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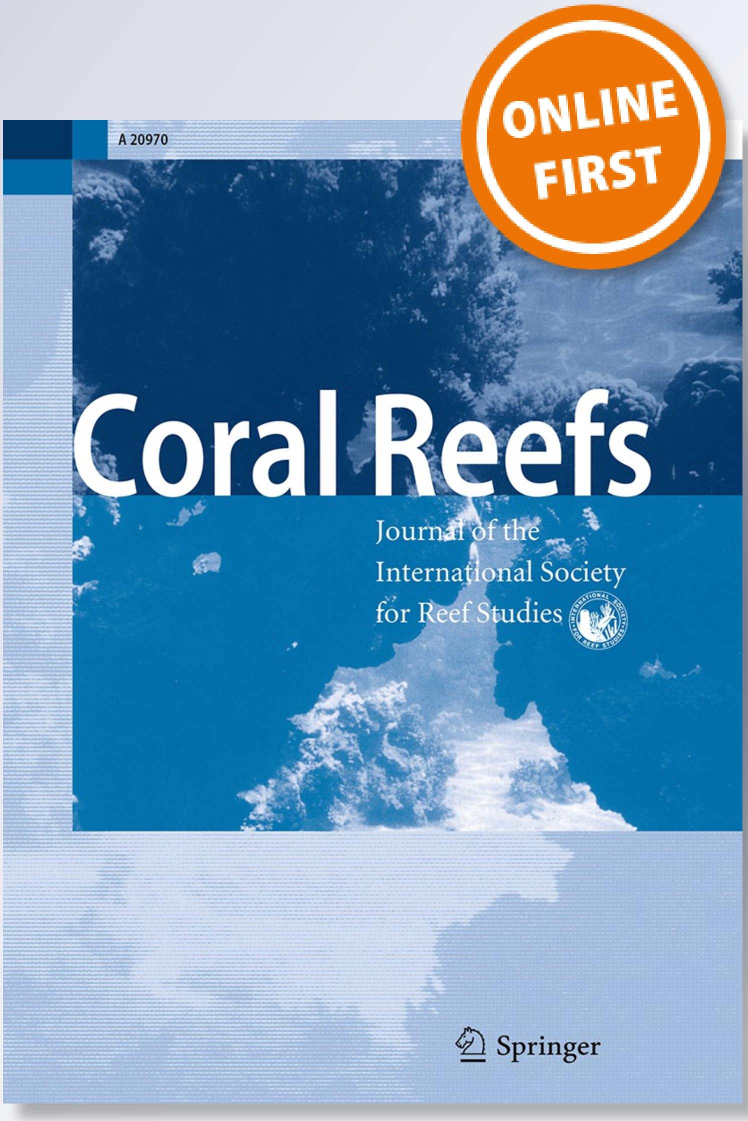

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REPORT

Sediments influence accumulation of two macroalgal species through novel but differing interactions with nutrients and herbivory

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Abstract Despite increasing concern that sediment loads from disturbed watersheds facilitate algal dominance on tropical reefs, little is known of how sediments interact with two primary drivers of algal communities, nutrients and herbivory. We examined the effects of sediment loads on the thalli of two increasingly abundant genera of macroalgae, *Galaxaura* and *Padina*, in a bay subject to terrestrial sediment influx in Mo'orea, French Polynesia. Field experiments examining (1) overall effects of ambient sediments and (2) interacting effects of sediments (ambient/removal) and herbivores (caged/uncaged) demonstrated that sediments had strong but opposite effects on both species' biomass accumulation. Sediment removal increased accumulation of *Padina boryana* Thivy 50% in the initial field experiment but had no effect in the second; rather, in a novel interaction, herbivores overcompensated for increases in tissue nutrient stores that occurred with sediments loads, likely by preferential consumption of nutrient-rich meristematic tissues. Despite negative effects of sediments on biomass, *Padina* maintained rapid growth across treatments in both experiments. In contrast, positive growth in *Galaxaura divaricata* Kjellman only occurred with ambient sediment loads. In mesocosm experiments testing interactions of added nutrients and sediments on growth, *Galaxaura* grew at equivalent rates with sediments (collected from thalli on the reef) as with additions of nitrate and phosphate, suggesting sediments provide a nutrient subsidy. For *Padina*, however, the only effect was a 50% reduction in growth with sediment. Overall, retention of thallus sediments creates a positive feedback that *Galaxaura* appears to require to sustain net growth, while *Padina* merely tolerates sediments. These results indicate that sediments can modify nutrient and herbivore control of algae in ways that differ among species, with the potential for strong and unexpected effects on the abundance and composition of tropical reef macroalgae.

Keywords Sediments · Macroalgae · Selective herbivory · Fringing reef · Nutrients · Tissue nutrients

Introduction

The global occurrence of phase shifts on coral reefs toward macroalgal dominance (Hughes et al. 2007) has heightened the need to elucidate how anthropogenic impacts affect the drivers of macroalgal biomass accumulation. Two of the primary processes structuring macroalgal communities that humans have altered are nutrient availability and herbivory, particularly by fish (for a review see Fong and Paul 2011). Anthropogenic increases in nutrient loads may release macroalgae from nutrient limitation, increasing growth and potentially abundance, particularly of opportunistic species (e.g., Littler et al. 2006). A concurrent reduction in herbivores lessens their ability to compensate for increased productivity and maintain low levels of algal

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biomass (e.g., Thacker et al. 2001). However, sedimentation on reefs is also increasing (Fabricius 2005), particularly on fringing reefs exposed to the stresses of watershed development via agricultural land use (De'ath and Fabricius 2010). On some reefs, these changes have become so widespread that many believe the baseline has shifted toward a new ambient condition of heightened sedimentation (McCulloch et al. 2003; Richmond et al. 2007; Prouty et al. 2010) and reduced herbivory (Hughes et al. 2010). There is substantial correlative evidence that macroalgae (>1 cm) are more abundant under higher sediment loads (McCook 1996, 1999; De'ath and Fabricius 2010), yet it is not known how increased sediment loads interact with nutrients and herbivory to influence algal dynamics.

One of the primary effects of increasing sediment loads may be changes in resources available for macroalgal growth. Reef sediments, particularly those with a substantial terrigenous component, often contain high levels of organic and inorganic nutrients (Weber et al. 2006) that can enrich surrounding waters when water column nutrients are low (Stimson and Larned 2000). There is some evidence that certain algal species may use nutrients in sediments for growth (Schaffelke 1999; Larned and Stimson 1996; Stimson and Larned 2000). Studies of direct effects of sediments on macroalgal growth on tropical reefs, however, are rare and primarily limited to *Sargassum* spp. on the Great Barrier Reef. Further, these effects appear to be context dependent, as one study showed sediments provided nutrient benefits (Schaffelke 1999), while another demonstrated negative impacts across demographic parameters (Umar et al. 1998). On temperate reefs, where the consequences of sediment loads for macroalgae are better studied, the effects on growth are primarily negative (e.g., Kawamata et al. 2012) by blocking light and gas or nutrient exchange (reviewed by Airoldi 2003; but see Kawamata et al. 2011). Yet one study (Gorgula and Connell 2004) showed that nutrient enrichment in the sediments increased algal turf cover. Thus, while sediments may significantly alter resource availability and therefore nutrient limitation in reef macroalgae, it is unclear whether this is the primary or even a consistent effect.

