagoons of a few mid-oceanic atolls where P/R was estimated to be ≈ 1 (net P ≈ 0) (reviewed in Hatcher 1988; Smith 1988; D'Elia 1988; D'Elia and Wiebe 1990). When net production ≤ 0 , efficient recycling can account for all of the nutrient requirements of a reef system, and outside nutrient sources are not needed to support high levels of gross production (Smith 1983). The problem is that such views have been generalized to whole reef systems, and to coral reefs world-wide. It is not surprising that atoll lagoons have a P/R ≤ 1 , and are heterotrophically dependent on inputs from surrounding reefs or oceans, but it is not clear that forereef areas should be expected to be functionally similar to such lagoons and reef flats. Other factors to consider are that continental and high-island reefs differ significantly from atolls with regard to their potential for terrestrial nutrient inputs (Littler et al. 1991), and that the nutritional input to coral reefs via import of particulates by planktivores has not been included in most nutrient budgets. The export of organics from coral reefs to oceanic and coastal waters is also poorly studied, and an important determinant of nutrient requirements and tolerances. Furthermore, Smith (1983) shows that even for atoll lagoons, increased nutrient supplies (e.g. upwelling) result in higher gross and net production.

Another short-coming of our present view of nutrients and coral reefs is that nutrient cycling, net production, P/R ratios and anthropogenic effects have been mostly considered from the 'production' (bottom up) end of things, even though it is well accepted that most of the primary production is normally rapidly transferred to consumer pathways (i.e. top-down control by high grazing rates; Lewis 1986; Hatcher 1988, 1990). For instance, increases in algal biomass are generally viewed as signs of increases in nutrient supply (Lapointe 1989; Shinn 1989; Hallock et al. 1993), when in fact they could just as well be symptomatic of decreases in grazing (e.g. aftermath of the *Diadema* die-off; Hughes 1994). Furthermore, estimates of nutrient requirements and sufficiency based on the scaling of elemental ratios for production have mostly considered the larger primary producers (Atkinson and Smith 1983; Atkinson 1988), primarily turf and macroalgae with high C:N:P ratios of $\geq 500:30:1$, and not those of zooxanthellae with ratios similar to the Redfield ratio (106:16:1) or those of the consumers such as fishes, which have low C:N ratios of ca. 4:1. Studies of coral reef nutrient dynamics should consider the factors that determine how much consumption of primary production a coral reef can accommodate, and the nutrient requirements of the consumers.

NEW SYNTHESIS

The ideological foundation of the model of nutrient dynamics that I present here is that the inherently high topographic complexity [m^2 of total area/ m^2 of planar area] of coral reefs is essential to their ability to acquire and retain nutrients, maintain high levels of gross production and consumption, and maintain coral dominance over algae, especially under moderately elevated nutrient fluxes. High topographic complexity provides the habitat for coral reefs to accommodate highly complex food chains that contribute to relatively low levels of net community production in spite of high levels of gross production.

The essence of habitat complexity are the massive and branching scleractinian corals. Coral skeletons, live and dead, modified by bioerosion, provide the habitat for the rest of the reef community. The amount and types of corals, and their health, will in turn be dependent on a diversity of reef consumers, especially herbivores, that keep algal biomass under control (Birkeland 1988a,b; Done 1992).

The first topic that merits revisiting is that of the nutrient conditions under which healthy coral reefs can exist. The issue of nutrient concentration vs flux is fundamental to the problem, but a difficult one to address logistically. The measurement of nutrient concentrations is relatively simple and inexpensive compared to that of estimating the hydrodynamic parameters needed to calculate fluxes. However, the common and acceptable assumption is that under any given flow regime, higher nutrient concentrations will result in higher nutrient fluxes. While coral reef nutrient concentrations are definitely low compared to temperate estuarine conditions (earlier references), they are not always as low as many people think (Table 1). Coral reefs on the Pacific coast of Panama experience both elevated nutrients ($PO_4 > 2 \mu M$; D'Croz et al. 1991) as well as lowered temperatures, as do reefs off upwelling zones such as the coast of Oman, Houtman Abrolhos, Canton, Fanning and Tarawa (Smith and Jokiel 1978; Kimmerer and Walsh 1981; Hatcher and Collins 1993; and others). Mechanisms that induce upwelling are numerous and common in reef areas. Upwelling mostly occurs along the outer shelf margins, but nutrients can move onto narrow or even wider shelves (e.g. Halimeda banks behind outer ribbon reefs in GBR; Marshall and Davies 1988). Since many of these events may be episodic and of short duration, they are easily missed during expeditionary sampling programs.

