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REPORT

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Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats

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Abstract We explored the role of food quality in herbivore preference for macroalgae by comparing consumption of *Acanthophora spicifera* with and without elevated tissue nitrogen and phosphorus concentrations. Algal enrichment effects on herbivory were examined in coral, seagrass, and mangrove habitats along a sparsely populated Honduran island protected from fishing. Nutrient enrichment led to significantly increased grazing by herbivores across habitats. Consumption of enriched algae increased by 91% compared to controls among the mangrove roots, where herbivory rates were generally lowest. In the heavily grazed seagrass and coral habitats, nutrient enrichment increased consumption by 30 and 20%, respectively, with the effect more spatially variable than among the mangrove roots. We suggest that, at least on the local scale, intact herbivore populations may be able to compensate for effects of increased nutrient supply by locating and consuming nutrient-enriched algae, but that the importance of this mechanism varies both among and within habitats.

Keywords *Acanthophora* · Herbivory · Honduras · Macroalgae · Nutrients

Introduction

Factors controlling growth and biomass accumulation of benthic algae are gaining considerable interest as concern over the health of the world's coral reefs builds (e.g., Szmant 2001). A small body of direct experimental evidence documents negative effects of macroalgae on corals (reviewed by McCook et al. 2001) through overgrowth (Coyer et al. 1993; Hughes 1989), colonization of coral lesions (Meesters and Bak 1993; Meesters et al. 1994, 1997; van Woesik 1998), or abrasion through contact with algae (Coyer et al. 1993; Miller and Hay 1996). In addition, many experiments have indirectly revealed, and observational and correlative studies support, a negative relationship between measures of algal proliferation and coral decline (McCook et al. 2001). While it is often not clear whether algae caused coral declines or recruited after other damages occurred, phase shifts from coral- to algal-dominated reefs have been widely documented over the last two decades (Littler and Littler 1984; Lapointe 1989, 1997; Done 1992; Hughes 1996; Miller 1998; McCook 1999).

Increases in human-derived nutrient supply to coastal areas in the tropics have been implicated in observed increases in cover or biomass of algal species in shallow habitats (Bell 1992; Lapointe 1997; Adey 1998). Increased nutrients (nitrogen, N and/or phosphorus, P) have been found to enhance productivity of many tropical algal species and assemblages (Hatcher and Larkum 1983; Lapointe 1987, 1989, 1997; Lapointe et al. 1987; Williams and Carpenter 1988; Larned and Stimson 1997; Schaffelke and Klumpp 1997, 1998a, 1998b; Larned 1998; Fong et al. 2003), although not all species/assemblages responded to nutrient enrichment or not in all seasons (Hatcher and Larkum 1983; Degaldo et al. 1996; Miller et al. 1999; Koop et al. 2001).

Despite experimental evidence for nutrient limitation of a number of tropical macroalgae, the extent and importance of nutrients to algal biomass accumulation in the field are unclear (e.g., Szmant 1997; McCook 1999). This is partly because herbivores, when abundant, exert strong control over macroalgae through biomass removal in nearshore tropical habitats (reviews by Hatcher 1983; Steneck 1988; Carpenter 1997) and are thought to counter the effects of ele-

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vated nutrients on algal growth (Hughes et al. 1999; McCook 1999). Szmant (1997) hypothesized that as long as there is sufficient topographic complexity in a reef for herbivore refuge and no major losses of important herbivore species, reef communities should be able to incorporate relatively high levels of nutrients without a shift to algal dominance.

While there is strong evidence that herbivores are important to community structure on reefs (e.g., Lewis 1986; Hay 1997), few manipulative experiments have tested the effects of nutrient enrichment on herbivore responses. In Australia, Hatcher and Larkum (1983) found inorganic nitrogen limited turf algal growth on an outer reef slope, but that grazing controlled standing crop. Recently, researchers at a low nutrient, fishery-managed reef in Hawaii found enhanced nutrients to promote fleshy macroalgal growth when large herbivores were excluded and growth of crustose coralline algae with herbivores present (Smith et al. 2001). Two other studies in which nutrient supply was manipulated in the field did not find a clear pattern of algal response, and thus were limited in their assessment of herbivore responses to increased nutrients (Miller et al. 1999; Thacker et al. 2001). Overall, these experiments have found strong top-down (e.g., herbivory) effects controlling algal biomass and community structure, but the relationship between nutrient enrichment and herbivory remains seldom tested and largely unresolved.

Enhanced nutrient supply can influence not only the quantity, but also the quality of primary producers as food for herbivores. Elevated nutrient content of plant tissues can increase the efficiency with which a consumer converts food into biomass (e.g., Mattson 1980; Sterner and Hesson 1994). Faster grazing rates or overall greater consumption of N- and/or P-enriched algae suggest a preference for such high quality foods in temperate locations (Nicotri 1980; Yates and Peckol 1993; Hauxwell et al. 1998; Giannotti and McGlathery 2001; Plath and Boersma 2001). However, some grazers are more selective than others with regard to food quality (Cruz-Rivera and Hay 2000).