In addition to modifying macroalgal growth potential, sediments may reduce herbivory by blanketing thalli and decreasing tissue access or palatability. Thin layers of sediments can inhibit herbivory on early life stages of macroalgae (temperate reefs: Kawamata et al. 2011), and experiments on palatable tropical turf algae (<1 cm) have shown that reduction in sediment loads can increase rates of herbivory (Bellwood and Fulton 2008) in all parts of the reef (Goatley and Bellwood 2012). Thus, the presence of sediments may allow for increased algal biomass accumulation, particularly in reef zones with intense herbivory (Goatley and Bellwood 2013). However, these effects may be specific to certain environmental contexts (Bonaldo and Bellwood 2011; Gordon et al. 2015); for example, at moderate sediment depths (e.g., 2–4 mm) fish herbivory may only be inhibited when sediments cause anoxic conditions (Clausing et al. 2014). Currently, most evidence of the effects of sediments on herbivory comes from temperate systems (e.g., urchins: Kawamata et al. 2011) or tropical turf algae (e.g., fish: Bellwood and Fulton 2008; Bonaldo and Bellwood 2011; Goatley and Bellwood 2012; Gordon et al. 2015); we know little about the impacts of sediments on herbivory of macroalgae, particularly in tropical reef ecosystems.

Differences in morphologies, nutrient use strategies and responses to environmental context among macroalgal species may affect how and to what extent sediments interact with herbivory and nutrients (Airoldi 2003). Both temperate (Connell 2005) and tropical (e.g., Bellwood and Fulton 2008) turf algae have shown tolerance to heavy sediment loads, while crustose algae seem to be inhibited by sediments (Connell 2005). Yet there is also evidence, albeit correlative, of negative effects of sediment loads on tropical algal turf abundance (Begin et al. 2013). Species that are adapted to use nutrients fluxing from sediment porewater (Larned and Stimson 1996) or particulate matter (Schaffelke 1999) may gain a competitive advantage with increasing sediment loads (see also McClanahan et al. 2005). Moreover, algal species from different divisions contain unique pigments (Barsanti and Gualtieri 2014) that are likely to respond differently to the reduction in light with increasing sedimentation. These results, combined with evidence of sediments providing nutrients and inhibiting herbivory, suggest that benefits of sediments may exist, but they are likely to vary strongly between algal forms and species. Few studies, however, have experimentally examined species-specific mechanisms driving sediment effects (e.g., Umar et al. 1998; but see Schaffelke 1999; Kawamata et al. 2011; Clausing et al. 2014).

Our objective was to examine the impact of naturally accumulating thallus sediment loads on growth and biomass accumulation of tropical reef macroalgae and whether these effects are caused by changes in herbivory or nutrients. Specifically, we addressed the following questions for two dominant fringing reef macroalgal species that differ in morphology and nutrient use: (1) Do sediment loads affect biomass accumulation and, if so, is the effect consistently positive or negative? (2) Do sediments provide a source of nutrients? (3) Does the presence of sediment inhibit herbivory? To test these questions, we conducted field and mesocosm experiments. First, the effect of sediments on biomass accumulation of these two algae was assessed in an in situ sediment removal experiment. Second, the effects of sediments and nutrient addition on algal growth were compared in a mesocosm experiment. Third, we evaluated how sediments alter or interact with the effects of herbivory on algal biomass accumulation in a factorial field experiment manipulating herbivory and sediment loads. In all experiments, we examined changes in tissue nutrients to identify underlying mechanisms.

Methods

Study site and species

Experiments were conducted in May 2012 on Gump Reef, a fringing reef of Mo'orea, French Polynesia, near the mouth of Cook's Bay (17°32′S, 149°50′W). Runoff both from the agricultural watershed and from adjacent developed land delivers sediments into Cook's Bay (Adjeroud and Salvat 1996). As is common along developed coasts (Nemeth and Nowlis 2001), storms can create sediment plumes over the reef that deposit organic-rich sediments, and the proportion of terrestrial sediments increases with proximity to the head of the bay (83.3 vs. 6.3% non-calcareous matter at the head vs. mouth of the bay; P. Fong et al., unpublished data). On Gump Reef, windy afternoon conditions in April and May cause nearly daily sediment resuspension and water turbidity.

All experiments were conducted on the macroalgae *Padina boryana* Thivy (hereafter *Padina*) and *Galaxaura divaricata* Kjellman (hereafter *Galaxaura*) because, though they differ in ecology and morphology, both genera have become dominant on the study reef (Fong and Fong 2014) as well as globally on inshore reef flats (e.g., Fox and Bellwood 2007; reviewed by Fong and Paul 2011; Rasher et al. 2012) where sediment loads can be higher. *Galaxaura* is a calcified branching red alga that is unpalatable to herbivores (Mantyka and Bellwood 2007) and rapidly becomes nutrient limited (Clausing and Fong 2016), likely because of a low internal nutrient storage capacity (Aisha et al. 1995). *Padina*, in contrast, is a lightly calcified foliose brown alga that is readily consumed by herbivorous fish (Mantyka and Bellwood 2007; Fong and Fong 2014) and responds more variably to water nutrient inputs (Clausing and Fong 2016). In Mo'orea, sediment adheres to fine hairs on the thallus surface in both of these species on the reef flat (Fig. 1; see also Schaffelke 1999 for *Padina*).

Environmental conditions

Environmental conditions prior to and during experiments were characterized using rainfall and solar radiation data obtained with permission from the Mo'orea Coral Reef Ecosystem Long-Term Ecological Research (LTER) network (Washburn and Brooks 2014). Light and rainfall prior to the experiment may indirectly affect growth during the experiment by altering initial algal tissue nutrient content. Rain may increase nutrient availability and thus tissue nutrients unless extreme low light conditions limit uptake. For both the week prior to and the duration of each experiment, accumulated rain (mm) was summed by day and solar radiation (kW m^{-2}, 300–1200 nm) was averaged over daylight hours (0600–1800 hrs) for estimates of daily rainfall and daytime irradiance. Because light data were collected above water, and rainfall increases turbidity on this reef (Clausing and Fong 2016), evaluation of the environmental context requires joint consideration of light and rainfall data.

