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Nutrient and growth dynamics of *Halimeda tuna* on Conch Reef, Florida Keys: Possible influence of internal tides on nutrient status and physiology

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Abstract

We conducted a manipulative nutrient enrichment study to examine the physiological and growth dynamics of the common tropical reef alga *Halimeda tuna* from shallow and deep coral reef environments on Conch Reef, in the Florida Keys. Paradoxically, *H. tuna* exhibited higher growth rates at depth (low light and below saturating irradiances) than at shallow sites (high light and at or above saturating irradiances). We hypothesized that the differences in growth rates were caused by differing nutrient environments at the two sites potentially caused by the influence of internal tidal bores that elevate nutrient concentrations with depth on Conch Reef. We tested this hypothesis by manipulating nutrients in a 10-d field experiment, after which we assessed growth, photosynthetic pigments, tissue nutrients, and other physiological parameters. *H. tuna* from the shallow back reef site exhibited nutrient limitation, as indicated by increases in growth rates, pigmentation, tissue nutrients, segment size, and photosynthetic rates, after enrichment. At the deep site, growth rates were not significantly different between controls and nutrient-enriched algae. Shallow enriched samples achieved levels of growth that were not significantly different from deep control or enriched samples. Algae from the deep site responded positively to enrichment for some physiological parameters; this suggests an opportunistic strategy in an environment that is known to experience frequent and significant pulses of nutrients from internal tides. Our results document differential nutrient limitation for *H. tuna* from two sites on Conch Reef where, in general, algae from the shallow site were more nutrient limited than those from the deep site. Finally, this provides some evidence that tropical reef communities may be adapted to large-scale physical processes such as internal tides.

Reef algae are an important component of many tropical marine ecosystems, including coral reefs, where their productivity can sustain higher trophic levels and their morphological diversity provides habitat and shelter for a number of fish and invertebrate species. Reef-building corals are generally considered to be the dominant components of healthy or pristine coral reefs, but inconspicuous turfs and encrusting coralline algae contribute substantially to reef primary production in these areas (Odum and Odum 1955; Hatcher 1997). The abundance of large frondose macroalgae is typically inversely related to coral abundance; macroalgae are common on reef flat, back reef, and inshore fringing reef areas, whereas corals are more common on reef slopes. Herbivorous grazing of algae on the reef crest and slope and higher levels of nutrients found near shore in association with terrestrial influence may drive these generalized differences in community structure (Odum and Odum 1955; Littler and Littler 1984; McCook 1996; Szmant and Forester 1996). However, the relative importance of top-down and bottom-up factors in structuring marine communities can also depend on many other factors acting alone or interactively, such as resource availability, competitive interactions, physical disturbance, and past history, all of which may vary widely within or among reefs (Hughes and Connell 1999; McCook 1999, 2001; McCook et al. 2001).

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Phase shifts from coral to algal dominance and large-scale algal blooms on tropical reefs have become increasingly common over the past several decades (Hughes et al. 1999; McCook 1999). Understanding the underlying mechanisms that drive shifts from coral to algal dominance is an active area of research across a wide range of geographic locales, including Hawaii (Smith et al. 2001, 2002; Stimson et al. 2001), Guam (Thacker et al. 2001), Florida (Szmant and Forrester 1996; Lapointe 1997; Miller et al. 1999; Lerman and Biber 2000), many Caribbean Islands (Littler and Littler 1984; Littler et al. 1991; Hughes 1994; Hughes and Connell 1999; Aronson and Precht 2000; Williams and Polunin 2001), and Australia (Hatcher and Larkum 1983; Bell 1992; McCook 1999, 2001). The results of these studies have been mixed—some have shown strong nutrient effects, others have shown strong herbivore effects, and others have documented interactive effects between both factors. This variability suggests that (1) these studies are not comparable because of various artifacts of the experimental design (e.g., the duration of experiments and levels of nutrient enrichment vary widely among studies) and/or (2) that factors that influence algal abundance on reefs can vary significantly between or within geographic locations. Longer-term studies with consistent enrichment and herbivore exclusion protocols are needed to clarify these differences.

Although determining community-level responses to elevated nutrients and reduced herbivory is appealing, studies that address these issues on a species-by-species basis may be more informative. In many cases, algal blooms on coral reefs are dominated by a single species or species complex, which suggests that these organisms may possess novel physiological characteristics that allow them to out-compete other members in the benthic community. Numerous studies have documented the effects of nitrogen and phosphorous concentrations on the growth and physiology of individual macroalgal species (Smith 1984; Fong et al. 2001). Larned (1998) demonstrated that several species of algae from Kane'ohe Bay, Hawaii, differed in nutrient requirements and limitations. After simultaneous experimental incubations in aquaria, certain species of red, brown, and green algae showed nitrogen limitation, whereas a single green alga showed phosphorous limitation; growth rates among species were highly variable. Other researchers have demonstrated that photosynthetic responses to nutrient enrichment vary among species (Delgado and Lapointe 1994; Lapointe 1997; Schaffelke and Klumpp 1998*a*,*b*). Still others have documented differences among species in growth, uptake rates, tissue nitrogen levels, and phosphorous ratios after enrichment (Haines and Wheeler 1978; Rosenberg and Probyn 1984; Fujita 1985; Littler et al. 1988). Thus, it is clear that species can differ widely in their response to elevated nutrient levels, thereby precluding any predictable or universal single response to nutrient enrichment by all algae. Some algal species (fast-growing, opportunistic species) will therefore be more informative than others of nutrient enrichment and may be able to serve as potential indicator species (Umezawa et al. 2002).

Although coral reefs are generally considered to be oligotrophic, many recent studies have shown that the waters surrounding some reefs are markedly more dynamic where upwelling events, internal tides, and tidal bores may periodically deliver pulses of cool, nutrient-rich water into the reef environment (Andrews and Gentien 1982; Wolanski and Hamner 1988; Rougerie et al. 1992; Wolankski and Delesalle 1993; Szmant and Forrester 1996; Furnas and Mitchell 1996; Leichter et al. 1996, 1998, 2003; Leichter and Miller 1999). The effects of upwelling events on the productivity and physiology of marine macrophytes (Zimmerman and Kremer 1984; Fujita et al. 1985, 1989; Kiirikki and Blomster 1996) and phytoplankton (Maranon and Fernandez 1995; Kudela et al. 1997) in temperate regions have been extensively studied. However, few researchers have documented community or species responses to these events on tropical reefs. Some studies have shown changes in planktonic communities (Wolanski and Hammner 1988; Pineda 1994; Leichter et al. 1998) and coral growth (Glynn 1977) on reefs in association with these internal wave events; others have speculated the influence of these events on benthic algal communities (Wolanski et al. 1988; Ormond and Banaimoon 1994). Recently, Leichter et al. (2003) documented differences in tissue nutrient concentrations along a depth gradient for *Codium isthmocladum* on Conch Reef in the Florida Keys, which suggested that the alga was responding to an offshore nutrient source.