We are aware of no studies in tropical waters that have explicitly tested the relationship between algal tissue nutrients and herbivory. Across adjacent coral reef, seagrass, and mangrove habitats, herbivore assemblage composition (Taylor et al. 1986; Marguiller et al. 1997), age and size structure (Chong et al. 1990; Laegdsgaard and Johnson 2001), and grazing rates (Hay 1984; Lewis and Wainwright 1985; Carpenter 1986; Lewis 1986) can differ greatly; hence, it is difficult to predict how elevated tissue nutrients might influence the response of a particular grazer assemblage. We conducted an experiment to examine the importance of increased algal tissue N and P on herbivore grazing along a remote and relatively pristine island off the coast of Honduras. The objectives of this study were to test if: (1) elevated nutrient content of a palatable algal species increased consumption by herbivores, (2) effects on herbivory varied among coral reef, seagrass, and mangrove habitats, and (3) effects on herbivory varied spatially within these habitats.

Methods

We performed a three-factor experiment, with nutrient enrichment of macroalgae (+/−), habitat (coral, seagrass, and mangrove), and station (three locations along an island) as factors. We compared consumption of the coarsely branched red macroalga, *Acanthophora spicifera* , cultured in ambient or enriched (N + P) seawater, then placed (along with a paired caged sample to account for growth) at three stations in each of the three habitats.

This research was conducted at Cayos Cochinos Natural Monument, approximately 15 km from mainland Honduras, within the Bay Islands, in the Caribbean Sea (Fig. 1). The 460-km^2 marine reserve encompasses the Cayos Cochinos Archipelago, which includes two forested islands (Cochino Grande and Cochino Pequeño) and 12 sand cays. A field station operated by the Honduras Coral Reef Fund (HCRF) is located on the south end of Cochino Pequeño. One modest (10 rooms) commercial hotel/diving facility is located on the southwest side of Cochino Grande in addition to a few scattered vacation homes on the west and north coasts. Otherwise, the archipelago is inhabited only by three small villages of Garifuna, descendants of shipwrecked/escaped slaves from Africa, who intermarried with native Arawak and Carib islanders beginning in the mid-1600s (Gonzalez 1988). The Garifuna practice subsistence fishing, but no other private or commercial fishing is permitted within the reserve (Adoni Cubas, HCRF, personal communication), a policy strictly enforced by park rangers based at the field station (personal observations).

With its distance from the mainland, sparse population, and protection from fishing, the reserve presented a relatively pristine environment in which we could manipulate algal nutrient levels and study natural responses of herbivores. This research was conducted on the east side of Cochino Grande (Fig. 1) within three contiguous stands (>10 m long) of red mangrove (*Rhizophora mangle*), adjacent seagrass beds (*Thalassia testudinum*), and a fringing coral reef slope in which we deployed the experiment (stations 1, 2, and 3 from N to S; Fig. 2a). Station 3 was 20 m north of a Garifuna village of ~80 people (Adoni Cubas, personal communication).

On February 29, 2000, we collected *Acanthophora spicifera* from a backreef rubble/lagoonal area ~100 m north of station 1 in ~3-m-deep water. *A. spicifera* was chosen because it stores both N and P in response to enhanced nutrient supply (Fong et al. 2001, Fong et al. 2003) and is a preferred species for herbivorous fishes (Taylor et al. 1986), specifically for surgeonfishes and parrotfishes (Lewis 1985; Stimson et al. 2001). Algae were sorted in seawater to remove epiphytes, epizoa, and