Fig. 1 Ambient sediment loads on thalli of *Padina boryana* and *Galaxaura divaricata* at Gump Reef in Cook's Bay, Mo'orea, French Polynesia

To quantify [g dry weight (DW) sediment g^{-1} algal DW] and characterize (grain size, organic matter and nutrient content) the thallus sediment load of each species, *Galaxaura* ($n = 2$) and *Padina* ($n = 1$) were collected using Ziploc bags to fully engulf the thalli and retain the sediments dislodged when thalli were clipped from the substrate. We rinsed the sediments from the thalli using seawater settled in a header tank and decanted and dried both the resulting slurry and the cleaned algae at 60 °C. This collection method provides a conservative estimate of thalli sediments, particularly fine sediments, which are most easily lost. Additional samples of each species were collected in 2013 ($n = 3$) and 2014 ($n = 3$) for further comparison, as initial collections had limited sample sizes. Benthic sediment samples ($n = 4$) were also collected in 2014 to quantify differences between benthic and thallus sediments (see Electronic Supplementary Material, ESM, for methods).

Experimental approaches

For all field and mesocosm experiments, we focused on the effects of naturally occurring (ambient) sediment loads on algal thalli at the experimental reef. Thus, ambient reef condition (defined here as +sediment, −nutrients, +herbivores) served as the reference in all experiments. For each experiment, algae were collected from the shallow (<1.5 m) backreef zone in one 5 × 10 m area comprised of patchy hard bottom and sand. Using the same location ensured replicate thalli were exposed to the same nutrient history in the field, thereby minimizing differences in tissue nutrient stores within each experiment. Algal thalli were cleaned of sediment and epibiota, spun for 1 min in a salad spinner (Fong et al. 2003) and wet weighed. Only entire thalli with little fouling and intact apical growing tips were used. Five additional thalli of both species were kept from the initial collection for each experiment, cleaned, rinsed in freshwater and dried at 60 °C to measure initial tissue N and P content. For *Padina*, we also investigated the partitioning of calcification and tissue nutrients within thalli. All analyses were performed using the R programming language (version 2.15.1; R Core Team 2012).

Overall effect of sediment on in situ biomass accumulation

We examined how the natural, in situ accumulation of sediment loads on algal thalli affected biomass change in *Padina* and *Galaxaura* with a sediment removal field experiment. Treatments were ambient sediment loads (Amb. Sed; natural levels of accumulation) and sediment removal (−Sed). Cleaned individual thalli were attached to 10 cm × 10 cm squares of 1-cm metal mesh using cable ties and randomly assigned to a treatment ($n = 15$). Initial weights varied among replicates (20–30 g *Galaxaura*, 11–17 g *Padina*) to maintain intact thalli.

Experimental replicates were secured haphazardly to an 8 m × 8 m area of hard bottom with 10-cm masonry nails. We allowed natural sediment to accumulate on algal thalli in ambient treatments and removed accumulated sediment daily in removal treatments by disturbing the overlying water or gently brushing thalli. *Galaxaura* was deployed 2–9 May and *Padina* 4–11 May. After 7 d, thalli were collected, cleaned, re-spun and re-weighed. Five random replicates of each treatment were retained for tissue nutrient analysis (see below).

Differences in percent change in biomass between treatments were analyzed with a bootstrapped *t* test because data could not be transformed to achieve normality (Manly 1997). Bootstrapping simulates the null hypothesis and provides a conservative estimate of significance for non-normal data (Manly and Francis 2002).

Interacting sediment and nutrient mesocosm experiment

The effects and interactions of sediments and nutrients on growth of *Galaxaura* and *Padina* were examined with a two-factor mesocosm experiment. Treatments were: +Sed −Nut (added sediment only, modeling conditions on the reef); −Sed −Nut (sediments absent, no nutrients added); +Sed +Nut (sediments and nutrients added); and −Sed +Nut (sediment absent and nutrients added—manipulation of both relative to ambient field conditions) ($n = 8$). On 6 and 7 May, we collected and prepared *Galaxaura* and *Padina*, respectively, while retaining, sieving and decanting thallus sediment loads. *Galaxaura* thalli were standardized to 8 g samples to minimize differences in surface area, the basis for nutrient uptake. For the more delicate *Padina*, entire thalli were retained (8.0–9.3 g initial weight).

The ambient nutrient treatment was water collected from the reef during algal collections. The enriched treatment was ambient water with added inorganic N and P (17 and 1.7 µM additions of $NaNO_3$ and NaH_2PO_4, respectively). All experimental units received 700 mL of either enriched or ambient seawater. Sediment treatments also received 15 mL of a sediment slurry mixed from ambient treatment water and sediment retained from *Galaxaura*, a volume that approximated in situ sediment loads. We agitated each unit to allow sediment to settle on the algal thalli as occurs on the reef during times of turbulence or terrestrial runoff. Replicate units were placed haphazardly in a flow-through water bath to maintain constant temperature. To simulate the frequent sediment resuspension that occurs on the reef, each unit was agitated for 5 s on day 3 of the experiment.

After 6 d, we cleaned and re-weighed algae and calculated percent change in wet biomass. While these experiments do not simulate natural field conditions (nutrient supply, flow, competition) and thus are not predictors of algal growth on the reef, results can be compared among treatments. Five random replicates per treatment were retained for analysis of nutrient content. Change in biomass among treatments was analyzed with a two-way factorial ANOVA. Data were not transformed as assumptions of normality and homogeneity of variance were met when checked with Shapiro–Wilk and Levene's tests.

Interacting sediment and herbivory field experiment

The effects of sediments and herbivory on growth and tissue N and P content of *Padina* and *Galaxaura* were evaluated in a factorial field experiment manipulating levels of sediment and herbivory (16–23 May). Treatments were: ambient (+Sed +Herb); reduced sediment (−Sed +Herb); reduced herbivory (+Sed −Herb); and reduced sediment and herbivory (−Sed −Herb).

Algae were collected and prepared as before and trimmed to 5 g (*Padina*) and 8 g (*Galaxaura*) replicate thalli. Weight differences between algal species standardized volume to avoid differences in potential attractiveness to herbivores. For reduced herbivory treatments (−Herb), algal thalli were cable-tied to the bottom of metal mesh cylindrical cages (D × H: 10 cm × 15 cm) with 1-cm openings. Previous work using this caging material found no reduction in flow or effects on biota and a reduction in irradiance of <10% (Clausing et al. 2014). Replicates of +Herb treatments were attached to flat squares of the same metal mesh (10 cm × 10 cm) open to herbivores. Experimental units were then attached randomly to ropes that loosely secured them to the reef benthos, allowing agitation of individual units for sediment removal. We allowed sediment to accumulate naturally on +Sed replicates and removed sediment on −Sed replicates daily as described above. After 6 d, algae were collected, cleaned and reweighed. All 40 thalli of each species were retained for tissue nutrient analysis. Growth as percent change in wet biomass was analyzed using a two-way ANOVA for each species as data met assumptions (Shapiro–Wilk and Levene's tests).