Given the few reefs that have been studied, more reefs in naturally high nutrient conditions will be recognized, especially in continental and upwelling areas. Continental and high-island reefs also have higher potential nutrient inputs from terrestrial sources, including ground water percolation and runoff, and bird colonies can also enrich especially with PO_4 (Smith and Johnson 1995).

Even in areas where the dissolved inorganic nutrient concentrations are low most of the time, there are significant levels of dissolved organic and particulate nutrients (PN) in waters flowing onto reefs, that can be incorporated by reef microbes (Moriarty et al. 1985). The contribution of PN is especially under-recognized: large schools of planktivorous fishes line the forereefs day and night capturing both incoming and outgoing particles (Williams and Hatcher 1983; Hammer et al. 1988). These

fishes are important prey for larger fishes, and their feces have a high trophic value for benthic feeding invertebrates and fishes (Robertson 1982; Williams and Hatcher 1983; Rothans and Miller 1991). High densities of small planktivores require the abundant shelter from predation that high-complexity coral reefs provide.

Once nutrients are 'captured' by reefs, recycling is important to their continued availability to reef primary producers. The symbiosis of invertebrates and microalgae is well studied. However, there are many other biotic and abiotic pathways of recycling, for example storm resuspension of sediment nutrients, which can make re-available both nutrients stored in forereef sediments, and nutrients in lagoonal deposits leeward of the reef (Smith 1988; Szmant and Forrester 1996). Biotic pathways include mechanisms such as upstream transport of nutrients by fish schools during feeding migrations (Meyer and Schultz 1985).

Most of reef production is by benthic turfs, pockets of macroalgae, and algal endosymbionts (Odum and Odum 1955; Adey and Steneck 1985; Hatcher 1988). When nutrient concentrations of incoming waters are moderately high, reef producers can take up nutrients directly from the water column, and new reef production results. The ability of reef algae to remove nutrients from the lowest oceanic nutrient concentrations is poorly studied, but it can be expected that little net uptake will occur, and that primary production will be (e.g. Hanisak 1983; Fig. 1a,b). Nutrient concentrations close to the benthos are higher than those in incoming oceanic waters because of efflux from sediment nutrients and excretion from benthic fauna (Szmant-Froelich 1983; Szmant and Forrester 1996), and benthic nutrients are likely the direct source of nutrients to reef producers when incoming concentrations are low (Williams 1984; McGlathery et al. 1992). Resulting production is, however, recycled, not new, production. Flow rate will affect nutrient uptake by decreasing the thickness of the diffusional boundary layer over the algal surface, and increasing the uptake rate at low and intermediate nutrient concentrations (Carpenter and Williams 1993; Fig. 1a).

Increased production with increased nutrient concentration will likely first occur by increased growth rates of normal reef algae, but eventually competitive interactions between algal groups should result in high-nutrient adapted (=nutrphilic) species replacing normal reef species, and thus shifts in algal community composition (Fig. 1b). Grazing pressure will affect these community shifts (Littler and Littler 1985; Birkeland 1988b), but there are few quantitative studies on this topic.