Some studies have shown a rapid uptake response by tropical algae when they are exposed to short-duration pulses of enhanced nutrients in controlled experiments (Lapointe 1985; Schaffelke and Klumpp 1998*a*,*b*; Schaffelke 1999). After uptake, some species store excess nutrients, whereas others have limited storage capacity (e.g., *Ulva* spp.) because of their higher growth rates (Larned 1998). The success of many tropical algae in offshore environments may be tied to their ability to exploit transient nutrient sources associated with upwelling, internal tides or tidal bores. Wolanski et al. (1988) demonstrated that tidal jets and localized upwelling events in the northern Great Barrier Reef appear to provide the nutrients necessary to support extensive deep ($>$30 m) meadows of the calcified green alga *Halimeda.* Sediment cores in this area also determined that tidally driven upwelling events might have provided the physical conditions necessary for *Halimeda* growth in this area for much of the Holocene period.

The goals of the present study were to determine whether changes in growth and a suite of physiological characteristics of a common reef alga, *Halimeda tuna,* could be detected from two sites representing a depth and nutrient gradient (generated by internal tides) on Conch Reef in the Florida Keys (Leichter et al. 1996, 2003). Internal tides and associated nutrient pulses increase in frequency and magnitude with increasing depth on Conch Reef and Leichter and Miller (1999) further suggested that return times for these events are much greater (orders of magnitude) at 33 m on the reef slope than in the shallower 7-m back-reef environments. High nitrate and soluble reactive phosphorous (SRP) levels have been documented in conjunction with internal tides, and nutrient levels appear to be somewhat negatively correlated with temperature (Leichter et al. 2003). Although there are limited data linking elevated nutrient levels and internal tides with the benthic biological community, it

seems clear that these physical events are likely an important source of externally derived nutrients on this reef.

Work conducted by Vroom et al. (2003) demonstrated a marked difference in the stature and growth rates of *H. tuna* individuals at two sites along a depth gradient on Conch Reef. Somewhat paradoxically, deeper samples typically exhibit larger sizes and higher growth rates. Additionally, Beach et al. (2003) documented highly variable photosynthetic rates for *H. tuna* at these same locations and did not find differences between shallow and deep populations, despite differences in irradiance. On the basis of these findings, we hypothesized that the apparent differences and variability in growth and physiology arise from differing nutrient regimes at these sites. If nutrient pulses from internal tidal bores are more frequent at depth on Conch Reef (Leichter et al. 2003), perhaps these patterns would be reflected in common benthic macroalgae. A nutrient enrichment study was conducted to determine the possible effects of enrichment events on the ecophysiology of *H. tuna.* Because we were not able to coordinate data capture with an actual internal tide event, nutrient levels were manipulated by performing a short-term in situ enrichment experiment. Growth and physiological parameters were expected to exhibit larger nutrient effects at the shallow site, whereas samples from the deep site were expected to show some evidence of alleviated nutrient stress.

Materials and methods

Experimental design and site description—A randomized factorial block design was used to study the effects of nutrient enrichment, alizarin red-s (as a growth indicator), and site (depth) on the growth, physiology, and morphology of *H. tuna* in the Florida Keys National Marine Sanctuary, on Conch Reef, Key Largo, Florida. Two sites were selected that represented two different depths to allow for physiological and growth comparisons between locations: Pinnacle (PIN), ~21 m depth, and Shallow Conch (SC), ~7 m depth. The PIN site (24°56′870″N, 80°27′276″W) is a gradually sloping spur and groove community to the west with a steep ledge dropping quickly to 35 m depth to the east. The SC site (24°57′047″N, 80°27′657″W) is ~700 m to the west-northwest of the PIN site and is a level back-reef community (Fig. 1).

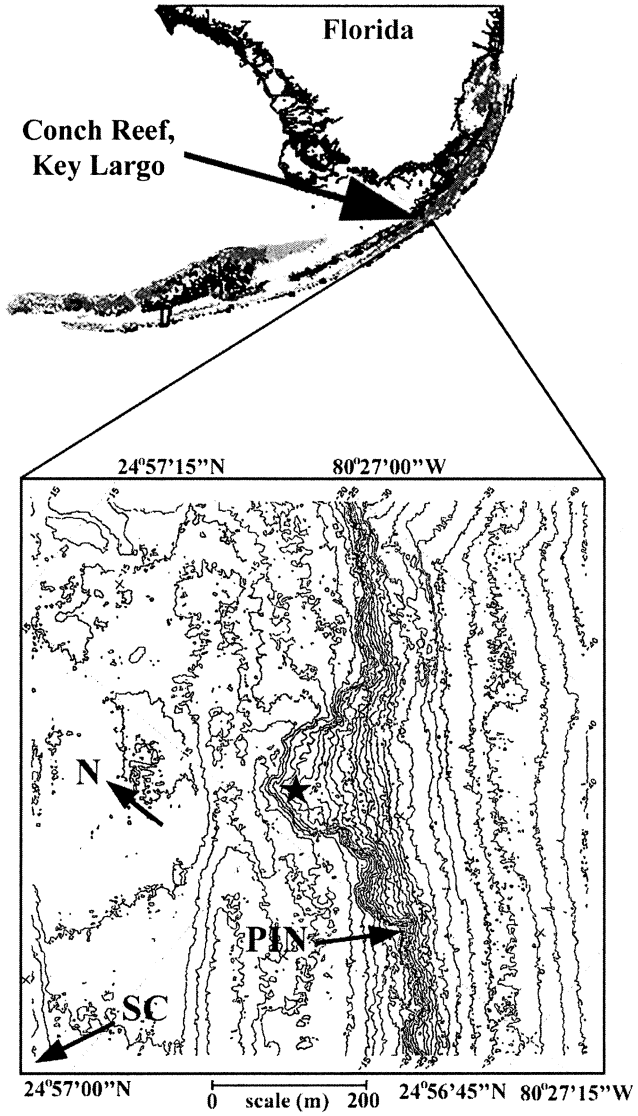

Fig. 1. Map of southern Florida and the Florida Keys, highlighting the research-only Conch Reef area. Detail: Bathymetric map of research area showing the topographic complexity associated with the PIN vs. the SC site; N, north; star, location of the Aquarius underwater research facility.