Tissue nutrients

Analytical methods to quantify tissue N and P content as % DW are described in ESM. Because growth can dilute tissue nutrient content even when uptake is occurring, change in tissue nutrients was calculated as percent change in N and P mass between the onset and end of each experiment (see ESM for calculations). The percentages were estimated based on total DW of the thallus, without removing calcium carbonate ($CaCO_3$). Despite potential effects of varying rates of calcification on calculation of tissue N incorporation, we chose to include $CaCO_3$ in the DW to give a realistic perspective of the energetic costs that the herbivores face to get the nutrition contained in the thallus. We analyzed percent change in nutrient mass using the same model used for each experiment. All data met assumptions of normality and homogeneity of variance where necessary (ANOVA models) except change in tissue N mass of *Padina* in the mesocosm experiment, which required a natural log transformation.

Calcification versus nutrient content within *Padina* thalli

To assess potential differences in palatability within thalli of *Padina*, $CaCO_3$ and nutrient content were quantified in thallus sections of differing age. Algal thalli ($n = 9$) were collected from Gump reef in April 2013 and cleaned, rinsed and dried at 60 °C. Prior to drying, thalli were partitioned into three parts along concentric rings of calcification at 2-cm intervals to ensure division by age within and between thalli. The oldest, basal tissue is typically thicker, tougher and more degraded; we hypothesized decreasing calcification and increasing relative nutrient content in newer tissue (toward the apical meristem). After removing roughly 0.01 g of each sample for nutrient analysis, we decalcified the remaining sample with dilute hydrochloric acid (0.1 M), rinsed it in deionized water and dried it at 60 °C overnight. Percent calcification was determined by change in weight. Tissue N content was analyzed at the UC Davis Stable Isotope Facility (SIF) using combustion. Tissue N % was based on entire DW, without removing $CaCO_3$. Both calcification and nutrient data were analyzed with mixed effects models using the function "lme" in the add-on package "nlme" in R. The model included section of the thallus (outer, middle or inner) as a fixed factor and replicate thalli as a random effect.

Results

Environmental and species characterization

Conditions on the reef prior to and during the three experiments varied. A weeklong storm (23–30 April; 198 mm rain) concluded one (*Galaxaura*) or three (*Padina*) days before the overall effect experiments began (Fig. 2a). Light was reduced during the storm (0.23 kW m^{-2} average daytime solar radiation; Fig. 2b), but was high ($\sim$0.43 kW m^{-2}) during the experiment. It remained dry and sunny for the remainder of the experiments (0 mm rainfall; 0.42–0.45 kW m^{-2}; Fig. 2a, b). Thus, although resuspension and deposition of benthic sediments on algal thalli occurred continually, after 1 May there would have been little new input of terrestrial sediments or nutrient inputs associated with runoff. Initial tissue N concentrations in both *Galaxaura* and *Padina* were significantly higher in the overall effect field experiment (2, 4 May) than in the second field experiment two weeks later (16 May; Fig. 2c, d), indicating the storm elevated nutrient supplies that subsequently decreased with time. Neither %P nor N/P ratios changed significantly for either species (ESM Fig. S1a–d). Relatively low tissue N concentrations (0.78–1.11%) in both species across experiments may be explained, in part, by calcium carbonate content which increases the weight by which the concentrations are determined, as has been found in previous work (Fong et al. 2001, 2003).

Sediment loads on thalli of *Galaxaura* and *Padina* appeared similar between species and year (Table 1), although low sample sizes prevent conclusions about changes over time. Organic content of thallus sediments ranged 5.9–8.1% across collections and species (Table 1). Organic content of the benthic sediment was only 2.5%.

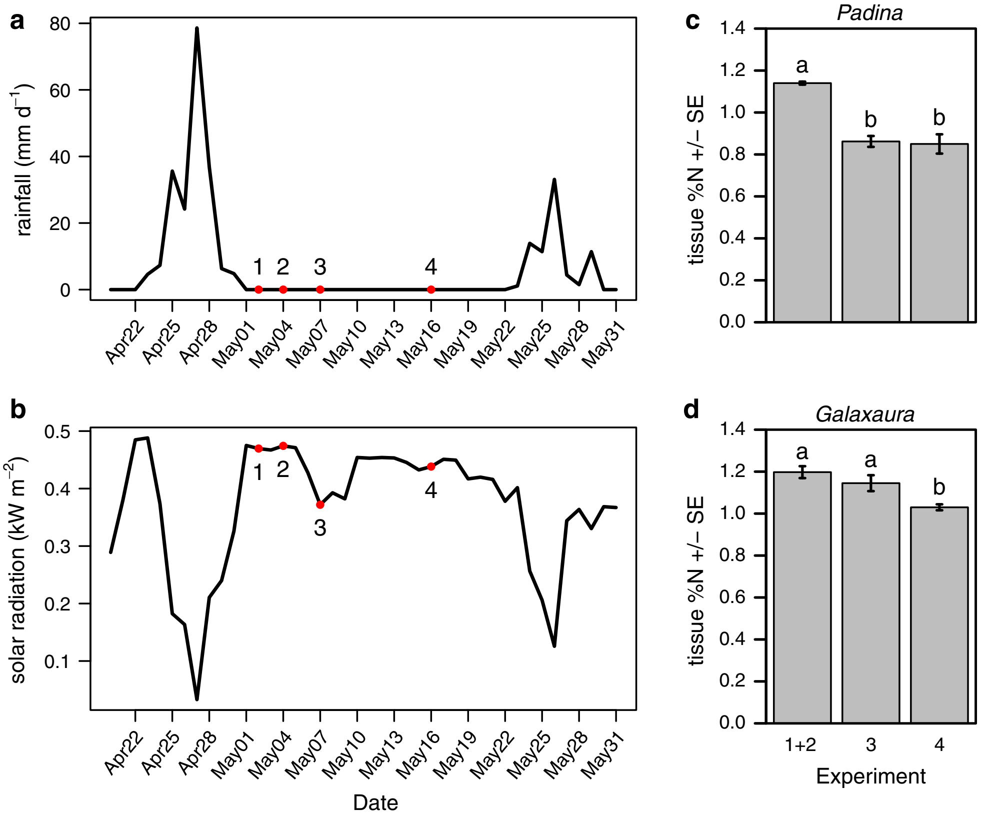

Fig. 2 Environmental and biotic data describing the conditions in the field during the experimental period. **a** Daily rainfall and **b** average daytime (0600–1800 hrs) solar irradiance (kW m^{-2}) over the course of each experiment. *Red dots* indicate onset of each 6-d experiment: overall effect field experiments on *Galaxaura* (*1*) and *Padina* (*2*); mesocosm experiment (*3*); interaction field experiment (*4*). **c**, **d** Tissue nitrogen concentrations at the onset of each experiment in *Padina* (**c**) and *Galaxaura* (**d**). *Letters* indicate significant differences at $p < 0.05$ (Tukey's HSD test). *Error bars* are standard errors