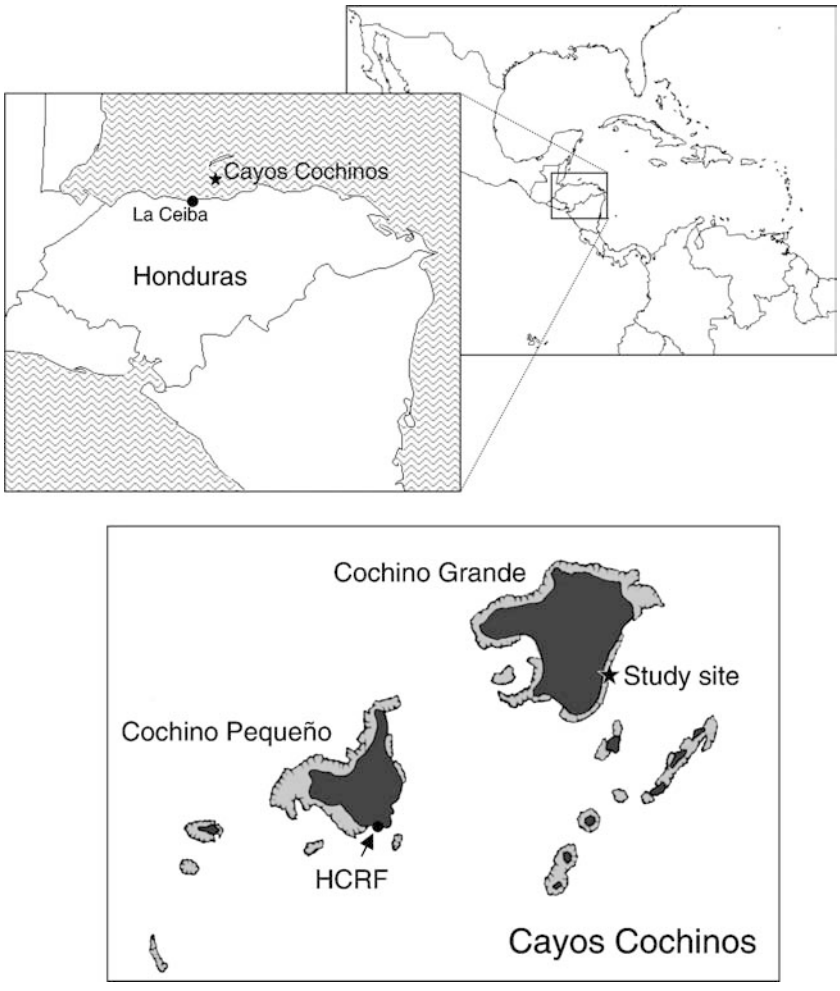

Fig. 1 Study location in the Cayos Cochinos Archipeligo, Bay Islands, Honduras (15°58′76″ N, 86°28′67″ W). The Honduras Coral Reef Fund's field station is located on the south side of Cochino Pequeño. *Darker coloring* indicates islands, with *lighter fringe* demarcating shallow reef environments

other debris and then placed in outdoor batch culture for 3 days, in ambient seawater either with or without added nutrients (20 μm N and 2 μm P). This level of nutrient enrichment was sufficient to increase tissue N and P content of *A. spicifera* in cultures from Puerto Rico (Fong et al. 2003). A second dose of N and P was added to the enriched tank after 24 h. After 3 days, tissues in enriched algae increased by 8% in both N (0.73–0.79% dry mass) and P (0.040–0.043% dry mass); methods of analysis are described below.

Algae were spun (~30 g at a time) for 1 min in a lettuce spinner to remove excess water, then divided into 5-g portions and bound together with a small cable tie (Fig. 2b). Half of the 5-g units from each nutrient treatment were attached to 15-cm segments of polypropylene rope while the other half were sewn into mesh bags (15×15 cm, flat) made from fiberglass window screening (cages) and then cable-tied to a 15-cm rope.

All 180 experimental units were labeled and placed in coolers filled with ambient or nutrient-enhanced seawater for transport to the field. Within each habitat, at each station (Fig. 2a), we laid out 5-m polypropylene ropes attached at both ends to concrete blocks. Ropes were anchored to the substratum by covering them with rock and coral fragments found at the site. In the mangrove habitat, each rope was stationed beneath the aerial roots, ~10 cm from the seaward edge in ~1-m deep water. In the seagrass habitat, each rope was placed ~5 m from the landward edge of the seagrass bed in ~1-m deep water. In the coral habitat, each rope was placed among coral and coral rubble on the reef slope in ~3-m deep water.

Experimental units were attached to the long ropes so that the algae rested on the substratum (Fig. 2b, c), permitting access to both benthic and pelagic herbivores. Four experimental units (with or without cages, with or without nutrient enrichment) were grouped in haphazard order at five replicate positions along each long rope; each group of four was separated by ~1 m of rope covered with rubble and coral to minimize visual cues. Within each group, ~8 cm separated each of the four experimental units. While ropes and cages may have attracted or inhibited grazers, algae with or without nutrient-enriched tissues provided identical visual displays and thus were considered to provide a valid assessment of relative responses of grazers to our treatments.

After 48 h, grazing in some locations had been high, but in no cases complete. Algae were removed from mesh bags and cable ties, rinsed gently in seawater, spun

