Phosphorus-rich waters at Grovers Reef, Belize?

Coral reefs worldwide are experiencing increasing anthropogenic impacts on local, regional and global scales. Two major human impacts—nutrient enrichment and overfishing—were recently assessed by McClanahan et al. (2002) at Grovers Reef, an atoll offshore the Belize Barrier Reef in the western Caribbean Sea. The most significant finding from this experimental study was the dramatic effect of phosphorus enrichment in stimulating increased cover of algal turf and macroalgal blooms of the green seaweed Enteromorpha. These results are important because many coral reef biologists have thought that algal blooms on Caribbean reefs in recent decades resulted only from reduction of grazing pressure (top–down controls) via overfishing of herbivorous fishes (parrotfishes, surgeonfishes) and/or mortality and die-off of the long-spined sea urchin Diadema antillarum (Hughes, 1994; Jackson et al., 2001). However, as was evident in the McClanahan et al. (2002) study, nutrient availability—not consumption by grazers—is a critical factor that regulates growth and reproduction of macroalgae. Inasmuch as grazing studies on coral reefs rarely include consideration of nutrients, the essential role of nutrient availability has been confounded within much of the “top–down” literature (Lapointe, 1999). As such, the McClanahan et al. (2002) study provided an important and much needed demonstration of the effects of nutrient enrichment (bottom-up controls) in triggering proliferation of algal turfs and macroalgae in coral reef environments.

The McClanahan et al. (2002) study could have been improved even more by considering previous work on nutrient limitation of macroalgae on the Belize Barrier Reef. McClanahan et al. (2002) stated that “phosphorus is likely to be among the most limiting and influential nutrient in this carbonate environment” and accordingly, their experiments focused on phosphorus (P) enrichment. While the primary importance of P may be true, supporting data for this assumption—such as ambient concentrations of dissolved inorganic nitrogen (DIN = NH$_4^+$ + NO$_3^-$ + NO$_2^-$) or macroalgal tissue carbon:nitrogen (C:N) ratios from Grovers Reef—were not provided to ensure that nitrogen (N) was not also limiting growth. Lapointe et al. (1987) reported relatively low concentrations of NH$_4^+$ (<0.41 μM), NO$_3^-$ (<0.16 μM) and PO$_4^{3-}$–P (<0.03 μM) from the back reef at Curlew Reef on the outer Belize Barrier Reef 15 km west of Grovers Reef (Table 1). Experimental nutrient enrichment assays with red, green and brown macroalgae indicated that both N and P were limiting the productivity of macroalgal communities in these oligotrophic waters of the outer Belizean Reef—but that the relative importance of N and P were species- and site-specific (Lapointe et al., 1987). Studies by Tomasko and Lapointe (1991) provided further evidence of very low or undetectable DIN concentrations on the Belize Barrier Reef, including Grovers Reef (Table 1). Lapointe et al. (1993) reported very low or undetectable DIN and PO$_4^{3-}$–P concentrations at Curlew Reef and Tobacco Reef on the outer Belize Barrier Reef (Table 1) and also high C:N ratios (>36:1) in a variety of macroalgae that were above the mean value for marine plants (22:1, Atkinson and Smith, 1983) and indicative of N-limitation.

McClanahan et al. (2002) did provide some background measurements of PO$_4^{3-}$–P concentrations from their experimental sites at Grovers Reef. They reported mean PO$_4^{3-}$–P concentrations of 0.03 mg/l for the “control” site and 0.06 mg/l for the “fertilized” site, although it was unclear exactly how many samples were analyzed. They converted these weight/volume units to molar concentrations of 0.35 and 0.77 μM for the “control” and “fertilized” sites, respectively, to facilitate comparison with the marine chemistry literature. Apparently, their conversion of “measured” PO$_4^{3-}$–P from mg/l to molar concentrations was incorrect, as 0.03 mg/l is equivalent to ~1.0 μM, not 0.35 μM as they stated; likewise, their 0.06 mg/l would be ~2.0 μM, much higher than their reported 0.77 μM. These PO$_4^{3-}$–P concentrations would be considered high for many coastal water, but especially for oligotrophic waters that typically occur on Caribbean coral reefs. Table 1 provides published PO$_4^{3-}$–P data (equivalent to soluble reactive phosphorus, SRP) for several carbonate-rich Caribbean reefs, including Grovers Reef, which shows that concentrations are typically <0.1 μM. Accordingly, the background PO$_4^{3-}$–P concentration (0.03 mg/l) reported by McClanahan et al. (2002) would appear some twenty-fold higher than concentrations reported previously for Grovers Reef and at last ten-fold higher than those reported for coral reefs experiencing eutrophication and associated macroalgal blooms in the Florida Keys and Jamaica (Table 1).
However, a more serious problem arises with the analytical method that McClanahan et al. (2002) used for PO$_4^{3-}$P analysis that is inappropriate given the very low PO$_4^{3-}$P concentrations reported for the Belize Barrier Reef and other Caribbean coral reefs (Table 1). McClanahan et al. (2002) used a Hach DR 3000 spectrophotometer and the ascorbic acid method to measure PO$_4^{3-}$P in the "low range of 0–2.0 mg/l". However, because of inherent optical and instrumental limitations, this method has an estimated detection limit (EDL) of only 0.01 mg/l, or ~0.35 µM, for PO$_4^{3-}$ (Hach, Method 8048). Consequently, this method does not have sufficient sensitivity to accurately measure PO$_4^{3-}$P concentrations that are typically <0.1 µM on the Belize Barrier Reef and Glovers Reef. For this reason, more sensitive analytical methods commonly used for monitoring nutrient concentrations on coral reefs have low detection limits (e.g., use of spectrophotometers with 10-cm cells can provide detection limits for PO$_4^{3-}$P of ~0.03 µM, Lapointe et al., 1993), which together with "clean handling techniques," are required to obtain high quality data representative of these environments.