Table 1 Comparison of sediment characteristics (a) between the thalli of *Galaxaura divaricata* and *Padina boryana* and (b) between the thalli of each macroalgal species and the benthos

Species	Year	Load	%N	%P	N:P	Organics (%)	Sand (%)	Clay (%)	Silt (%)
(a) Comparison of thallus sediments between species									
Padina	2012	0.25	0.25	0.033	16.2	7.0	–	–	–
	2013	0.29 (0.04)	0.13 (0.01)	0.011 (0.001)	25.4 (2.0)	6.2 (0.13)	–	–	–
Galaxaura	2012	0.24	0.32	0.048	14.8	8.1 (0.09)	53.2 (1.3)	27.5 (3.8)	19.3 (2.5)
	2013	0.27 (0.03)	0.16 (0.01)	0.027 (0.007)	15.1 (4.0)	7.7 (1.4)	–	–	–

Spp	%N	*n*	Organics (%)	*n*	$CaCO_3$ (%)	*n*	Sand (%)	Clay (%)	Silt (%)	*n*
(b) Comparison of benthic and thallus sediments (both species)										
Padina	0.155 (0.002)	3	6.19 (0.13)	2	–	–	–	–	–	–
Galaxaura	0.183 (0.001)	2	5.91 (0.28)	2	78.1	1	66.2	5.6	28.2	1
Benthos	0.038 (0.003)	4	2.47 (0.083)	4	90.8	4	87.5 (3.97)	7.1 (1.3)	5.4 (3.7)	4

(a) N/P are molar ratios. Sediment load is calculated as g dry weight sediment per g dry weight algal tissue. Values are means with standard errors in parentheses; 2012: $n = 1$ for all samples except *Galaxaura* organic content and grain size ($n = 2$); 2013: $n = 3$ for all samples

(b) Samples collected in 2014 from Gump reef collection site

Moreover, %N was 4.4 times greater in thallus sediments than in benthic sediments. Sediments on the thalli of *Galaxaura* contained more than five times the silt content of benthic sediments, roughly 30% fewer larger-grained sand particles and 15% less $CaCO_3$ (Table 1). Nutrient concentrations were greater in thallus sediments of

Galaxaura than those of *Padina* in all years, although this pattern could not be confirmed statistically in the year of experimentation due to low sample size (Table 1).

Experimental results

Overall effect of sediment on in situ biomass accumulation

Biomass accumulation of *Padina* increased by ~50% with the daily removal of ambient sediment loads (Fig. 3a; $p = 0.009$). In contrast, ambient sediment loads positively affected *Galaxaura*, which only gained biomass in the presence of sediment (Fig. 3b; $p = 0.014$). Sediment loads significantly reduced both tissue N and P content of *Padina* (Fig. 3c, d; N: $p < 0.001$; P: $p = 0.02$), causing nutrient loss even though biomass increased. In contrast, tissue N and P of *Galaxaura* varied across treatments with no significant trends (ESM Fig. S2). Actual tissue N and P concentrations are reported in ESM Table S1.

Interacting sediment and nutrient mesocosm experiment

Padina grew ~50% more without sediments (both −Sed treatments) compared with the ambient sediment treatment (Table 2; Fig. 4a). Added nutrients appeared to increase growth, but the effect was not significant. Further, tissue N and P content showed no pattern (ESM Table S2; ESM Fig. S3a, c).

In contrast, nutrient addition ameliorated the negative effects of sediment removal in *Galaxaura*, resulting in a significant interaction of sediment and nutrients on growth (Fig. 4b; Table 2). At ambient nutrient levels, replicates with sediments grew more than double those without. Yet the addition of nutrients to replicates without sediments (−Sed +Nut) resulted in growth rates similar to those of the ambient treatment (+Sed −Nut), indicating sediments caused a boost in growth equivalent to the addition of nutrients. Thus, in low nutrient conditions, sediments may provide a similar benefit to *Galaxaura* as added nutrients, but may have little effect on growth when nutrients are replete (+Sed −Nut compared to −Sed +Nut). Despite effects on biomass, no trends were observed in either tissue nutrient (ESM Table S2; ESM Fig. S3b, d). Actual values and percent change in tissue N and P concentrations are reported in ESM Table S3.

Interacting sediment and herbivory field experiment

Protection from herbivory increased biomass accumulation of *Padina* by roughly an order of magnitude compared to open units where herbivory resulted in negligible change in biomass (Table 3a; Fig. 5a). In contrast to the previous experiments, sediment had no effect on *Padina*, regardless of herbivore treatment. This lack of effect may relate to the different environmental conditions on the reef prior to experimentation, which resulted in substantially reduced initial tissue nutrient stores (Fig. 2). Changes in tissue N mass, however, revealed a significant interaction between sediment and herbivory (Table 3a). When herbivores were present (Fig. 5b left two bars), ambient sediment loads