At each site, a total of 15 blocks were established. Each block was ~25 m^2 in size and was divided into four 2.5 × 2.5 m subplots. Within each subplot, one *H. tuna* sample was haphazardly selected, marked, and numbered with colored surveyors tape. Treatments (nutrient enrichment and alizarin red-s; *see below*) were then randomly and independently assigned to subplots within each block. Samples in each subplot were separated by at least 3 m, and adjacent blocks were separated by 5 m.

Physical parameters—Temperature was recorded throughout the duration of the experiment ~300 m away from the PIN site, at the Aquarius underwater research laboratory (20 m depth) using an S4 current and conductivity-temperature-depth meter (Inter Ocean). Temperature was recorded from 10 August to 7 September 2000 every 60 s. Instantaneous photosynthetically active radiation (PAR) was recorded (every 15 s) at both sites from 5 to 10 September with LI-COR 4 pi spherical quantum sensors and LI-COR LI-1400 data loggers in underwater housings. Each unit was attached to the substratum with the sensor sitting ~0.25 m off of the benthos.

Nutrient enrichment and quantification—The nutrient-enrichment treatment was accomplished by placing a 5-cm fertilizer spike (13 : 4 : 5 N : P : K; Jobes Inc.; Miller et al. 1999) inside a 6 cm long × 1.5 cm diameter piece of PVC tubing. Tubes were perforated by drilling 15 5-mm holes, dispersed evenly to allow the release of fertilizer. Tubes were closed off at the ends with duct tape and then loosely tied with cable directly onto the basal portion of *H. tuna* individuals.

SCUBA divers collected water samples every 3 d throughout the experiment, beginning ~1 h after initial deployment. Samples were obtained on a transect moving away from the enrichment source at four distances (0, 0.25, 1, and 5 m) in replicates of three at each site on each sampling date. Ambient water samples were collected on each sampling date ~10 m from the experimental area. Samples were collected using sterile 140-ml syringes. Before collection, each sample was rinsed through syringes three times. Samples were then returned to the surface, where three 20-ml aliquots were filtered through Whatman 2 GF/F glass-fiber filters and rinsed into 60-ml Nalgene sample bottles. Finally, the remaining 60 ml of sample was filtered into sample bottles and placed immediately on ice. All samples were frozen on return to shore. Nutrient concentrations were determined using an Alpkem autoanalyzer for nitrate, nitrite, ammonium, and phosphate. Differences among sites, distances, and times were examined for all nutrients analyzed, to determine the extent of enrichment both spatially and temporally. Total dissolved inorganic nitrogen (DIN) and SRP levels were also analyzed with site, treatment (enriched, samples taken at the base of algal samples, or ambient-both averaged across all sampling intervals), and time as factors to determine whether significant levels of enrichment occurred.

Alizarin red staining—The alizarin staining treatment was accomplished by placing a 1-ml aliquot of a 1% (w/v) solution of alizarin red-s dye into a 1.5-ml Eppendorf tube, according to the method of Vroom et al. (2003). One tube was placed into a 4-liter plastic bag that was then filled with seawater by SCUBA divers and affixed around the base of each alga using rubber bands. Once bags were stable, the Eppendorf tubes were opened, and the stain was moved throughout the bag by gently massaging the contents. Bags were left in situ for 24 h and were then removed by divers. Immediately after the removal of bags, the nutrient treatments were deployed on appropriate algal samples. Because the effects of alizarin red-s stain on *H. tuna* growth have been shown to be negligible and are presented elsewhere (Vroom et al. 2003), only data from alizarin and alizarin plus nutrient–enriched treatments will be presented here.

In-laboratory measurements—All algae that were stained were left undisturbed in situ for the duration of the experiment. On day 10, algal samples were harvested, placed in separate labeled plastic bags, and returned to the laboratory for analysis. Samples were placed in a 4% bleach solution for 10 min, to remove natural pigmentation. Any new growth was excised from each algal sample, and the numbers of new and old segments were counted. Algal material was weighed wet and dried at 70°C until a constant weight was achieved, then reweighed. Before drying, the dimensions of the largest newly expanded segment on each sample was determined.

Tissue nutrient analysis—After completion of the experiment, five algal samples were randomly selected from each site and treatment combination for tissue nitrogen and phosphorous measurement. Algae were rinsed briefly in freshwater, dried to a constant weight at 70°C, decalcified using a 5% HCl solution, rinsed in fresh water again, and dried at 70°C until a constant weight was reached. Carbon, nitrogen, and phosphorus content were determined using standard methods and a Perkin-Elmer 6500 ICP spectrophotometer at the University of Hawaii Diagnostic Services Center.

Photosynthetic pigment analysis—Photosynthetic pigments were quantified for algae that were not stained from 12 randomly selected blocks within each treatment and site combination. To minimize any bias associated with the deposition of inorganic carbon and the weight of algal tissue, only recently expanded segments that were not completely calcified were used for pigment extraction. These new segments were also expected to show the most significant treatment effects, because they were produced during the experimental interval. Between 0.05 and 0.10 g of tissue was removed from each algal sample. Chlorophyll *a* and total carotenoid concentrations were determined spectrophotometrically using N,N-dimethylformamide extraction (Moran and Porath 1980). Calculations of Chl *a* and *b* concentrations were based on the extinction coefficients of Porra et al. (1989). An estimate of the relative carotenoid content was determined by the use of equations suggested by Henley and Dunton (1995). All pigment values were normalized to tissue fresh weight.

Pulse amplitude–modulated florescence (PAM)—Relative photosynthetic electron transport rates (RETR), calculated from chlorophyll fluorescence parameters, were used as a relative measure to estimate the photosynthetic efficiency of *H. tuna* throughout the duration of the experiment in situ using an underwater pulse amplitude modulation device (Diving-PAM; Waltz). Rapid light curves (White and Critchley 1999) were generated for alizarin and alizarin/nutrient-treated samples within three randomly selected blocks every 3 d at approximately the same time of day for each site. Only new segments were used in generating these data, to avoid any influence that alizarin staining may have had on photosynthesis. Rapid light curves (RETR vs. actinic light) were used to estimate various fluorescence parameters: relative maximum electron transport rate ($RETR_{max}$), alpha (slope of initial rise in the light response curve), beta (slope of downturn at irradiances above saturating levels), and saturating irradiance (I_k). Different algal samples were selected on each sampling day, to avoid possible confounding effects of inhibition from previous high-irradiance exposures. All parameters were estimated from the nonlinear three-parameter model in Frenette et al. (1993). In all cases, data fitted the model well, with significant r^2 values ($r^2 > 0.995$ and $p < 0.001$, data not shown). PAR values were corrected for declining intensity as battery voltage declined.