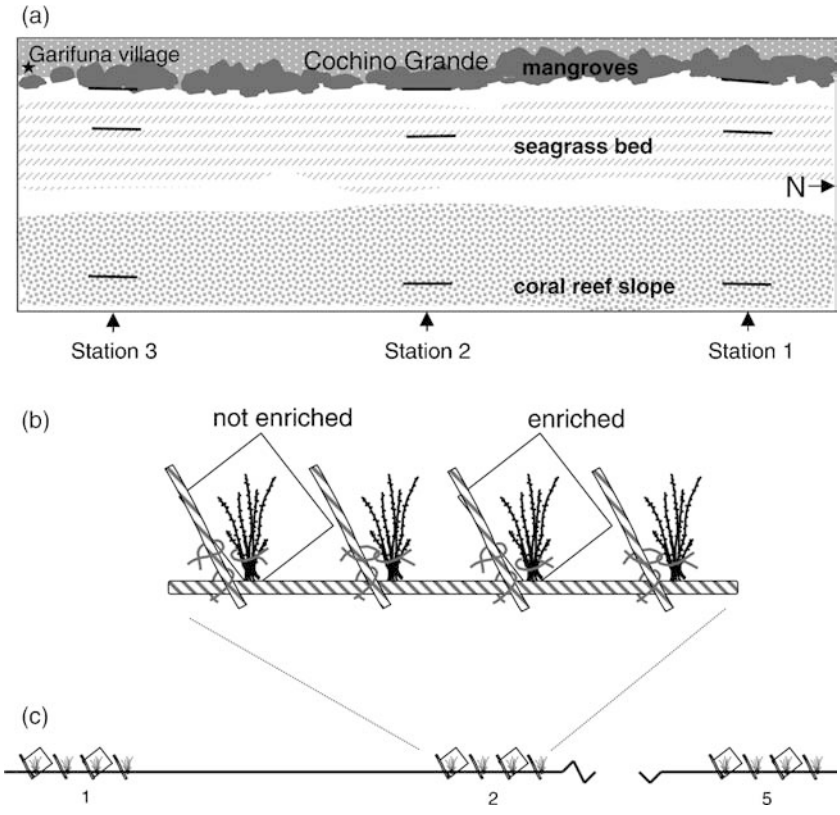

Fig. 2 **a** Experimental arrays were deployed at three stations within each of the three habitats (mangrove, seagrass, coral) along the east side of Cochino Grande. Station 3 was nearest the Garifuna village. **b** Schematic of experimental units. Assembly with cable ties is shown loosely for clarity. **c** Each group of four units was repeated in haphazard order at five replicate positions along a rope anchored to the benthos

for 1 min in nylon bags in a lettuce spinner, and then weighed. Values from caged samples were used to calculate percentage change from initial wet mass as a measure of algal growth when excluded from herbivores. We did not expect much growth due to the experimental conditions (bundled algae), but needed to account for any growth in calculating herbivory rates. Consumption of algae was quantified by subtracting the wet mass of the uncaged algae from the adjacent caged sample that had been subjected to the same nutrient treatment, and expressed as percent change from initial wet mass. While light reduction by cages (~30%) could limit growth within them, our calculations generated a conservative estimate of consumption.

Samples were rinsed in freshwater, placed in clean mesh bags, and air-dried outdoors at the field station. Samples were dried at 60 °C to a constant weight upon return to UCLA. Since uncaged samples often lacked sufficient biomass, samples from within the cages only were analyzed for total N and P content (DANR Analytical Laboratory, University of California, Davis) after grinding with a mortar and pestle. Total N was determined by N gas analyzer, using an induction furnace and thermal conductivity (Sweeney 1989). The total P analysis used microwave acid digestion dissolution (Sah and Miller 1992) with determination by atomic emission spectroscopy. Percent change from initial nutrient concentration was calculated based on the mean initial N or P content.

All data were analyzed using 3-factor ANOVA to test for differences by habitat (mangrove, seagrass, or coral), station (1, 2, or 3), nutrient treatment (enriched or not), and their interactions. A logarithmic transformation—log (x + 1)—was used to achieve homogeneity of variances on the wet mass data. Following a significant ANOVA, multiple comparisons were made using the T-method on wet mass data (equal sample size) or the Tukey-Kramer method on nutrient data (unequal sample size due to a few samples that had insufficient mass for analysis; Sokal and Rohlf 1995). All errors presented are ±1SE.

Results

As expected , *Acanthophora spicifera* in cages changed little in wet mass during the experiment, but patterns emerged by both habitat and station (Table 1). Caged algae placed in the seagrass habitat had the highest average growth (2.4%), significantly greater than in the mangroves (−0.9%) but similar to the coral habitat (1.0%). Algal growth was greatest overall at station 2 (2%), significantly greater than at station 3 (−0.6%), and intermediate at station 1 (1%). There were no significant effects of algal nutrient treatment on growth, and no significant interactions.

Consumption of *Acanthophora spicifera* differed by habitat, station, and nutrient treatment (Table 1, Fig. 3). Overall removal of algae was similar within the seagrass beds and coral reefs (means across stations = 31 and 33%, respectively); however, herbivory in both habitats was greater than in the mangrove habitat

Table 1 Statistical results of 3-factor ANOVA on % change in algal wet mass (*Growth*caged only; *Consumption* uncaged corrected for paired caged sample) and tissue N and P concentration (caged only). Error *df* = 72 for wet mass, 70 for N, and 68 for P (see methods). Results of multiple comparison tests are indicated by letters below significant *P* values (*a*lowest value); shared letters indicate no difference at $\partial = 0.05$