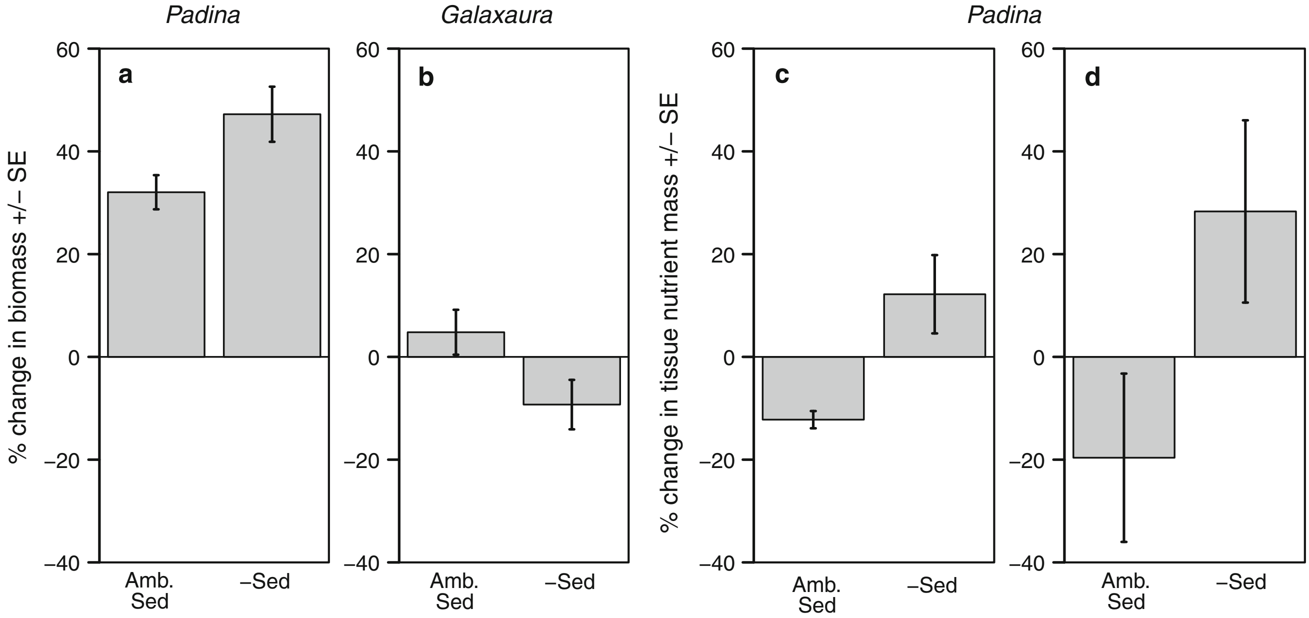

Fig. 3 Overall effect of ambient sedimentation versus sediment removal on mean biomass accumulation over 7 d of **a** *Padina* and **b** *Galaxaura*. **c**, **d** Tissue nutrient content of *Padina* only, where nutrients are **c** nitrogen (N) mass and **d** phosphorus (P) mass. Comparisons in all panels are significantly different (bootstrapped two-sample comparison, $p < 0.05$). *Error bars* are standard errors

Table 2 Results of two-way ANOVAs on percent change in biomass of *Padina* and *Galaxaura* over 6-d mesocosm experiment with and without nutrient addition and sediments

	df	MS	*F*	*p*
Padina				
Nutrient	1	68.22	2.72	0.110
Sediment	1	192.56	7.68	0.010**
Sediment/nutrient	1	22.56	0.90	0.351
Error	28	25.09		
Total	32			
Galaxaura				
Sediment	1	107.9	1.97	0.172
Nutrient	1	320.4	5.84	0.022
Sediment/nutrient	1	1026.6	18.71	<0.001***
Error	28	54.9		
Total	32			

Significance at ** $p < 0.05$; *** $p < 0.01$

resulted in three times lower gains in N mass than when sediment was removed. In contrast, in the absence of herbivores (Fig. 5b right two bars) ambient sediment loads resulted in three times higher gains in N mass than when sediment was removed. This interaction suggests that herbivores were mediating the accumulation of N in the tissue. Similarly, sediment removal in the absence of herbivores (−Sed −Herb) resulted in a reduced gain in tissue P relative to thalli with sediments intact (+Sed −Herb) (Fig. 5c). Sediment removal in the presence of herbivores, however, had no effect, resulting in a marginally significant interaction (Table 3a).

Across treatments, *Galaxaura* either maintained or lost biomass (Fig. 5d). Lower initial tissue N concentrations for this experiment may indicate that nutrient limitation was strong enough after two weeks without rain that respiration exceeded photosynthesis (see Fig. 2d). While *Galaxaura* appeared to lose more biomass without sediments, this difference was only marginally significant (Table 3b). Herbivory had no main or interactive effects. In contrast, for tissue nutrients, herbivores significantly decreased P accumulation, but only marginally reduced N. Sediments had no significant effect (Table 3b; Fig. 5e, f), nor were there interactive effects (Table 3b). Actual tissue nutrient percentages are reported in ESM Table S4.

Calcification and nutrient content of *Padina*

$CaCO_3$ content in *Padina* was 10% greater in the older, basal portion of the thallus than in either the mid or apical sections (Fig. 6a; Table 4a). In contrast, nutrient content was significantly greater in the outer apical area of the thallus compared with the mid or basal sections (Fig. 6b; Table 4b).

Discussion

We have demonstrated that sediments interacted with herbivory and nutrient availability in a novel way on coral reefs, where the nutrient benefits of sediments to the brown alga *Padina boryana* were masked by herbivory that overcompensated for increased tissue nutrients with

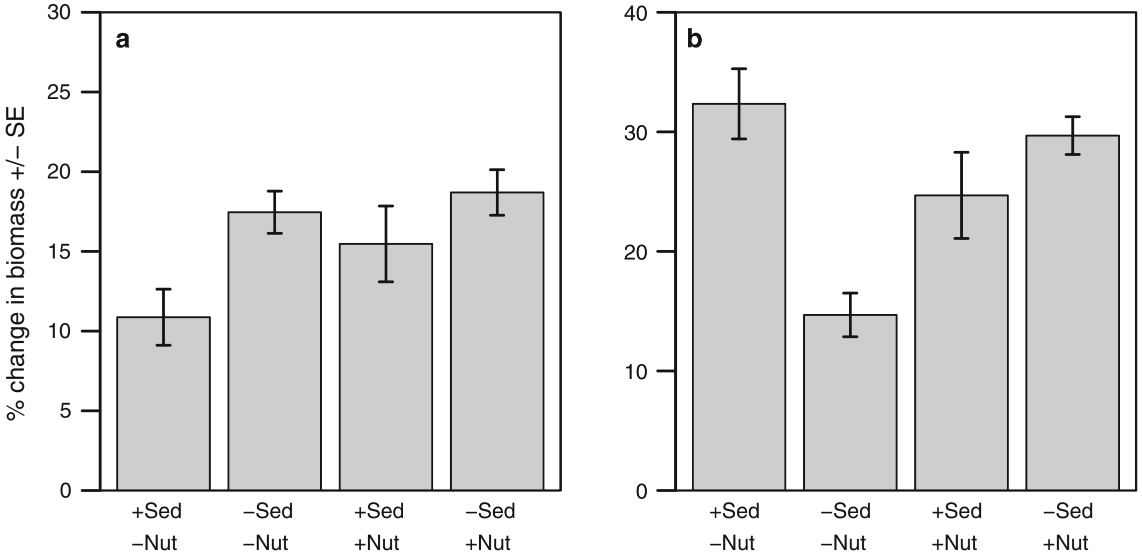

Fig. 4 Individual and interacting effects of sediments and nutrient addition on growth of **a** *Padina* and **b** *Galaxaura* over 6 d in mesocosms. The +Sed −Nut treatment simulates conditions on the reef (natural sediment loads, ambient nutrients), −Sed −Nut indicates the absence of sediment, +Sed +Nut represents both sediment and nutrient addition, and –Sed +Nut indicates the absence of sediment with added nutrients. *Error bars* are standard errors

Table 3 Results of two-way ANOVAs on the interacting effects of sediment and herbivory on % change in biomass and in tissue N and P of (a) *Padina* and (b) *Galaxaura*, comparing the impact of sediment and herbivore removal on growth and tissue nutrient stores over 6-d field experiments

