Nutrient Enrichment as a Factor Driving Macroalgal Blooms on the Belize Barrier Reef Complex

El Enriquecimiento de Nutrientes como un Factor que Impulsa las Floraciones de Macroalgas en el Complejo del Arrecife de Coral de Belice

Enrichissement en Eléments Nutritifs en Tant que Facteur de Prolifération des Macroalgues sur le Complexe de Récifs de la Barrière du Belize

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EXTENDED ABSTRACT

Representing a significant portion of the world's second largest coral reef complex and encompassing a World Heritage site, the Belize Barrier Reef Complex (BBRC) has experienced increasing blooms of macroalgae in recent decades. Considerable debate has centered on the ecological factors causing macroalgal blooms on Caribbean coral reefs, and top-down controls, such as reduced grazing by herbivorous fishes and/or or sea urchins, and nutrient enrichment from natural or anthropogenic sources, have long been recognized as interacting factors (Lapointe 1997). Recent research on the BBRC, where herbivores (scarids and acanthurids) have been banned from exploitation since 2009 (Tewfik et al. 2017), suggests that the worsening macroalgal blooms are not the result of overfishing of herbivorous fishes as many coral reef biologists have previously suggested, but more likely related to external factors, such as local and regional scale nutrient enrichment (Suchley et al. 2016).

Because historical nutrient data for seawater and macroalgae were collected in the BBRC in the 1980s (Lapointe et al., 1987; Tomasko and Lapointe, 1991; Lapointe et al., 1992), we re-sampled the same sites in South Water Caye (SWC) marine reserve (e.g. Man-O-War Caye, Twin Cayes, Tobacco Reef, Curlew Reef), and various sites at Glovers Reef (GR) marine reserve (e.g. Middle Caye, patch reefs, fore reef) in June 2017 and 2018. Seawater samples, along with cistern and groundwater samples from Middle Caye, were collected in triplicate (n = 3) into clean, HDPE bottles, and placed on ice in a cooler. The samples were filtered through 0.7 µm GF/F filters, and frozen until analysis for DIN (ammonium + nitrate) and SRP (soluble reactive phosphorus) on a SEAL AA3 at FAU-HBOI in Ft. Pierce, FL. Macroalgae samples were collected by divers/snorkelers into nylon mesh bags, identified, cleaned of sediment and epiphytes, rinsed briefly (3 - 5 seconds) with deionized water (DIW), and dried in a laboratory oven at 65°C for 48 hours. The dried macroalgae were powdered with a mortar and pestle, placed into plastic screw-top vials, and analyzed for stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes, % N, %C, and %P at the Center for Applied Isotope Studies, University of Georgia, Athens, GA.

In the 1980s, DIN and SRP concentrations were relatively high at Man-O-War Caye (mangrove seabird rookery) and Twin Cayes (mangrove) due to natural enrichment (Lapointe et al. 1992). At Tobacco Reef, Curlew Reef, and Glovers Reef in the 1980s, however, DIN and SRP concentrations were very low or undetectable (Lapointe et al., 1992; Tomasko and Lapointe 1991). Decades later in 2005 (Anton 2006) and 2017/2018, Glovers Lagoon had significantly higher DIN and SRP concentrations than in the 1980s, with values of 0.5 – 1.0 µM DIN and > 0.10 µM SRP. Because these DIN and SRP concentrations are at or above the ecological nutrient thresholds for macroalgal blooms on coral reefs (Lapointe 1997), such "bottom-up" forcing by nutrient enrichment helps to explain the widespread blooms now occurring in the BBRC (Figure 1).

In 2017, macroalgae C:N ratios were lower at Man-O-War Caye, Twin Cayes, Tobacco Reef and Curlew Reef (C:N of 15 to 26) compared to higher baseline values (28 to 40) in the 1980s, suggesting large-scale nitrogen enrichment of these habitats. Low C:N ratios of 13 to 16 occurred at Middle Caye (GR) and Man-O-Way Caye (SWC), indicating nitrogen enrichment at these sites by humans and seabirds, respectively. In contrast to C:N ratios, C:P ratios of macroalgae increased from the 1980s to 2017 at all four sites, especially Tobacco Reef and Curlew Reef, which ranged between 1,200 and 1,500. This indicates that the growth of these macroalgae is currently more P-limited than in the 1980s, which would be expected from the C:N data showing simultaneous and strong N enrichment.

Stable nitrogen isotope values ($\delta^{15}N$) in the macroalgae helped to identify nitrogen sources supporting the macroalgae blooms. Values were generally elevated (+3 to + 7 o/oo) at Middle Caye (GR) and Man-O-War Caye (SWC), the two sites that were directly impacted by N enrichment from humans and/or seabirds, but also suggests contributions from other N sources, such as atmospheric deposition or submarine groundwater discharge. DIN sampling of the groundwater at Middle Caye showed elevated ammonium (~ 10 µM) that could result from human and wildlife activity; however, much higher concentrations of nitrate (30 µM) were measured in the cistern water, suggesting significant and widespread reactive N enrichment of habitats at Glovers Reef from rainfall.

Observations from patch reef and fore-reef benthic surveys highlight that the original main structural components of living corals (*Acropora* spp., *Siderastrea* spp. and *Orbicella* spp.) are in decline with much of the hard bottom habitats,

Figure 1. Left: Heavy macroalgal epiphyte loads on turtle grass (*Thalassia testudinum*) in the back reef at Tobacco Reef in SWCMR, June 2017.
Right: Thick overgrowth of macroalgae (*Hypnea musciformis*, *Laurencia papillosa*) on patch reefs in Glovers Reef lagoon.

including coral skeletons, now dominated by fleshy macroalgae (*Dictyota* sp., *Lobophora* sp.) as well as several excavating sponges (*Cliona* spp.) (Tewfik 2016, Tewfik et al. 2017). The comparative nutrient data presented here support recent suggestions that nutrient enrichment is a significant factor driving the widespread macroalgal blooms. In addition, increased N:P ratios, which cause P-starvation and metabolic stress in stony corals (Rosset et al. 2017), helps explain the coral decline from diseases and/or bleaching. The loss of broader ecosystem services generated by the BBRC includes critical livelihoods associated with fishing and tourism as well as coastal protection from more frequent and severe weather events.

KEYWORDS: Macroalgal blooms, nutrient enrichment, coral reefs

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