Source of variation	df	% change in wet mass				Nitrogen (total)				Phosphorus (total)			
		Growth		Consumption		Concentration		% change		Concentration		% change	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat	2	5.80	0.0046	17.34	0.0001	64.10	0.0001	65.04	0.0001	22.14	0.0001	22.12	0.0001
Mangrove			a		a		c		c		b		b
Seagrass			b		b		a		a		a		a
Coral			ab		b		b		b		a		a
Station	2	3.59	0.0326	3.46	0.0367	4.39	0.0160	4.44	0.0152	2.97	0.0579	2.78	0.0688
1			ab		a		a		a				
2			b		b		ab		ab				
3			a		ab		b		b				
Nutrients	1	0.37	0.5443	12.54	0.0007	2.17	0.1457	27.62	0.0001	6.72	0.0117	0.27	0.6023
−					a				b		a		
+					b				a		b		
Habitat x station	4	1.19	0.3225	0.84	0.5064	1.78	0.1421	1.84	0.1313	2.77	0.0341	2.70	0.0380
Habitat x nutrients	2	2.67	0.0760	0.85	0.4336	0.76	0.4738	1.40	0.2524	0.39	0.6777	0.57	0.5703
Station x nutrients	2	0.10	0.9094	0.76	0.4728	0.96	0.3880	1.00	0.3733	2.25	0.1137	2.07	0.1347
Habitat x station x nutrients	4	0.71	0.5866	0.67	0.6187	1.93	0.1143	1.99	0.1054	0.67	0.6185	0.61	0.6568

(15%). Algal consumption was highest overall at station 2 (33%), lowest at station 1 (22%), and intermediate at station 3 (24%).

Enhanced algal tissue nutrient concentrations resulted in highly significant increases in consumption across habitats (Table 1, Fig. 3). In the mangrove habitat, where herbivory was generally lower than in other habitats, nutrient enrichment resulted in 91% greater consumption than on non-enriched algae. In the more heavily grazed seagrass and coral habitats, nutrient enrichment increased mean algal removal by 30 and 20%, respectively. The nutrient effect on herbivory was consistent across stations in the mangrove habitat, but less so in the seagrass and coral habitats. For example, at station 2, where herbivory was the highest in both the seagrass and coral habitats, there was no effect of added nutrients on herbivory.

The final N concentration of the caged algae depended on the habitat and station into which the experimental units were placed, but was not affected by initial algal tissue enrichment (Table 1, Fig. 4a, b, c). Overall, algal samples in the mangrove habitat ended with 12 or 16% greater tissue N (0.85% dry mass) than in the coral (0.76%) and seagrass (0.73%) habitats, respectively. Samples in the coral habitat were also significantly higher in tissue N than in the seagrass habitat. Overall, algal tissue N levels ended significantly higher at station 3 (0.80%) than at station 1 (0.76%), with station 2 levels intermediate (0.78%). Tissue N concentrations became similar among nutrient treatments during the 2-day period in the field.

Samples placed in the mangrove habitat increased in N by 5–30% (mean = 12%), while those in the seagrass habitat decreased (−4%), and in the coral habitat

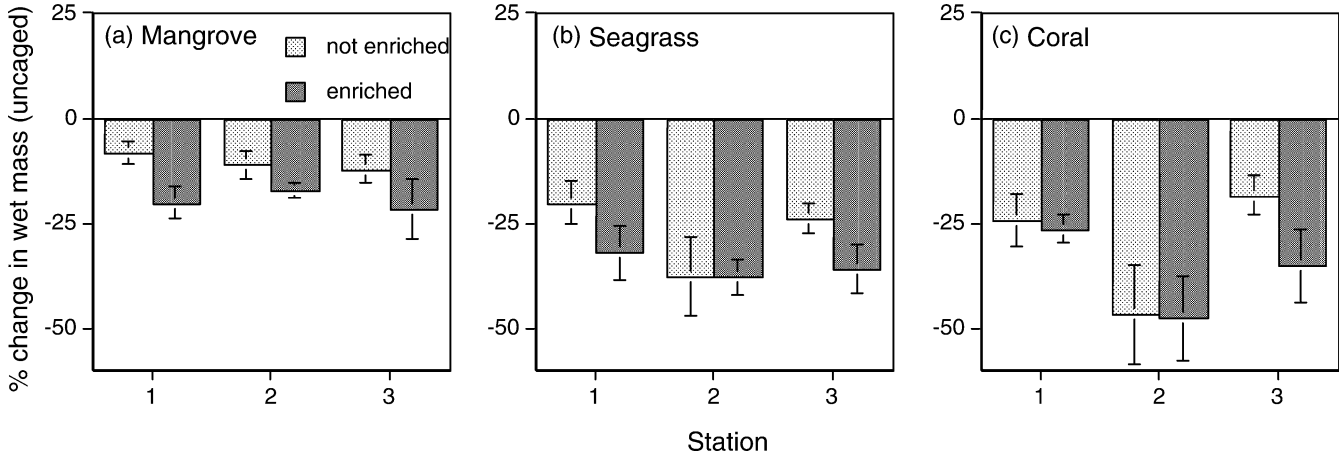

Fig. 3 Percentage change in wet mass of uncaged algae (adjusted for growth using corresponding caged sample), indicating consumption of algae enriched/not enriched with nutrients, at the three stations within the **a** mangrove, **b** seagrass, and **c** coral habitats