	(a) *Padina*				(b) *Galaxaura*			
	df	MS	*F*	*p*	*df*	MS	*F*	*p*
% Change in biomass								
Sediment	1	31.2	0.12	0.737	1	601	4.01	0.053*
Herbivores	1	2550	9.40	0.004***	1	56.4	0.38	0.543
Sed/Herb	1	50.3	0.19	0.670	1	30.6	0.21	0.654
Error	33	272			36	150		
Total	37				40			
% Change in tissue N mass								
Sediment	1	7.7	0.04	0.837	1	81.1	0.42	0.522
Herbivores	1	136	0.76	0.390	1	773	3.99	0.053*
Sed/Herb	1	1445	8.07	0.008****	1	230	1.19	0.283
Error	33	179			36	194		
Total	37				40			
% Change in tissue P mass								
Sediment	1	919	3.67	0.064*	1	621	3.90	0.056*
Herbivores	1	95	0.40	0.542	1	999	6.27	0.017**
Sed/Herb	1	874	3.49	0.071*	1	0.02	0.001	0.991
Error	33	250			36	159		
Total	37				40			

* Significance at $0.05 < p < 0.1$; ** $p < 0.05$; *** $p < 0.01$; **** $p < 0.001$

sediment loads. Unlike in algal turfs, where sediment may protect algae from herbivory (e.g., Bellwood and Fulton 2008; Goatley and Bellwood 2012), sediment loads induced herbivory that caused proportionally larger loss of tissue nutrients, likely through selective consumption of the more nutrient-rich peripheral meristem. Despite that herbivory, nutrient availability and sedimentation are three major ecological processes that are altered by human impacts (e.g., Thacker et al. 2001; Fabricius 2005; Littler et al. 2006; Prouty et al. 2010), this is the first study examining the interplay of all three processes in controlling macroalgal proliferation on reefs. Previous work demonstrating that sediments can provide algae with nutrient subsidies (*Sargassum* spp.; Schaffelke 1999) and that herbivory is greater on nutrient-enriched tissue not only on reefs (Boyer et al. 2004), but also in mangroves (Onuf et al. 1977) and seagrass communities (Williams and Ruckelshaus 1993; Goecker et al. 2005) suggests such interactions may be widespread across a range of marine ecosystems. Evidence of selective herbivory of preferred tissues within thalli is limited in marine algae (but see Poore 1994; Cronin and Hay 1996); however, apical tissues have been shown to be more nutritious under enriched conditions (Hay et al. 2011), suggesting that this mechanism could occur with other palatable reef species. Targeted consumption of young meristematic tissue with sediment loads is likely to reduce the ability of algae to tolerate both sediments and herbivory, particularly if either increases (Poore 1994; Hay et al. 2011). Thus, the examination of these processes (sediments, nutrients, herbivory) in isolation may provide an incomplete picture of their role in controlling algal proliferation on impacted reefs.

This study identified a novel positive feedback in which algal morphology may facilitate growth through the retention of finer, more nutrient- and organic-rich sediments settling on the thalli. *Galaxaura* appeared to depend on these sediments to support positive growth in certain environmental contexts. Although sediment loads with high organic content have been shown to cause anaerobic conditions (>2% organic content; Clausing et al. 2014), H_2S production and microbial activity (>5%; Weber et al. 2012), the frequency of sediment resuspension and the flexible nature of both species' thalli may preclude the accumulation of sediment deep enough to cause such negative effects on this reef. Environmental modification by plants that increase soil moisture retention and alter the microclimate is well documented (reviewed by Scheffer and Carpenter 2003). Moreover, strong evidence exists for positive feedbacks in corals, which may indirectly inhibit algal biomass accumulation by providing habitat structure that acts as a refuge for urchin herbivores (Lee 2006; Norström et al. 2009). Similar mechanisms have been postulated by which algae can maintain dominance. For example, some frondose algae may prevent N limitation by isolating spaces over the sediment that allow sediment-derived dissolved inorganic N to accumulate (*Dictyosphaeria cavernosa*; Larned and Stimson 1996). On

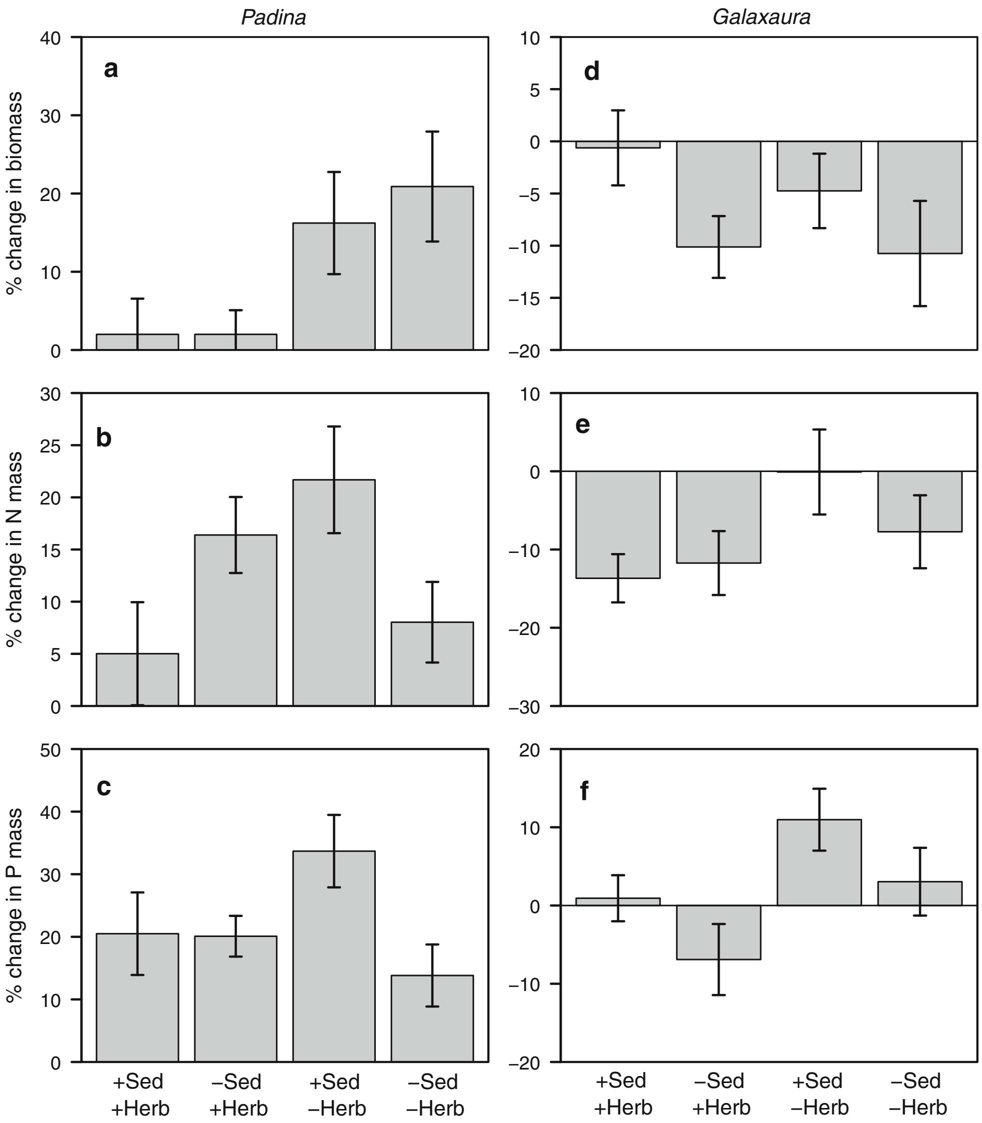

Fig. 5 Individual and interacting effects of sediments and herbivory on biomass accumulation and tissue nutrients on the reef of **a**–**c** *Padina* and **d**–**f** *Galaxaura*. Tissue nutrients are % change in tissue nutrient mass of **b** N and **c** P on *Padina* and **e** N and **f** P on *Galaxaura*. All responses are % changes over a 6-d experimental duration where the +Sed +Herb treatment is unmanipulated to experience ambient reef conditions (natural sediment loads and herbivory), −Sed +Herb indicates the removal of accumulating sediment, +Sed −Herb represents thalli caged from herbivorous fish and −Sed −Herb both sediment removal and cages to prevent herbivory. *Error bars* are standard errors