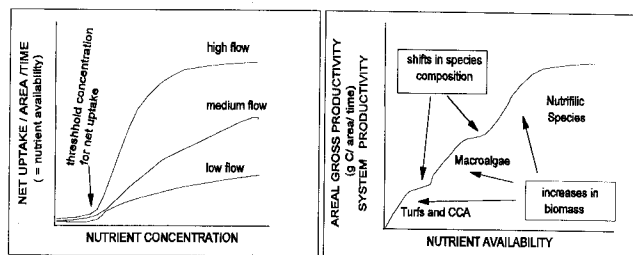


Fig. 1: (left) Hypothetical relationship between nutrient concentration, advective flow and nutrient availability. (right) Hypothetical effect of nutrient flux on primary production and algal community composition.

Re-examination of coral reef productivity data summarized by Kinsey (1985) shows that GPP (gross primary production) per area of reef or lagoon can vary by a factor of 2 to 3 (from 2.3 to 6.0). The striking feature of the data is how the consumption rates of those reef systems were able to increase in pace with the level of production, so that the estimated P/R and E (excess or net community production) was reportedly always near 1.0 and ca. 0, respectively!!!

So, how does one explain the proportional increases in primary production (P) and consumer abundances (R) on those coral reefs? Differences in nutrient fluxes are obviously partially responsible for the differences in primary production between reefs, but I suggest that the topographic complexity (=surface area) of those reefs allowed their producer communities to respond to the increased nutrient availability, and their consumer communities to respond to the increased primary production. Adey and Steneck (1985) and others have demonstrated a correlation between reef topography and GPP, and Grigg

(1994), and others have shown that fish numbers and diversity increase in proportion to complexity measures. While fish are critical contributors to reef trophodynamics, they are but one small part of a reef's consumer community. Macro- and micro- invertebrates, meiofauna and microbial populations also increase as a function of habitat complexity, and are quantitatively a greater proportion of the consumer biomass than are fishes (Johnson et al. 1995).

The major tenet of the proposed conceptual nutrient dynamics model is that nutrient and carbon cycling are dependent on how reef topographic complexity influences the relative and absolute abundances of primary producers and consumers (Fig. 2). As the complexity increases, up to some maximum, more canopies of producers ($\therefore$ more algae to take up nutrients) can co-exist, and more reef substrate is available for infaunal and epifaunal consumer groups to inhabit ($\therefore$ more trophic complexity). Therefore, GFP will be a function of both alloctonous nutrient supply and of surface area for algal growth, while consumption will be a function of primary production and of habitat for shelter.

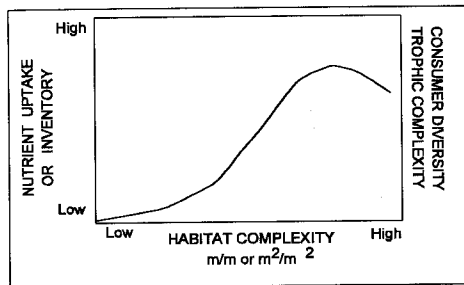


Fig. 2: Hypothesized effect of reef complexity (bottom axis) on: reef's ability to take up and store nutrients (left axis) and diversity of consumer trophic levels (right axis).

Another way to conceptualize the relationship between habitat complexity and nutrient dynamics is encompassed in the proposed 'intermediate nutrient hypothesis' (Fig. 3), explained in the figure caption. The significance of this hypothesis is that it encompasses the ability of reefs to thrive under a range of nutrient fluxes, but also to exhibit what are generally considered classic symptoms of eutrophication (shifts to algal dominance) without changes in nutrient flux *if* either habitat complexity is reduced (loss of coral due to natural physical disturbance, coral mining, destructive fishing practices, etc.), or where there is overfishing or herbivore die-off.