Data analysis—Analysis of variance (ANOVA) was used to test for factor effects in all data sets. ANOVA assumptions were satisfied in all cases by evaluating homoscedasticity and performing residual analyses to confirm normal distributions of error terms. In cases where there were positive correlations between the mean and SD, data were log transformed before analysis. For analysis of proportion data sets, arc-sin square-root transformations were performed. In all

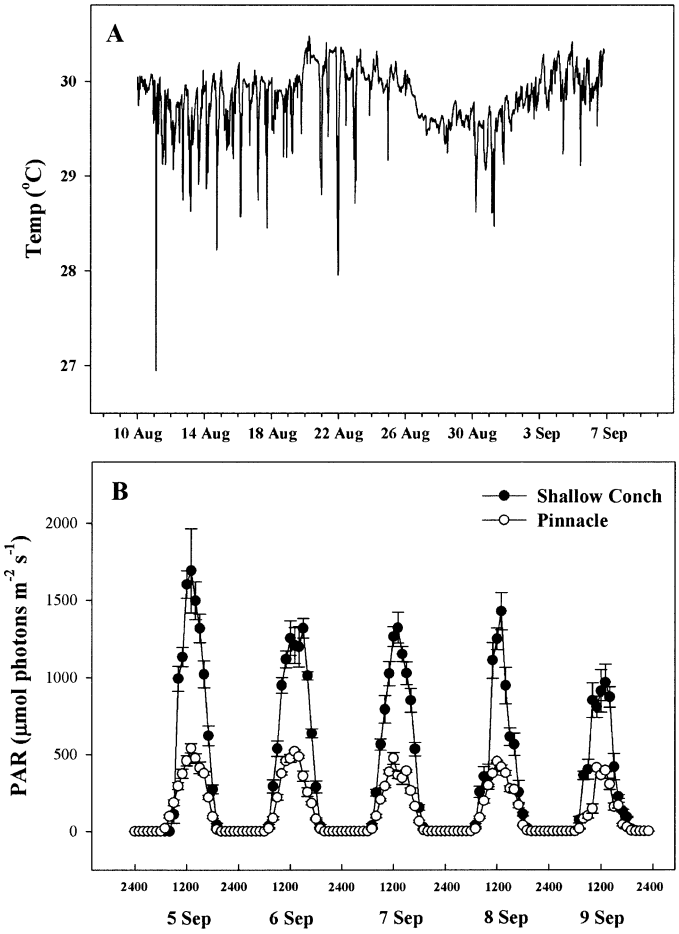

Fig. 2. (A) Temperature (°C) at the PIN site during the experimental interval. (B) PAR at both the SC and PIN sites from a 6-d interval during the experiment.

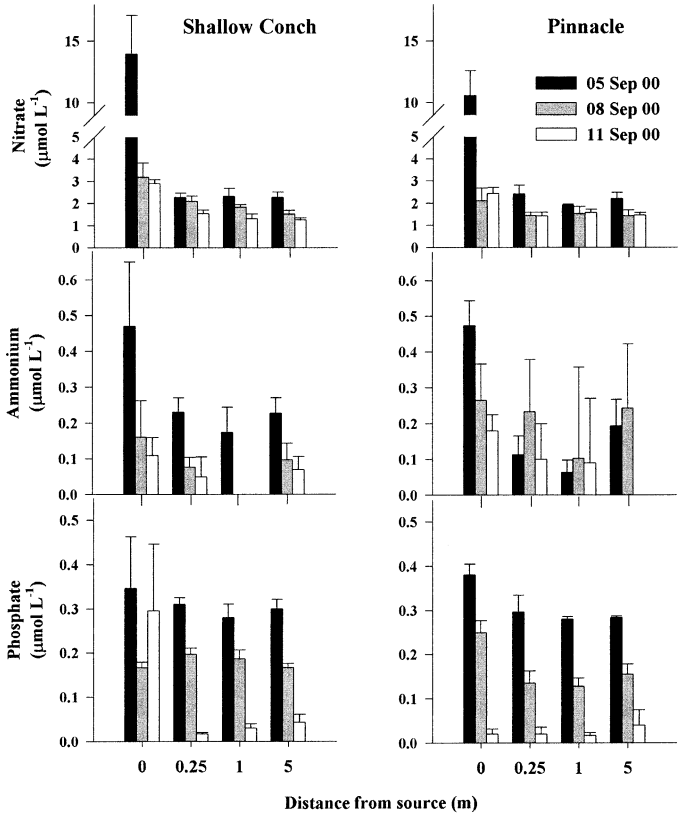

Fig. 3. Experimental nutrient enrichment results (mean ± 1 SE for nitrate, ammonium, and phosphate, $n = 3$) for water-column samples taken over a 6-d interval beginning 1 h after the deployment of treatments. Different-colored bars represent different sampling dates; distance from source refers to the distance away from the enriched alga.

tests examined, experimental factors (treatment, site, time, etc.) were treated as fixed variables, with the block factor treated as a nested, random factor. The error term was used as the denominator in all *F* tests, because there was no a priori reason to assume interactions between fixed and blocking variables. When significant interactions were detected between fixed factors, Tukey's multiple comparisons were used to determine significance among treatment combinations and main effects were assumed to be uninterpretable (model I ANOVA).

Results

Physical parameters—Seawater temperatures from 10 August to 7 September are shown in Fig. 2A. Values ranged between 25.98° and 32.09°, with a mean of 29.76° (±0.005°). Diurnal measurements of PAR were significantly greater at the SC site ($p < 0.001$) than at the PIN site (Fig. 2B). The mean PAR for daylight hours was 665.5 (±61.3) and 219.2 (±20.4) μmol quanta m^{-2} s^{-1}, with a maximum of 1691.7 and 539.2 μmol quanta m^{-2} s^{-1} for the SC and PIN sites, respectively.

Nutrient enrichment quantification—Mean ($n = 3$) concentrations of nitrate, ammonium, and phosphate at four distances from the source of enrichment on three sampling dates were variable (Fig. 3). A large pulse of enrichment is evident on day 1 for all of the nutrients analyzed. For nitrate, the large pulse (>10 μmol) quickly diminished, but concentrations remain elevated above ambient for the duration of the experiment. Concentrations of ammonium and phosphate showed a more gradual and variable decline over time and with distance from the enrichment source.