disturbed reefs, accumulation of terrestrially derived sediments may promote dominance of particular functional forms of algae, providing a potential mechanism by which the algal state may persist.

The benefit of sediments to algae may be via a nutrient subsidy, at least in some environmental conditions. Both species showed increased tissue nutrient content with thallus sediments in at least one experiment, provisionally supporting this mechanism. Mixed results over time may relate to the complexity of nutrient uptake and storage processes under temporally variable nutrient supplies (Fong and Paul 2011), particularly in species where calcification can influence apparent nutrient incorporation. Thus, future work on calcified macroalgae would benefit from additional comparison of tissue nutrient change based on $CaCO_3$-free dry weight. In addition, sediment nutrient benefits varied between species: In *Galaxaura* they were manifest directly in growth, while nutrient gains in *Padina* were annulled by herbivory. Previous work supports differential effects of sediment nutrients among species (e.g., Schaffelke 1999), where those with lower uptake and storage capacities of water column nutrients may best utilize sediment nutrients (Larned and Stimson 1996). A low capacity for tissue nutrient storage (Aisha et al. 1995) and tendency toward nutrient limitation (Clausing and Fong 2016) in *Galaxaura* indicates that nutrients from thallus

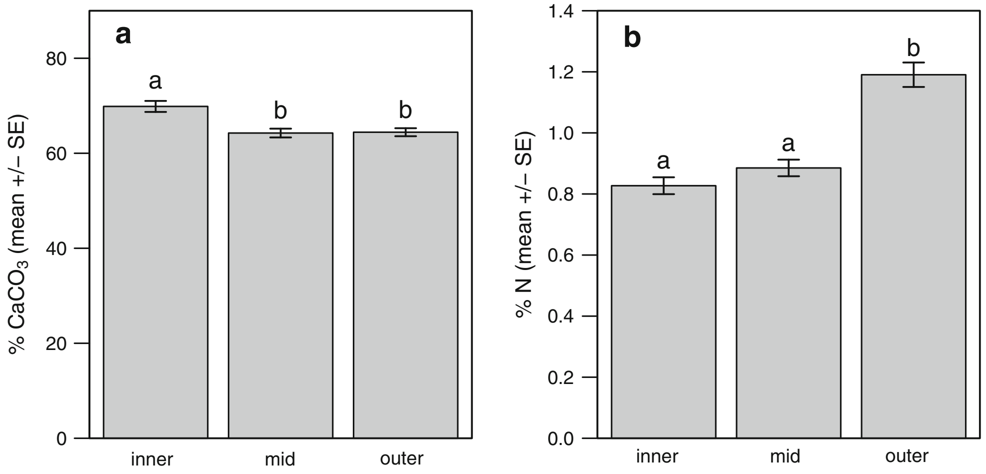

Fig. 6 Percent calcification **a** and percent nitrogen **b** of inner, mid and outer thallus sections of *Padina.* Thalli were partitioned along concentric rings of calcification; the innermost section is the oldest tissue and the outer section is the new apical growth

Table 4 Mixed effects models on (a) % calcification and (b) % N of *Padina* thallus sections of differing age

	Estimate	SE	*df*	*t*	*p*
(a) % Calcification					
(Intercept)	69.9	1.002	14	69.7	<0.0001
Midsection	−5.6	1.377	14	−4.1	0.0011
Outer section	−5.4	1.417	14	−3.8	0.0018
(b) % Nitrogen					
(Intercept)	0.83	0.030	14	27.8	<0.0001
Midsection	0.058	0.038	14	1.5	0.14
Outer section	0.37	0.041	14	9.0	<0.0001

(a) The random effect of thallus section was removed because it accounted for <0.001% of the variance

(b) The random effect of thallus section accounted for 33.0% of the variance

sediments could be an important mechanism facilitating its proliferation. Mat-forming algal species have also been shown to benefit from release of nutrients from sediment when water column nutrients are low (Larned 1998; Stimson and Larned 2000; Kamer et al. 2004). An alternative explanation for high nutrient content in thallus sediments (relative to benthic sediments) could be nutrient leakage from the thalli. However, nutrient release occurs variably both among seasons and species (Haas et al. 2010) and does not explain the increased proportion of fine thallus sediments relative to the benthos. Nevertheless, further investigation is needed to evaluate in which species and environmental contexts sediments confer nutrient benefits and whether they facilitate macroalgal dominance on reefs.

Galaxaura and *Padina*, two dominant genera of coral reef macroalgae (Fox and Bellwood 2007; Fong and Paul 2011), may have different mechanisms of persistence under increasing sediment deposition. In *Padina*, maintenance of positive growth despite overall negative effects of sediment indicates the ability to survive through tolerance; *Galaxaura*, in contrast, directly benefited from increased supplies of nutrient-rich terrestrial sediment. Species with ecological strategies that profit from human disturbances (e.g., *Galaxaura*) may become more dominant in impacted habitats (e.g., Argentine ants: Suarez et al. 1998). Yet disturbance-tolerant species (*Padina*) may also thrive on sedimented reefs by maintaining relatively higher rates of growth than less tolerant species (Littler and Littler 1980). Moreover, if herbivory is concurrently reduced, palatable species like *Padina* may gain advantage through increased tissue nutrients.

Overall, our research suggests that sediments may alter coral reef macroalgal community structure through unique interactions with herbivory and nutrient availability. Additionally, differential effects among species could lead to unexpected effects in impacted communities (i.e., “ecological surprises”; Paine et al. 1998; Nyström et al. 2000), particularly if the focus remains on nutrient and herbivore control of algae without considering sediment modulation of these processes. In light of recent studies demonstrating reduced coral reef resilience to phase shifts under multiple human stressors (Fung et al. 2011; Muthukrishnan and Fong 2014; Goatley et al. 2016), it may be particularly important to manage sediment inputs onto reefs, as they may disrupt nutrient cycles and patterns of herbivory.

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