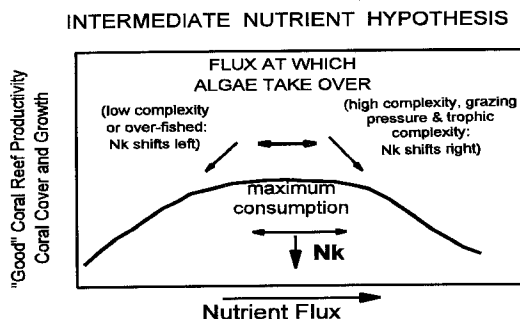


Fig. 3: The intermediate nutrient hypothesis. Coral reefs respond to and benefit from increased nutrient fluxes, with increased productivity, coral cover and coral growth, until the point where consumers cannot consume all of the production, and there is a biotic shift in dominance from corals to algae (N_k). The nutrient flux at which this shift in dominance occurs is a function of habitat complexity, which determines the amount of available shelter for grazers and other consumers (as well as surface area for producers), and factors such as fishing pressure, which reduce grazer densities.

Let us consider how the progression from [low complexity/low diversity/low productivity] to [high complexity/high diversity/high productivity] may develop over the history of a reef's formation during the Holocene (Fig. 4). The diagrams illustrate that as corals were able to become established after reflooding due to sea level

rise, they created habitat for other organisms, leading to opportunity for increased nutrient processing, biomass accumulation and trophic complexity. An important asset that accrues to hard-bottom systems along with higher complexity is the formation of sediment pockets that form within interstices in high complexity reliefs, and which serve as important sites of detritus entrapment and microbial remineralization (Szmant-Froelich 1983). In the absence of such "trapping" microhabitats, detrital materials are easily washed out of the system before they can contribute to reef trophodynamics.

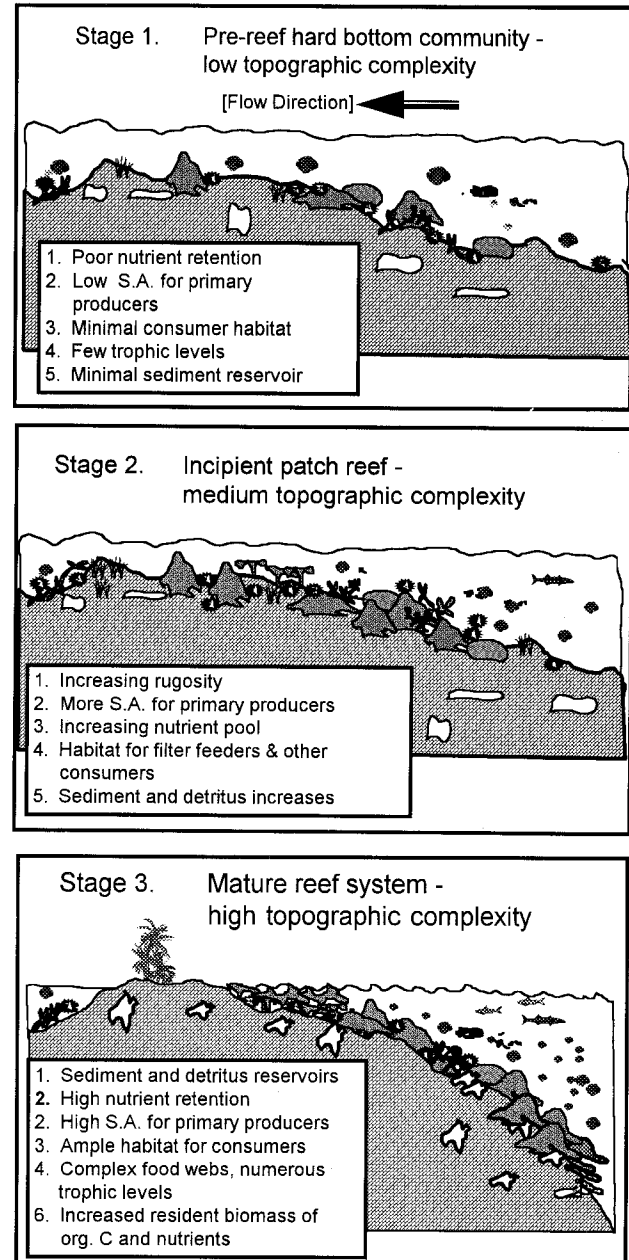


Fig. 4: Illustrations of the hypothetical increase in structural and community complexity during the development of coral reefs on low-relief hard-bottom areas during periods of sea-level rise. S.A. = surface area.