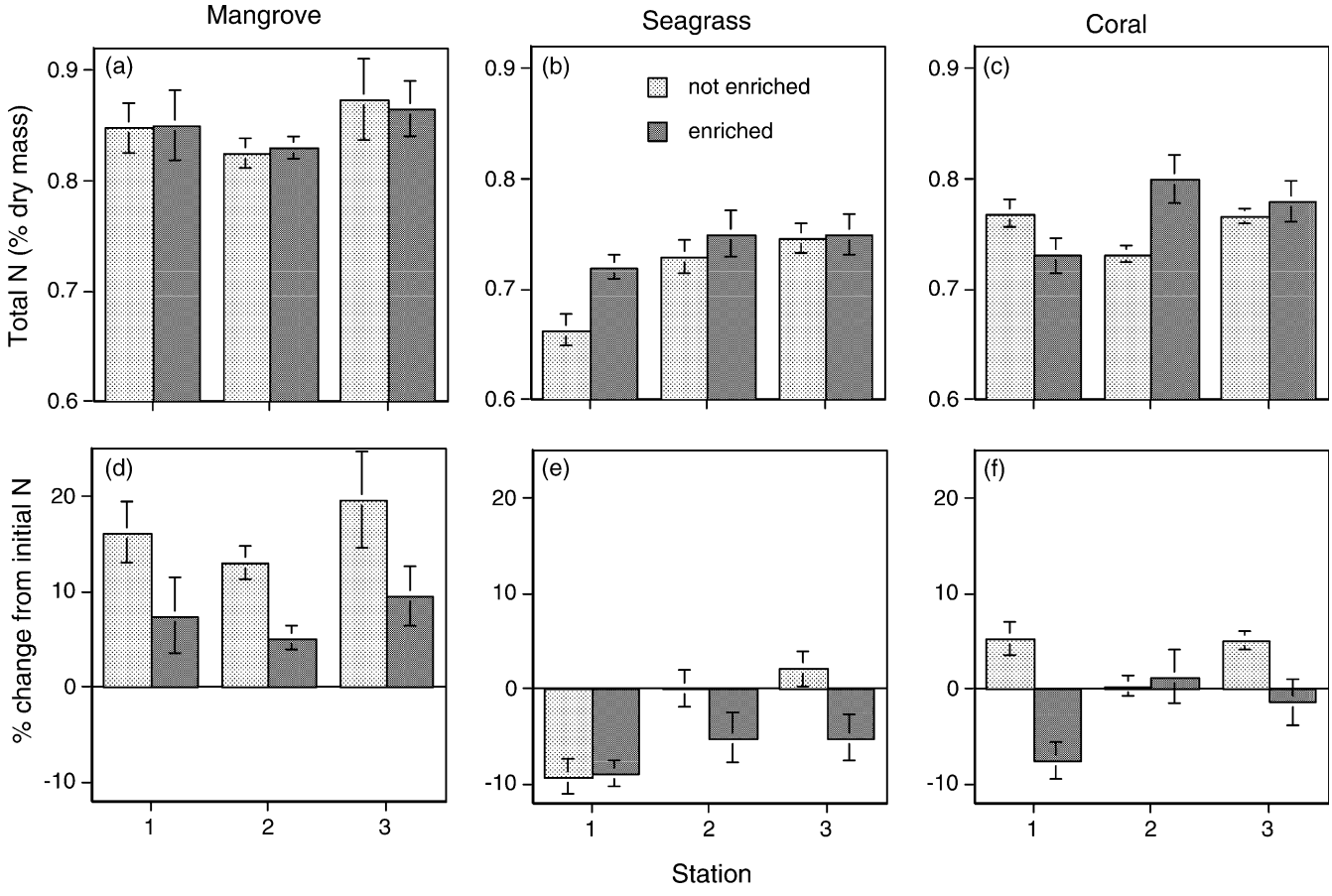

Fig. 4 Algal tissue total N (as % dry mass) and percentage change from initial mean N concentration after 2 days in the **a** and **d** mangrove, **b** and **e** seagrass, and **c** and **f** coral habitats

changed little (0.5%; Fig. 4d, e, f). On average, algal N increased by 5% at station 3, significantly more than at station 1 (0.6%) but similar to station 2 (2.5%) (Table 1). Unlike final N concentration measures, percent change in N concentration differed by nutrient treatment with more positive changes for the non-enriched treatment; this resulted in convergence in final N concentrations among nutrient treatments. In the mangrove habitat, algae from the non-enriched treatment increased in N by 15% above initial levels; however, nutrient-treated algae, which started out 8% higher in N, only gained about 7%. In the seagrass habitat, algae from both nutrient treatments declined in N, but the nutrient-enriched treatment declined more on average. In the coral habitat, algal N levels across stations increased in the non-enriched treatment, and decreased or remained the same in the enriched treatment.