This analytical limitation undermines McClanahan et al.'s (2002) conclusion that their data "do not support a threshold hypothesis" for PO$_4^{3-}$P concentration at which macroalgal blooms can develop at Glovers Reef. Previous field studies along natural nutrient gradients on the Belize Barrier Reef (Lapointe et al., 1993) and Jamaican fringing reefs experiencing eutrophication from land-based runoff (Lapointe, 1997, 1999; Lapointe and Thacker, 2002) all suggest a DIN threshold of ~1.0 µM (Table 1). This threshold is supported by detailed laboratory and field studies that have quantified DIN-limited growth rates of a variety of tropical macroalgae that typically occur at concentrations of ~0.5–1.0 µM; above these concentrations, growth rates become DIN-saturated in a fashion similar to Michaelis–Menten kinetics (Lapointe, 1999). Considering that macroalgae require N:P in a ratio of ~10:1, a corresponding PO$_4^{3-}$P threshold concentration of ~0.05–0.1 µM would be needed to support P uptake and balanced growth for the development of algal blooms. Indeed, macroalgal blooms have been reported for tropical coastal waters having this range of PO$_4^{3-}$P concentrations (Table 1) as a result of P enrichment from natural sources (mangroves, seabird guano) in localized areas of the Belize Barrier Reef (Lapointe et al., 1993) or on much larger spatial scales due to escalating anthropogenic nutrient enrichment (sewage, agricultural runoff) of the Negril Marine Park, Jamaica (Lapointe and Thacker, 2002) and Looe Key in the Florida Keys National marine Sanctuary (Lapointe et al., 2002). These quantitative relationships between macroalgal blooms and PO$_4^{3-}$P concentrations illustrate why removal of grazers via overfishing on oligotrophic coral reefs with very low PO$_4^{3-}$P concentrations (<0.03 µM) do not result in macroalgal blooms (Lapointe, 1999), but rather the expansion of more diminutive algal turfs as predicted by the Relative Dominance Model (RDM, Littler and Littler, 1984).

Although McClanahan et al. (2002) found a significant and dramatic effect of PO$_4^{3-}$P enrichment on macroalgal cover and blooms of Enteromorpha, even greater nutrient effects could have occurred had stronger DIN enrichment been utilized in their experimental design. Many green filamentous seaweeds in the genera Enteromorpha, Chaetomorpha and Cladophora are well-known indicators of "nutrient enrichment" and typi-
cally form blooms around mangrove islands from P-rich seabird guano (Lapointe et al., 1993) or in coral reef habitats impacted by land-based nutrient pollution from sewage, agricultural runoff and top soil loss (Lapointe, 1997; Lapointe and Thacker, 2002). In locations like the Negril Marine Park and Discovery Bay, Jamaica, DIN-rich groundwater inputs from the limestone watersheds typically have very high N:P ratios (>35:1), which result in strong P-limitation of macroalgal growth on downstream reefs (Lapointe, 1997; Lapointe, 1999). However, such high DIN concentrations, N:P ratios and strong P-limitation would not be expected at Glover’s Reef, which is a remote offshore atoll with relatively little groundwater DIN input. Instead, the water column at Golvers Reef would likely have lower N:P ratios (<15:1, see DIN:PO4 ratio in Table 1) that would favor co-limitation by both N and P and an overall “weaker” degree of P-limitation. Indeed, comparative studies of reef macroalgae from Discovery Bay, Jamaica and Curlew Reef on the outer Belize Barrier Reef using alkaline phosphatase activity (APA) as an index of P-limitation showed significantly (two-fold) lower values on the more oligotrophic Belizean site as a result of lower DIN concentrations and P-limitation (Lapointe et al., 1997). The land-based DIN enrichment (largely via submarine groundwater discharges) on reefs offshore Discovery Bay enriches the percentage N content of the brown seaweed Lobophora variegata to at least 36 m depths, supporting increased P-limitation in the super-abundant and multi-layered macroalgal blooms that have developed on those reefs in recent decades (Lapointe et al., 1997). Despite the offshore location of Golvers Reef, satellite imagery shows that land-based runoff via river discharges from Honduras have impacted this remote area periodically during the rainy season over the past several decades, especially following Hurricane Mitch in late October, 1998; the recurrent sedimentation and nutrient enrichment associated with these events helps to explain the recent phase shift from hermatypic corals to macroalgae in the Golvers Reef lagoon (Andrefouet et al., 2002).

Acknowledgements

This correspondence was supported by a grant from the United States Environmental Protection Agency through the Ecology and Oceanography of Harmful Algal Blooms program. This is contribution No. 1534 from the Harbor Branch Oceanographic Institution, Inc.

References


Brian E. Lapointe
Division of Marine Science
Harbor Branch Oceanographic Institution, Inc.
5600 US 1 North Ft. Pierce
FL 34946
USA
Tel.: +1-772-465-2400; fax: +1-772-468-0757
E-mail address: lapointe@hboi.edu