



# Nutrients and herbivory, but not sediments, have opposite and independent effects on the tropical macroalga, *Padina boryana*

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## ABSTRACT

Multiple anthropogenic stressors including overfishing, nutrient loading, and sediments are major drivers that may support the proliferation of macroalgae on coral reefs; however, few studies have investigated all three simultaneously. We evaluated the effects of all three stressors (nutrient enrichment, small and large sediment grain sizes, and herbivory) on biomass accumulation of the dominant coral reef macroalga *Padina boryana* in a multifactorial field experiment on a fringing reef in Mo'orea, French Polynesia. Biomass accumulation of *P. boryana* was controlled by the separate, but not interactive, effects of herbivory and nutrients; although we did not detect effects of sediments, these may have been obscured by high variability leading to low statistical power. With herbivores, biomass remained the same or decreased up to 50% in 12 days compared to ~50–100% increases in biomass without herbivores. Overall, enriched *P. boryana* grew ~ 4-fold greater compared to ambient treatments, both with and without herbivory. Our results suggest that any release from bottom-up and/or top-down controls that may occur simultaneously on these nearshore reefs may facilitate proliferation of this tropical macroalga, and, in contrast to the prevailing paradigm, we found these effects can function independently.

## 1. Introduction

Coral reefs are increasingly subject to anthropogenic impacts including overfishing of herbivores, addition of nutrients, and loading of sediment, all of which have been linked to coral decline and the proliferation of primary producers such as macroalgae (Hughes et al., 2003). Macroalgal dominance may be especially common on fringing reefs due to their proximity to multiple anthropogenic stressors (e.g., Clausing et al., 2014, 2016; Fong and Fong, 2014). It is well documented that herbivorous fishes strongly limit proliferation of tropical algae and that overfishing can result in increased macroalgal abundance (e.g. Hay and Steinberg, 1992; Paul et al., 2001; Hughes et al., 2007; Bellwood and Fulton, 2008). This top down control allows coral reefs to recover following disturbance by preventing competitive overgrowth by macroalgae (e.g. Hughes et al., 2007). However, the importance of nutrient enrichment on tropical reefs remains a controversial topic (e.g. Lapointe, 1997; Thacker and Paul, 2001; Littler et al., 2006; Fong and Paul, 2011). While many studies conclude that enrichment may have mixed or limited effects on algal proliferation (e.g., Thacker and Paul, 2001), other studies have found that elevated

nutrient levels lead to increased growth (e.g., Fong et al., 2003).

The effects of sediments on algae are understudied relative to nutrients and herbivory, and the few studies that exist have obtained contrasting results. Sedimentation rates on reefs can increase as a result of human settlement, development, and deforestation near the coast (Maina et al., 2013). Sediment particles smother reef organisms, increase turbidity, and reduce light for photosynthesis (Rogers, 1990). While increased sediment loads have been demonstrated to negatively impact corals (Rogers, 1990; Fabricius, 2005), the extent of the impact of sedimentation on marine macroalgae is unclear. For example, sediments may benefit algal turf by reducing herbivory (Bellwood and Fulton, 2008; Goatley and Bellwood, 2012) but may also result in anoxia, inhibiting growth (Clausing et al., 2014). For macroalgae, sediment loading may provide a source of nutrients for certain species such as *Padina boryana* Thivy (Clausing et al., 2016), but may decrease growth and survivorship of others such as *Sargassum microphyllum* recruits (Umar et al., 1998). Further, sediment effects may vary with grain size. For example, filaments on the surface of *P. boryana* can trap fine-grained sediments, providing nutrients to the macroalgae (Clausing et al., 2016). While one recent study found that a species of parrotfish

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preferred algal turf with fine-grained and nutrient-enriched sediments (Gordon et al., 2016), another study found that a species of surgeonfish preferred algal turfs with coarser sediments (Tebbett et al., 2017). Together, these studies suggest that sediments of differing grain size may interact with nutrient addition to influence top-down controls on coral reef algae.

Human impacts often simultaneously affect top-down and bottom-up controls resulting in a complex set of interactive responses to different combinations of stressors (Crain et al., 2008). The importance of pairwise interactions has been well documented and may influence many processes including ecosystem functioning (Vinebrooke et al., 2004) and primary producer abundance (Burkpile and Hay, 2006). Coral reefs have experienced progressive deterioration that has been attributed, at least in part, to multiple co-occurring anthropogenic stressors (Hughes et al., 2003). For example, nutrient supply has been found to promote algal proliferation, even in the presence of herbivory, if threshold nutrient levels are exceeded (Lapointe, 1997; Smith et al., 2001; Lapointe et al., 2004; Littler et al., 2006). However, Burkpile and Hay's (2006) meta-analysis found that interactions between nutrients and herbivory were common, with nutrient effects only apparent in the absence of herbivores (e.g. Burkpile and Hay, 2006; Smith et al., 2010). Further, herbivores often preferentially consume enriched macroalgae, which may mask nutrient effects (Chan et al., 2012). Other studies found strong interactions where sediments reduced herbivory (Bellwood and Fulton, 2008; Goatley and Bellwood, 2012). However, the extent to which these three stressors interact remains relatively unstudied (but see Muthukrishnan and Fong, 2014; Clausing et al., 2016; Fong et al., 2018), and none study the effects of sediments of different grain size on macroalgae. As the magnitude of anthropogenic impacts continues to grow, it will be critical to evaluate interactive effects of multiple stressors on coral reef ecosystems, especially on fringing reefs that may face the most intense impacts.