It is interesting to speculate that differences in the amount of habitat complexity created during subaerial erosion may have been one of the factors contributing to the variability in success of Holocene reef initiation. Areas with more suitable habitat for fish and sea urchin shelters might have had higher levels of grazing, and thus made it easier for corals to get established. Figure 4 summarizes how the substrate complexity of an antecedent platform might have influenced the probability of a reef

forming under differing nutrient regimes. Hallock and Schlager (1986) proposed that high nutrient fluxes precluded reef formation in areas with upwelling and/or other local high nutrient fluxes. On the other hand, there are good examples of large reef complexes forming within upwelling areas (cited above), and it is thought that many reflooded shelf areas had relatively higher nutrient regimes (Adey 1978). If habitat for sufficient grazers occurred in such areas, nutrient-tolerant corals may have been able to get a strong hold and form reefs under somewhat elevated nutrient levels, and possibly at higher growth rates than in lower nutrient regimes.

HYPOTHETICAL TOPOGRAPHY-BASED SCENARIOS FOR HOLOCENE REEF FORMATION

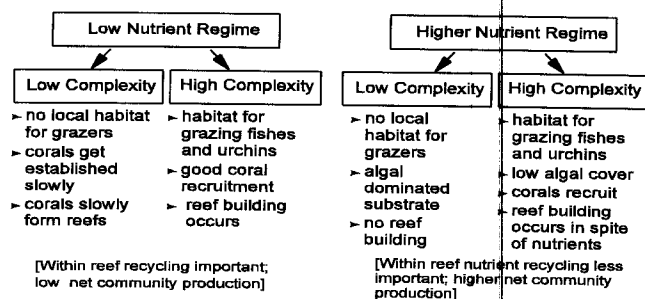


Fig. 5: Consequences of topographic complexity on the formation of coral reefs under low and high nutrient levels.

TROPIC ASPECTS OF NUTRIENT DYNAMICS

New nutrients can enter coral reef food webs as either dissolved inorganic and organic nutrients, or in particulate form. Once new nutrients, regardless of source (natural or anthropogenic, chronic or episodic), are assimilated by reef primary producers or suspended particulate feeders, they move through the food web to other biotic/trophic groups either through direct consumption of the producers or planktivores by herbivores and piscivores, or by detrital pathways. Coral reefs are estimated to have at least 6 major consumer levels, each with transfer efficiencies of ca. 17 % (Grigg et al. 1984). These diverse consumer organisms release unassimilated N and P as ammonium, phosphate or feces. Feces can either re-enter the food web via coprophagy, or settle into the sediments, where together with other detrital material (e.g. algal fragments) they are remineralized by detritivores and microbes (Hatcher 1983; Moriarty et al. 1985). In order to truly understand biogeochemical cycles of coral reefs, we need to know the biomass of each of these biotic/trophic groups, the flux rates of each of the transfers, and their rate controlling processes.

Reflecting on this conceptual summary of coral reef nutrient dynamics, some special features and linkages are worthy of re-visiting:

1) The enormously high rates of GPP reported for coral reefs are a function of the large number and diversity of primary producers, but, under balanced trophic flow the producer biomass doesn't accumulate (except for symbiotic cnidarians) because it is quickly passed up the food web.

2) Reef corals are the major contributors of structural complexity, but contribute less to direct trophic flow, mostly through the excretion of mucus. Few animals eat corals and much of coral energy may be used to support calcification. However, mass spawning by corals can release large amounts of potential food into reef waters (e.g. 40 % of tissue C, 25 % of tissue N each year; Szmant 1991), and fishes and invertebrates feed on the spawn.