Total DIN and SRP concentrations were variable and generally showed a decrease in concentration in treatment plots over time while remaining relatively constant in control plots (Fig. 4). Total DIN concentrations for enriched plots significantly declined over time, as evidenced by the significant interaction between treatment and time ($p < 0.001$); ambient samples remained constant in concentration over time. In general, DIN concentrations for enriched samples at both sites declined over time, whereas control samples remained relatively constant. There was a significant day × site interaction for SRP concentration; concentrations steadily decreased over time at the PIN site, whereas more variability was seen at the SC site (Fig. 4, Table 1). There were no significant differences in DIN or SRP concentration in either

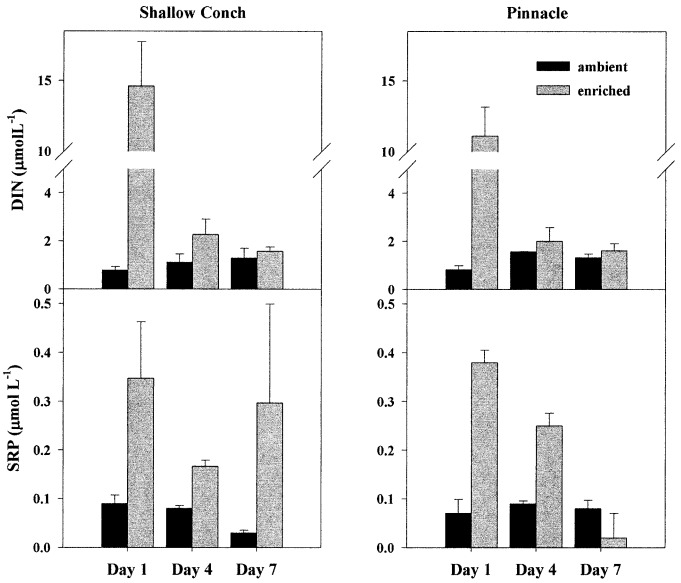

Fig. 4. DIN and SRP results (mean ± 1 SE, $n = 3$) for enriched (samples taken at the site of enrichment) and ambient (samples taken outside of the experimental area) water samples.

ambient or enriched plots between sites ($p = 0.984$ and 0.452, respectively).

Alizarin staining and nutrients—Several morphological parameters were measured to determine the physical response of *H. tuna* to elevated nutrient concentrations. Growth was estimated by quantifying newly produced biomass and the number of new segments produced during the 10-d experiment. To account for possible effects of thallus size on these variables, the relative percentage increase in both weight and segment number were also examined (Fig. 5). A significant interaction was present for the mean new dry weight produced during the experiment. Biomass production was greater for PIN individuals treated with alizarin ($p = 0.0024$) and with alizarin and nutrient ($p = 0.0042$) than for SC alizarin-treated individuals. SC alizarin and nutrient–enriched samples produced more biomass than SC samples that only received alizarin treatments ($p = 0.0028$). Overall, the largest weight gain occurred in the PIN stained samples, followed by PIN stained and nutrient-treated samples, then SC stained and nutrient-treated, and, lastly, the SC stained samples (Table 2). The mean percentage increase in dry weight biomass throughout the experiment was significantly greater for *H. tuna* at the PIN site than at the SC site ($p = 0.010$) and was greater for enriched samples than for control samples ($p = 0.025$). The mean percentage increase in biomass per day was similar for enriched samples at the SC site and the unenriched samples at the PIN site (1.248 ± 0.179 vs. 1.324 ± 0.160, respectively).

The absolute number of new segments and the percentage increase in segments per day was greater at the PIN site than at SC ($p = 0.009$ and $p < 0.001$, respectively). Again, the SC enriched samples showed a similar number of new segments produced per day as the PIN unenriched samples (3.54 ± 0.821 vs. 3.95 ± 0.768, respectively). *H. tuna* at the PIN site typically had a significantly greater number of segments per axis than samples at SC ($p = 0.043$, data not shown).

Table 1. ANOVA results for water chemistry: comparing dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) between ambient samples and enriched samples (treatment) every 3 days (time) after enrichment on day 1 between sites (SC and PIN), $n = 3$. Significance at $\alpha = 0.05$ is indicated in boldface type; Tr, treatment.

Factor	DIN		SP	
	$F_{1,1,2,1,2,2,2}$	p	$F_{1,1,2,1,2,2,2}$	p
Site	0	0.984	0.59	0.452
Treatment	48.63	**<0.001**	15.68	**0.001**
Time	10.35	**0.001**	1.44	0.257
Site × Tr	1.60	0.218	2.15	0.157
Site × time	0.15	0.861	3.59	**0.044**
Tr × time	28.86	**<0.001**	0.54	0.592
Site × Tr × time	0.36	0.699	0.48	0.625

Segment width (horizontal dimension) was significantly greater at the PIN site than at the SC site ($p = 0.007$) but did not change significantly with enrichment (Fig. 6A, Table 3). Segment length (vertical dimension) was also significantly greater at the PIN site ($p < 0.023$) and increased in response to nutrient enrichment ($p < 0.001$) at both sites (Fig. 6B, Table 3). Segment circumference was again greatest at the PIN site ($p = 0.004$) and increased in response to enrichment ($p = 0.031$, Fig. 6C, Table 3).

Nutrient enrichment generally led to increases in algal biomass, and this response was greatest at the SC site. Various parameters that measure thallus stature, including the total number of new segments, weight, and the size of new segments were greater at the PIN site than at the SC site and showed variable responses to enrichment (Figs. 5, 6).

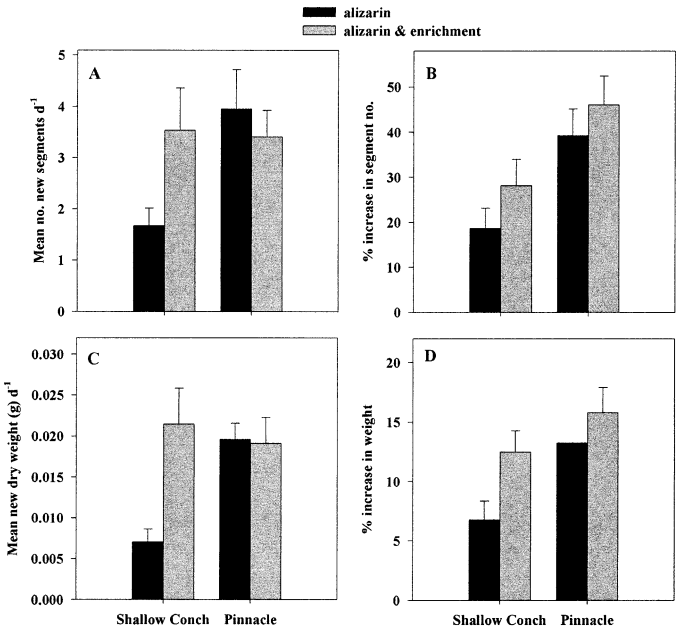

Fig. 5. Mean (± 1 SE, $n = 15$) of various morphological characteristics for *H. tuna* at SC and PIN sites in alizarin- and alizarin and nutrient–enriched treatments.