We evaluated the separate and interactive effects of herbivory, nutrient enrichment, and sediment grain size on biomass accumulation of the dominant tropical macroalga *Padina boryana* on an algal-dominated fringing reef. We hypothesized nutrients would have positive effects on *P. boryana*, but only in the absence of herbivory. We expected herbivores would consume *P. boryana*, but consumption would be reduced by addition of fine- rather than large-grained sediments as these would be trapped by fine thallus hairs.

## 2. Material and methods

### 2.1. Field characterization

We chose a relatively pristine fringing reef along the north shore of Mo'orea, French Polynesia (hereafter referred to as Sailing School;  $-17.491199^{\circ}\text{S}$ ,  $-149.851107^{\circ}\text{W}$ ) as our study site given that fringing reefs are relatively understudied, yet are the most susceptible to human impacts, particularly terrestrial input of nutrients and fine-grain sediments. Research was conducted in the wet season, between 21 January and 8 February 2016.

To characterize the study site, we quantified the abundance of herbivorous fishes and cover of benthic algae. Benthic surveys using the point intercept method were conducted between 0.5 and 2.0 m depths; cover categories for macroalgae were *Padina boryana*, *Turbinaria ornata*, *Dictyota bartayresiana*, *Sargassum mangarevense*, *Galaxaura divaricata*, while all other cover was grouped into a category called "other." Benthic surveys employed a 1 m<sup>2</sup> quadrat with 81 intersection points that was laid on the benthos at randomly generated points along a 30 m transect line. Because data was only recorded for quadrats that overlaid hard substrates, the number of quadrats along each of the 8 transects varied from 2 to 11, for a total of 45 quadrats. Benthic cover was identified underneath each intersection point and recorded. Data were collected in-situ.

Visual surveys of roving herbivorous fish within 2 × 50 m belt

transects were also conducted ( $N = 36$ ). Although other herbivorous fish families were occasionally observed, only roving herbivorous fishes in the family Acanthuridae and family Labridae, tribe Scarinae occurred in the transects. Because the data did not have equal variances, we used non-parametric Kruskal-Wallis tests to compare the percent benthic cover of five macroalgal species (listed above) and to compare the abundance of herbivorous fishes observed in the family Acanthuridae versus the family Labridae, tribe Scarinae. Following a significant Kruskal-Wallis test, we used non-parametric comparisons for all pairs using the Steel-Dwass method for the macroalgal benthic cover data. These analyses were conducted in JMP 13.0.0. We also analyzed data from the Mo'orea Coral Reef Long Term Ecological Research (LTER) to assess the diversity of herbivorous fish species at the nearest LTER site (LTER 1) from the data collection date closest to our experimental dates: August 2016 (Brooks, 2017). A literature search was then performed to confirm whether the herbivorous species present are known to consume *Padina boryana*.

The field experiment was conducted at the more pristine Sailing School site. However, sediments (small and large grain) were collected from Gump Reef, a fringing reef near the mouth of Cook's Bay also on the North Shore of Mo'orea, which is more impacted by terrestrial input ( $-17.490356^{\circ}\text{S}$ ,  $-149.825818^{\circ}\text{W}$ ). The addition of sediments from Gump Reef to *Padina boryana* at the Sailing School site was done in order to model how potential impacts of increased sedimentation from a more terrestrially-influenced source (Gump) would impact macroalgal growth at a more pristine reef (Sailing School). To estimate the range of natural sediment accumulation on macroalgal thalli on the fringing reefs of Mo'orea, *P. boryana* with natural sediment loads were collected ( $n = 3$ , each) from Sailing School and Gump Reef. Gallon-sized plastic bags were placed over samples of *P. boryana* and closed underwater to secure all algal fronds and associated sediments. Bags were returned to the lab where the algae were cleaned of sediments by brushing and shaking off sediments while algae were still in the water in the bags. Cleaned algae were placed into nylon bags, spun in a salad spinner to remove excess water, and wet weighed on a balance. A dry to wet weight ratio of 0.17 for *P. boryana* (Clausing et al., pers. comm.) was used to transform wet to dry weights. Sediments were settled, decanted, dried at 60 °C, and weighed. Sediment loads were visually observed to be composed primarily of fine sediments and were calculated as grams dry weight of sediment per grams dry weight of algae. Using JMP 13.0.0 we performed a two-tailed *t*-test comparing sediment loads between sites. To characterize sediment deposition at the study site, we also analyzed sedimentation rate data from the Mo'orea Coral Reef LTER at the site closest to our experimental site (LTER 1 Fringing Reef; Alldredge, 2012). Sedimentation rates for this site were only available from 3 December 2005–16 January 2010.

Given that all research was conducted during the wet season, we also quantified rainfall at the study site, given that temporal patterns in rainfall have been shown to influence macroalgal nutrient limitation in Mo'orea (Clausing and Fong, 2016). Rainfall data was accessed from the Mo'orea Coral Reef LTER data portal (Washburn and Brooks, 2016).

### 2.2. Algal collection and field experiment

We conducted a three-factor, fully-crossed field experiment evaluating the effects of sediment grain size (none, small, large), nutrients (ambient and enriched), herbivory ( $\pm$ ), and their interactions on biomass accumulation of *Padina boryana*. Experimental units contained thalli of *P. boryana* collected from Sailing School reef that were cleaned of sediments and wet weighed into 8 g subsamples. The thalli ( $n = 10$  replicates for each of the 12 treatment combinations,  $N = 120$ ) were attached by the holdfast to 13 × 13 cm flat hardware cloth bases. To exclude herbivores, half the thalli were placed in 13 × 13 cm (DxH) cylindrical cages made from the same hardware cloth with 1 cm<sup>2</sup> openings. Cages made of this material produced few artifacts in prior experiments on this reef (Clausing et al., 2014, 2016). Ten randomly

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