3) The importance of nutrient import and retention to coral reefs effected by planktivorous fishes has been underappreciated. Dense schools of planktivores feed in the water column on both windward and leeward sides of reefs, and intercept nutrient-rich particles before they can reach benthic filter feeders or be washed away from the reef. At abundances of 0.1 to 1.0 g AFDW per m² (Hamner et al. 1988), zooplankton could be the source of 1 to 10 mmol of N per m² of water passing over the reef. Williams and Hatcher (1983) found that planktivores numerically dominate some GBR reef fish communities (> 80 % of individuals) and constitute up to 20 % of their biomass, and Russ (1985) reported that reef areas with high fisheries yields have a large percent of their fish communities (and catch) made up

of planktivores. Planktivores are small and by virtue of their feeding mode, prone to predation, thereby providing a potentially short trophic connection between oceanic particulate nutrient inputs and higher trophic levels. Nutrients in the captured particulates become available to primary producers after they are excreted or defected and remineralized. As planktivore density is highly dependent on substrate complexity (Eklund 1996), this is a prime example of how topographic complexity can contribute to both nutrient acquisition and processing on coral reefs.

4) If nutrient concentrations or other factors shift algal species composition towards dominance by algae with low palatability (e.g. chemically or structurally defended), then the predicted increases in trophic flow may not occur and algal biomass may build up (to the detriment of corals). In such a case, flow through detrital pathways should also increase (Johnson et al. 1995)

5) Ammonium and phosphate are excreted by all animal groups into their habitats, much of it into the benthic boundary layer where it elevates local nutrient concentrations (Szmant-Froelich 1983), and enhances uptake by benthic algae. A minimal estimate of recycled N produced by NH₄ excretion, derived from too many papers to cite here, suggests that the major groups of coral reef consumers produce ca. 13.9 mmol/m²/d (fishes 0.5; echinoderms 4.5, molluscs 6.1; crustaceans 2.4; polychaetes 0.4). Using a C:N of 20-30 (Atkinson and Smith 1983), this excretion can support a GPP of 3-5 g C/m²/d, or 40 to 70 % of Kinsey's (1985) standard coral reef performance (7 g C/m²/d). The biomass estimates used were likely low and many taxa were not included, thus actual ammonium excretion rates are possibly twice these values.

6) Defecation products and algal detrital particles are either immediately consumed (Robertson 1982; Rothans and Miller 1991), or fall into the sediments where microbial groups and macro-detritivores will feed off them (Hatcher 1983; Moriarty et al. 1985), and in the process, remineralize nutrients. Reef sediments are typically low in nutrient content (Szmant and Forrester 1996), but they cover extensive areas of the reef, including the lagoon, sand channels on fore reefs, and trapped within topographic irregularities (Szmant-Froelich 1983). They can produce ca. 70 to 100 µmol NH₄/m²/day. Furnas et al. (1993) estimated that on the Great Barrier Reef, benthic remineralization is the largest component of the total gross nutrient supply.

7) Coral reefs, by virtue of their existence, must have a long-term net positive community production. Over geological time, as reefs grow, they accrete a biomass of 'living' nutrients in the biomass of their fauna and flora. In addition, reefs have small amounts of organic C (0.5-0.8 %) and nutrients (0.07 % N and 0.02 % P) in their carbonate accumulations. For example, Carrie Bow Cay, on the Belize barrier reef, has accumulated ca. 8 x 10⁶ m³ of carbonate under ca. 0.7 km² of reef area over a 6-7,000 year time frame. This amounts to burial of 17.6 g organic C/m²/yr (0.7 % of the Kinsey standard for GPP), 0.11 mol N/m²/yr, and 0.014 mol P/m²/yr. It is interesting to note that the C:N:P of the buried material as estimated is 105:8:1.

8) Coral reefs are reported capable of sustained fisheries yields of 5-15 mton/km²/year, and this also represents a form of net production. By comparison with sediment burial, fisheries production [3.4 g C/m²/yr, 0.05 mol N/m²/yr and 0.002 mol P/m²/yr] is small.