Algal tissue P levels were influenced by the habitat, but not significantly by the station, into which experimental units were placed (Table 1, Fig. 5a, b, c). Final algal P in the mangrove habitat (0.05% dry mass) was 22 and 16% higher than in the seagrass (0.041%) and coral habitats (0.043%), respectively, which were similar to each other. There was a non-significant trend of higher tissue P at station 3 that was driven by high values in algae from the mangrove habitat, and it appears that the difference in pattern in the mangrove habitat versus the others caused the significant interaction between habitat and station. Unlike final tissue N measures, there was a significant effect of nutrient pre-treatment on final tissue P levels.

P concentrations of macroalgae increased by 10–30% in the mangrove habitat in 2 days, significantly more so than in the seagrass or coral habitats (Table 1, Fig. 5d, e, f). Percent change in tissue P in the seagrass (−0.4%) and coral (4%) habitats was similarly low. As with P concentration, there were no significant effects of station on percent change in tissue P, but station 3 ranked highest due to relatively high values in the mangroves. Again, it was this pattern that resulted in a significant habitat x station interaction (Table 1). Nutrient treatment did not influence percent change in tissue P.

Discussion

We found that herbivores in mangrove root, seagrass, and coral habitats could differentiate between nutrient-enhanced and untreated algae and concentrate grazing on nutrient-rich food. Through modification of algal nutrient content, we documented a linkage between bottom-up and top-down forces that may be important to community structure in shallow tropical habitats, at least on the local scale. Selection of nutrient-enriched and, potentially, faster-growing algae may be an