Table 2. ANOVA results for various *H. tuna* growth statistics after 10 d of exposure to treatments. $n = 15$; treatment (trt), alizarin or alizarin and nutrients; site, SC or PIN; block is nested within site. Statistically significant values are given in boldface.

	New weight		% new weight		New segments		% new segments	
Factor	$F_{1,1,1,28}$	p	$F_{1,1,1,28}$	p	$F_{1,1,1,28}$	p	$F_{1,1,1,28}$	p
Treatment	5.76	**0.025**	5.79	**0.025**	1.49	0.235	1.48	0.237
Site	7.50	**0.012**	7.91	**0.010**	7.57	**0.009**	15.37	<**0.001**
Trt × site	8.68	**0.007**	1.18	0.288	2.65	0.117	0.92	0.347
Block (site)	1.17	0.354	1.37	0.227	0.47	0.972	0.48	0.969

Tissue nutrients—Total nitrogen (TN) and total phosphorus (TP) levels were the lowest for unenriched samples at both sites (Table 4, Fig. 7). TN was significantly greater at the PIN site ($p = 0.029$), and the enrichment treatment led to significant increases in TN levels ($p = 0.004$). TP was not significantly different between sites but did increase significantly with enrichment at both sites ($p = 0.026$). Tissue TN : TP ratios for *H. tuna* were greater than water-column N : P ratios and did not differ between sites or treatments ($p = 0.829$ and 0.124, respectively).

Pigment concentrations—Quantities and ratios of photosynthetic pigments extracted from samples at the end of the experiment generally responded to enrichment and site (Fig. 8). Significant treatment effects were detected for Chl *a* ($p = 0.042$), with nutrient-enriched samples exhibiting higher concentrations than control samples (Table 5). There were no significant differences observed for treatment, site, or block in Chl *b* concentrations. Caroteniod concentration had a significant treatment × site interaction ($p = 0.032$); nutrient-enriched samples had significantly greater carotenoid concentrations than control samples, and SC enriched samples had significantly greater carotenoid concentrations than SC control samples. There was a significant site effect for Chl *a* : *b* ratios ($p = 0.009$), with the SC site having more Chl *a* per Chl *b* than the PIN site. There were no significant site or treatment effects for the ratio of Chl *a* : carotenoid.

PAM fluorescence—Data were fitted to nonlinear models using equations from Frenette et al. (1993) to estimate the parameters $RETR_{max}$, alpha, beta, and I_k; in all cases, r^2 values were >0.998, with $p < 0.01$ (data not shown). Because of the consistent significance in these models, estimates of photosynthetic parameters were used in ANOVA analysis to test for differences among sites, treatments, and days (Table 6, Fig. 9). A significant treatment × time interaction ($p = 0.039$) was detected for $RETR_{max}$. In general, photosynthetic rates were higher at the SC site than the PIN site, but these rates increased in nutrient-enriched samples at both sites over time while remaining constant for controls (Fig. 10). The measure of photosynthetic efficiency, alpha, displayed a significant treatment × site interaction ($p = 0.001$, control PIN > control SC, $p = 0.0022$). Significant site and day effects ($p = 0.050$ and 0.013, respectively) were detected for beta; *H. tuna* samples at SC had greater negative values for beta than samples at the PIN site, and beta on day 10 was greater (more negative) than on day 1 or 4 ($p = 0.0217$, 0.0255, respectively).

Discussion

Our study experimentally demonstrated differences in nutrient limitation for a common reef alga *H. tuna* from two sites along a depth gradient on Conch Reef, Florida Keys. *H. tuna* samples from the deeper PIN site were less nutrient limited than those from the shallow back reef site, as determined by higher growth rates and less of an overall response to nutrient addition (*see Table 7 for summary*). These results are counterintuitive if one assumes that algae at shallow sites that are closer to shore are more likely to be exposed to elevated nutrients associated with terrestrial runoff, sewage input, and groundwater intrusion. However, SC is a back reef habitat that is located ~3 km from shore, and long-term water quality monitoring in the vicinity has not documented sustained elevated nutrient concentrations (http://www.fiu.edu/~serp/jrpp/wqmn/wqmn.html). A more likely explanation for the observed difference in growth and physiology is the frequent presence of internal tidal bores that have been documented on Conch Reef at the PIN site, which bring cool, nutrient-rich water up onto the reef slope (Leichter et al. 2003). Because of the bathymetry associated with many of these offshore reefs, tidal bores initially interact with the deeper offshore reef slope but then quickly mix, destratify, and dissipate before reaching the shallow waters of the back reef. It has been estimated that, although an occasional bore may reach the back reef, most of these events are associated with the deeper fore-reef environments (Leichter and Miller 1999). Therefore, nutrient input and its associated effects on benthic communities are likely to be most pronounced in the deeper reef-slope areas. This dynamic nutrient environment helps to explain the long-term trends observed by Vroom et al. (2003) of higher growth rates at the PIN site and the high variability in photosynthetic parameters observed by Beach et al. (2003) for the same plant populations at SC and PIN. On tropical reefs, physical forcing functions such as internal tides are likely to influence biological patterns and processes such as those observed here and elsewhere (Beach et al. 2003; Vroom et al. 2003).

Nutrient enrichment—The nutrient enrichment methods used in our study were effective at significantly increasing inorganic nutrient concentrations above ambient levels. Concentrations of all nutrients measured decreased both with time and distance away from the nutrient source (Fig. 3). It is of interest that ambient nutrient concentrations measured here were higher than those reported from Leichter et al. (2003) from Conch Reef but were similar to those reported