CONSEQUENCES/PREDICTIONS OF THESE HYPOTHESES

Johnson et al. (1995) produced a numerical model of carbon flow through a coral reef system, with two alternative pathways for C flow if algal cover increases. While their approach and objectives were different from the present one, they reached an important conclusion that is relevant to the present discussion: changes in relative abundance of major trophic groups can cause changes in trophic pathways and efficiencies at many different levels. Similar statements have been made by others (e.g. Birkeland 1988a; McClanahan and Shafir 1990; Done 1992; Hughes 1994).

Nutritification is blamed for many incidences of reef deterioration world-wide. However, most coral reefs have suffered from moderate or intense harvesting for longer than they have suffered from significant nutritification. Because fishermen travel far from home, over-harvesting can and has occurred in uninhabitable reef areas distant from human habitation (Roberts and Polunin 1994). Coral reefs in isolated or sparsely populated areas that are in poor health or deteriorated may be suffering from ecological

imbalance due to the removal of important trophic groups, and not from water quality deterioration.

Consequences of overfishing are most obvious when herbivorous fishes or sea urchins are harvested. Such harvesting may eventually lead to a change of benthic community structure (i.e. algal over-growth of corals). Natural mortality of herbivores can have the same effect (Hughes 1994). Herbivore loss will also affect the transfer of nutrients to other trophic groups that eat the herbivores, or the detrital materials they produce. It will also affect nutrient cycling since most of the nutrients that normally re-enter the coral reef food web as excretory and fecal products of these animals may remain on the reef as algae.

Harvesting of higher level consumers (piscivorous fishes, predatory molluscs and crustaceans) are predicted to also have important cascading effects on coral reef community structure and nutrient dynamics. Their exact manifestations are less simple to predict given the complexity of the feeding habits of these animals. Some estimates are that many reefs have <50 % of their natural fish biomass (Clark et al. 1989; McClanahan and Shafir 1990; Roberts and Polunin 1994; Russ and Alcala 1996). An example of possible secondary effects of fishing is the increase in damselfish abundance on Puerto Rican reefs over the past decade. These fishes have killed a large number of massive corals with their algal lawns (unpubl. observ.). I suspect that overharvesting of predatory fishes from these reefs has allowed damselfish populations to explode. On Florida reefs we see large numbers of large-sized individuals of the coral eating gastropod, *Corallophila*, actively feeding on their preferred food, acroporid corals: Could a snail population explosion be related to overharvesting of spiny lobster, which used to be abundant in *Acropora palmata* thickets? I am sure that readers can think of other such examples of potential cascading effects of fishing that impact corals other than via algal overgrowth. The nutrient dynamics consequences of these cases will be difficult to recognize without detailed studies of the trophodynamics and nutrient balances for each such example.

I must caution that the objective of proposing this hypothesis is not to minimize in any way the idea that excess nutrients are harmful to coral reefs. There are coral reefs located in areas receiving intolerably high inputs of anthropogenic nutrients that could not be absorbed even with high topographic complexity and intact community structure. On the other hand, we should not be too quick to blame every 'sick' coral reef on sewage pollution while ignoring or over-looking the effects of fishing and habitat destruction. The management consequences of such an attitude will be the expenditure of large sums of money to manage the sewage, with little to no benefit to the reefs in question.

Finally, from an academic point of view, nutrients as an agent of deterioration should be differentiated from the sediments and/or organics with which they are often associated. "Clean" nutrients, such as those from upwelling, have the potential to enter through the algal community and from there transfer through the food web in a balanced fashion. Nutrients associated with high organic loads will stimulate bacterial production, result in lower dissolved oxygen, increased growth of filter feeders and boring borers, and cause major changes in trophic flow (Birkeland 1988a; Done 1992). In such cases, the organics are the major problem, not the N or P. Sediments usually have an associated nutrient (and organic) component, but again, the abrasive and smothering properties of the particles can have negative effects separate from those of the nutrients. While measures to control sediment and organic inputs to coral reef waters usually simultaneously reduce nutrient inputs, the mechanism of any resulting benefit should not be misunderstood.

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