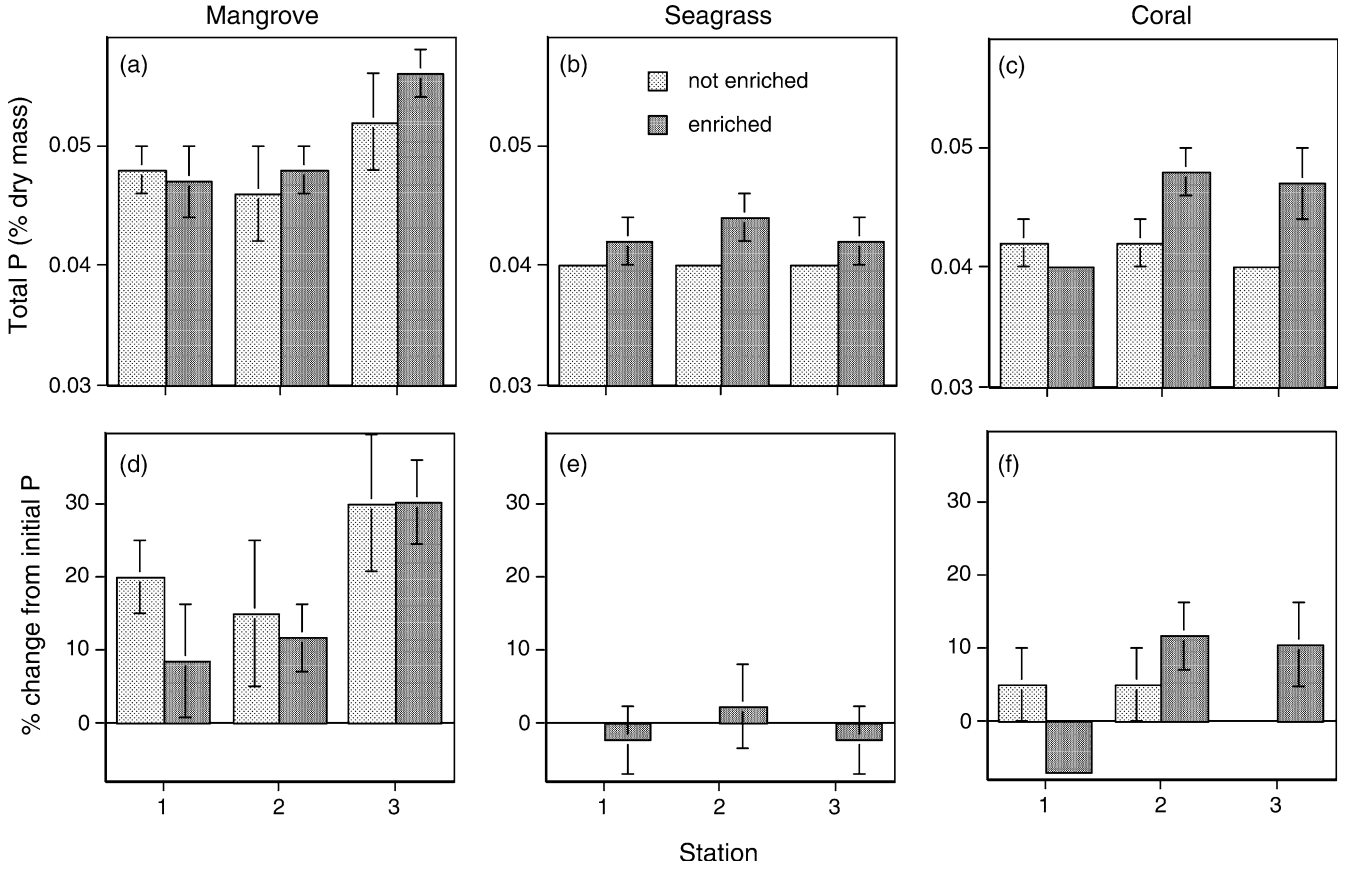

Fig. 5 Algal tissue total P and percentage change from mean initial P concentration, displayed as in Fig. 4. In panels *e* and *f*, *missing bars* indicate both mean and SE = 0

important mechanism that contributes to herbivore control of algal biomass accumulation in areas subject to nutrient enrichment.

Background differences in herbivory pressure among habitats and stations may have influenced responses of herbivores to nutrient-enhanced algae. There were higher rates of herbivory on *Acanthophora spicifera* in the coral and seagrass relative to the mangrove habitat, which may have resulted in reduced opportunity for grazers to be selective in their food choices. Similarly, in stations where herbivory rates were particularly high, the algal nutrient/herbivory relationship was less pronounced. Hence, the relationship between algal nutrient content and herbivory may be less coupled in habitats with higher herbivory pressure.

We found the mangrove herbivore guild exhibited the greatest percent response to enhanced algal nutrient concentration of the three habitats studied, suggesting either resident grazers or transient fish passing by and remaining after sampling the algae, were more selective in response to variation in food quality. Other studies found juvenile parrotfishes are the most common grazing fishes in the mangroves, with adults present in the adjacent seagrass beds (Lewis and Wainright 1985; Taylor et al. 1986). The protection from predation afforded to small grazers by mangrove roots (Austin 1971; Phillips 1981) might allow relatively more time to be devoted to selecting high quality food than in other, more exposed habitats.

Relative to coral and seagrass habitats, mangroves were a source of both N and P to the outplanted algal tissues across stations. Increased tissue nutrients in algae placed in the mangroves at station 3 suggest that the nearby Garifuna village contributes nutrients to nearshore waters. Sources probably include sewage (only ~40% of the villagers utilize pit latrines; Adoni Cubas, personal communication) and livestock wastes; both may seep through soils or flow into aquatic habitats during storms. It is less likely that the Garifuna village influenced tissue nutrients at the more distant mangrove stations. Others have found that mangrove root habitats supply higher N and P to macroalgae (including *Acanthophora spicifera*) than coral habitats, even along uninhabited islands (Lapointe et al. 1987). It is notable that algae did not grow significantly while in mangrove stations in our experiment, unlike algae at the seagrass habitat, which grew and decreased in nutrient concentrations as the result of "dilution" in greater biomass. If a delay in growth is typical after nutrient uptake within mangrove habitats (perhaps due to light or other limitations), then the time available for herbivores to respond to increased food quality may also be extended.

Our experiment simulated a short-term or pulsed nutrient input (3 days) over a small spatial scale and produced an immediate (within 2 days) increase in algal

consumption by herbivores. The herbivore guilds in all the habitats tested were capable of tracking and responding to changes in food quality that might result from pulsed or intermittent nutrient inputs. However, the effects of chronic and/or large-scale increases in nutrient supply are difficult to predict. Higher food quality should increase efficiency of transformation into herbivore biomass, such that less algal tissue needs to be consumed (e.g., Mattson 1980; Sterner and Hesson 1994). On the other hand, a sustained higher-quality food supply might lead to increases in herbivore abundance, such that continued control of algal biomass accumulation may be possible; however, such a scenario is possible only where fishing pressure is not strong enough to counter herbivore density increases.

We tested algal nutrient/herbivory relationships using a highly palatable alga, but herbivores may not respond in the same manner to nutrient enrichment of less palatable (e.g., chemically or physically defended) algae. In a pristine Hawaiian reef, calcareous algae proliferated in the presence of herbivores, probably because palatable species were preferentially removed (Smith et al. 2001). Introduction of *Acanthophora spicifera* to Kaneohe Bay, Hawaii, is hypothesized to have led to the steady gain of the less palatable alga *Dictyosphaeria cavernosa* on coral reefs (Stimson et al. 2001). Thus, the importance of herbivore detection and consumption of nutrient-enriched algae in control of algal biomass in tropical waters will likely vary not only within and among habitats, but with the composition of both the algal and herbivore assemblages present at any one site.

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