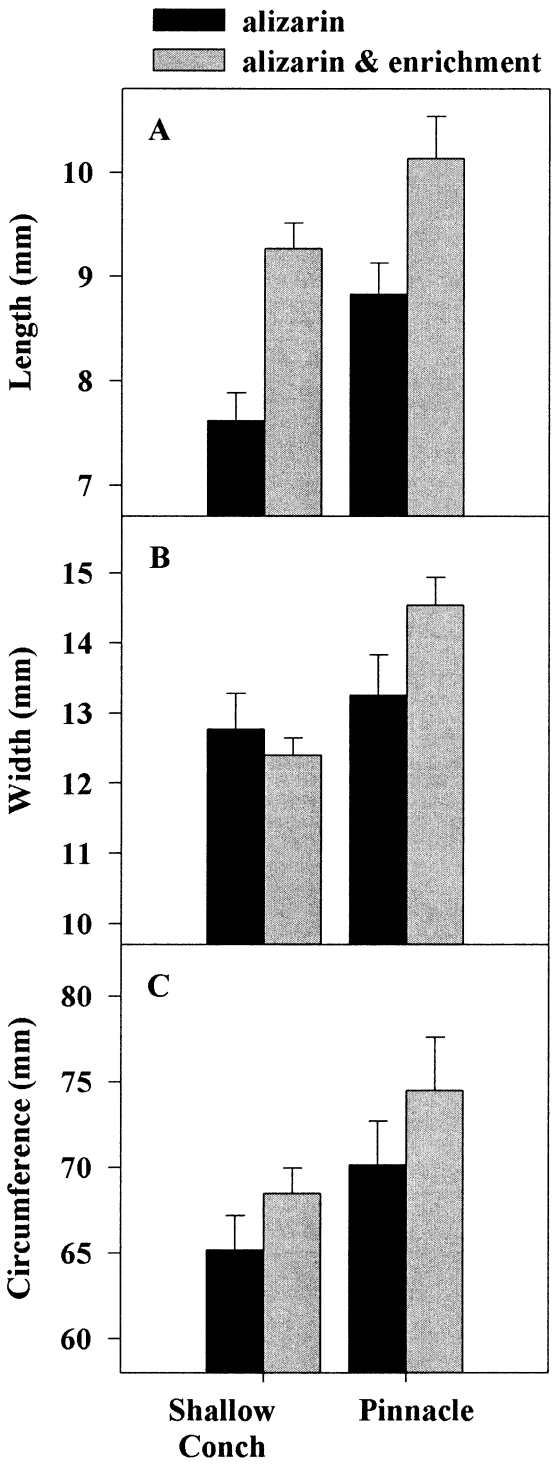

Fig. 6. Mean segment dimensions (±1 SE, $n = 15$) of *H. tuna*. (A) width, (B) length, and (C) circumference.

by Miller et al. (1999) on nearby Pickles Reef. It is unclear why DIN concentrations were high in these ambient samples, but they may have been associated with passing internal tide events. Temperatures recorded during the present study indicated that multiple small-scale upwelling events did occur. It is also possible that enrichment treatments had some effect on our ''ambient'' sampling—samples were taken only 10 m away from experimental treatments. Either way, enrichment treatments clearly increased nutrient concentrations above background levels. Nevertheless, the sampling reported here and elsewhere (Szmant and Forrester 1996; Miller et al. 1999; Umezawa et al. 2002; Leichter et al. 2003) emphasizes the dynamic nature of seawater nutrient chemistry and supports the need for more robust spatial and temporal sampling to accurately document the nutrient regime of a given location. The factors that affect variability in nutrient concentrations and delivery rates in coral reef habitats are still little known and represent an important area for future study.

Table 3. ANOVA results for *H. tuna* segment dimensions measured after the 10-d experiment ($n = 15$); treatment (trt), alizarin or alizarin and nutrients; site, SC or PIN; block is nested within site. Statistically significant values are given in boldface.

	Length		Width		Circumference	
Factor	$F_{1,1,1,28}$	p	$F_{1,1,1,28}$	p	$F_{1,1,1,28}$	p
Treatment	17.20	<**0.001**	0.49	0.492	5.30	**0.031**
Site	5.67	**0.023**	8.10	**0.007**	9.51	**0.004**
Trt × site	0.95	0.339	1.25	0.276	0.44	0.511
Block (site)	0.88	0.633	0.93	0.576	1.42	0.198

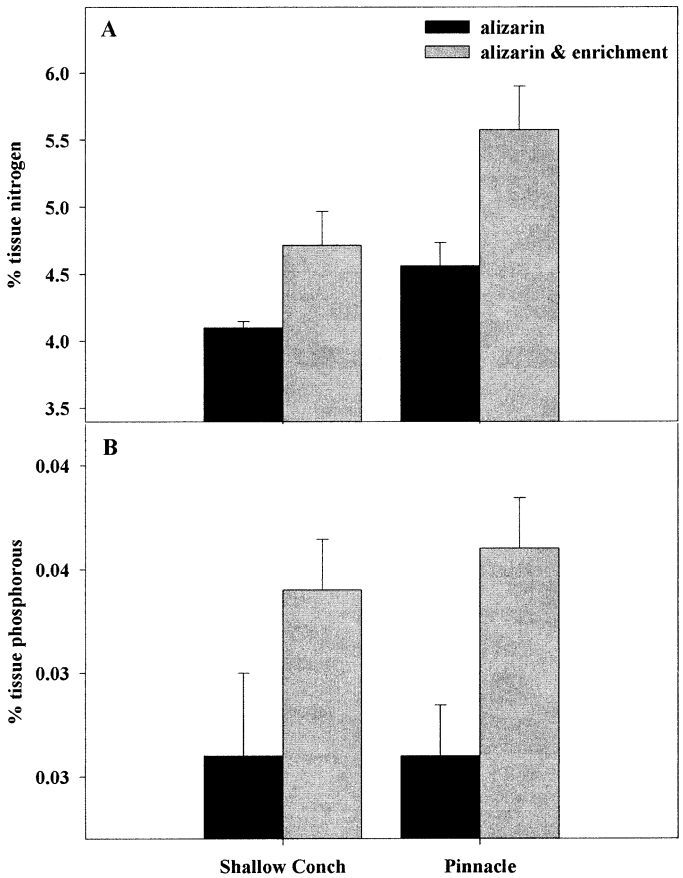

Fig. 7. Mean % tissue nutrients (±1 SE, $n = 5$). (A) nitrogen and (B) phosphorus.

Table 4. ANOVA results for % tissue nutrients after the completion of the 10-d experiment ($n = 5$; treatment (Trt), alizarin or alizarin and nutrients; site, SC or PIN. Statistically significant values are given in boldface.

	TN		TP		N : P	
Factor	$F_{1,1,1}$	p	$F_{1,1,1}$	p	$F_{1,1,1}$	p
Treatment	10.94	**0.004**	6.00	**0.026**	1.84	0.194
Site	5.77	**0.029**	0.07	0.789	0.05	0.829
Trt × site	1.01	0.329	0.07	0.789	0.18	0.678

Alizarin staining—Alizarin red-s is a biological stain that has been used to measure growth in a number of calcified organisms, including calcareous algae (Payri 1998; Vroom et al. 2003) and coral (Dodge 1984). Because the stain has been known to temporarily reduce growth rates in some organisms, we wanted to determine whether manual growth determination was a more appropriate technique to measure growth in *H. tuna*. Results found in the present study (data not presented) and by Vroom et al. (2003) suggest that alizarin produced little to no detectable effects on *H. tuna* growth.

Effects of nutrient enrichment on growth of H. tuna—For unenriched treatments, both the number of segments produced and the new dry-weight biomass for *H. tuna* was significantly greater at the PIN site than at the SC site. With the addition of nutrients, samples at the SC site responded significantly and, in most of the measurements, reached values equal to or greater than PIN unenriched samples. In terms of total dry-weight production, algal samples at the PIN site did not respond to enrichment, whereas those at the SC site did. This finding suggests that the growth of *H. tuna* was nutrient limited at the SC site but not at the PIN site. Morphometric measurements of *H. tuna* also showed interesting patterns in terms of depth and nutrient enrichment. The overall size of segments at the PIN site was larger than at SC, but, at both locations, segment size increased with nutrient addition. These findings suggest that nutrient concentrations may be related to segment size. Because of the siphonous nature of all *Halimeda* species and because members of this genus typically produce new segments rapidly during the night (Hay et al. 1988), it would seem logical that larger segments could be produced during periods of greater resource availability. Furthermore, there may be a possible adaptive advantage to producing larger segments in the presence of increased nutrient concentrations, because larger segments have a larger surface area, which thus allows for increased absorption of nutrients as well as light. Regardless of the underlying adaptive mechanism, our results suggest that changing nutrient environments can significantly influence segment size in *H. tuna.*

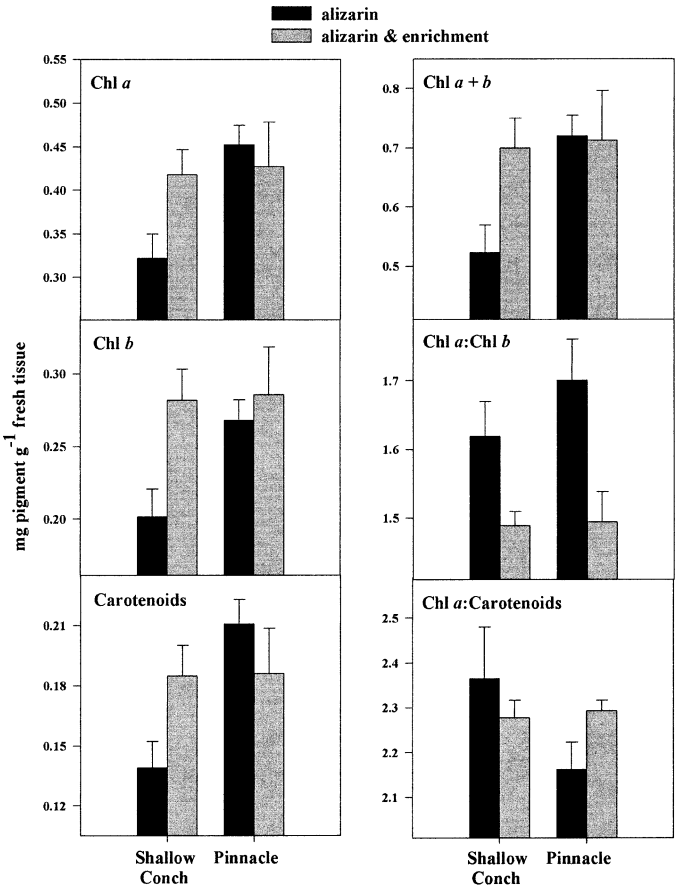

Fig. 8. Photosynthetic pigments (mean ± 1 SE, $n = 12$) and pigment ratios from *H. tuna* at the end of the experiment.

Effects of nutrient enrichment on H. tuna *physiology*—Experiments along a depth gradient present a complex and interacting series of factors, including irradiance load and day length, temperature, and episodic nutrient pulses, as well as isolating mechanisms leading to population responses. In the present study, alizarin-treated controls exhibited typical sun–shade acclimation (Falkowski and LaRoche 1991), with shallow samples having higher relative electron transport

Table 5. ANOVA results for photosynthetic pigments extracted from *H. tuna* after the 10-d experiment ($n = 12$); treatment, alizarin or alizarin and nutrients; site, SC or PIN. Statistically significant values are given in boldface.

	Chl *a*		Chl *b*		Carotenoid		Chl *a* : *b*		Chl *a* : carotenoid	
Factor	$F_{1,1,1,17}$	p	$F_{1,1,1,17}$	p	$F_{1,1,1,17}$	p	$F_{1,1,1,17}$	p	$F_{1,1,1,17}$	p
Treatment	4.83	**0.042**	3.54	0.071	5.82	**0.027**	1.57	0.227	2.28	0.149
Site	1.01	0.328	3.61	0.075	0.40	0.537	8.55	**0.009**	0.07	0.791
Trt × site	3.63	0.074	2.84	0.110	5.49	**0.032**	1.20	0.289	3.12	0.095
Block (site)	1.22	0.340	1.91	0.096	1.24	0.332	2.73	0.023	1.75	0.128

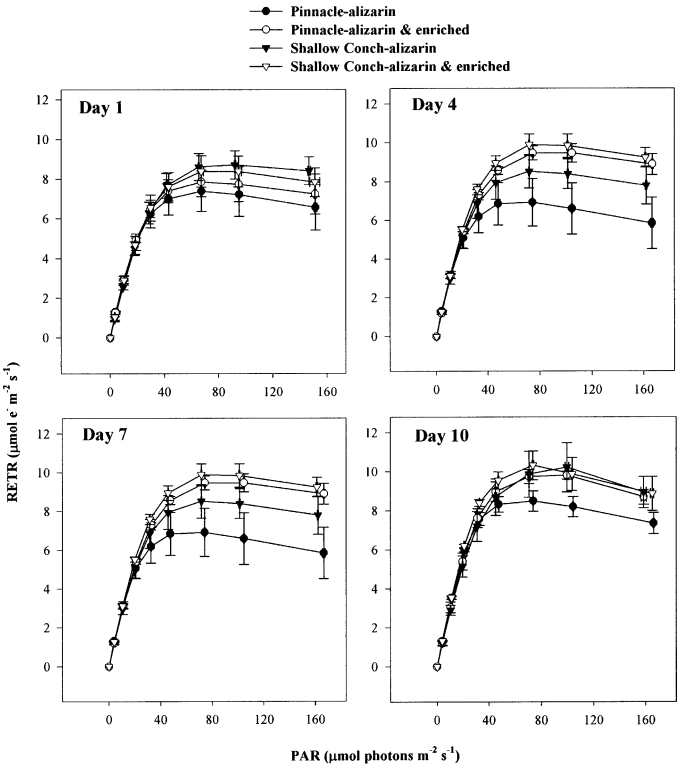

Fig. 9. Rapid light curves generated in the field using a PAM. Each curve represents the mean (±1 SE, $n = 3$) of three individually sampled *H. tuna* samples within each treatment and site combination. Curves were run on samples every 3 d during the 10-d nutrient enrichment experiment and began on day 1, immediately after enrichment.

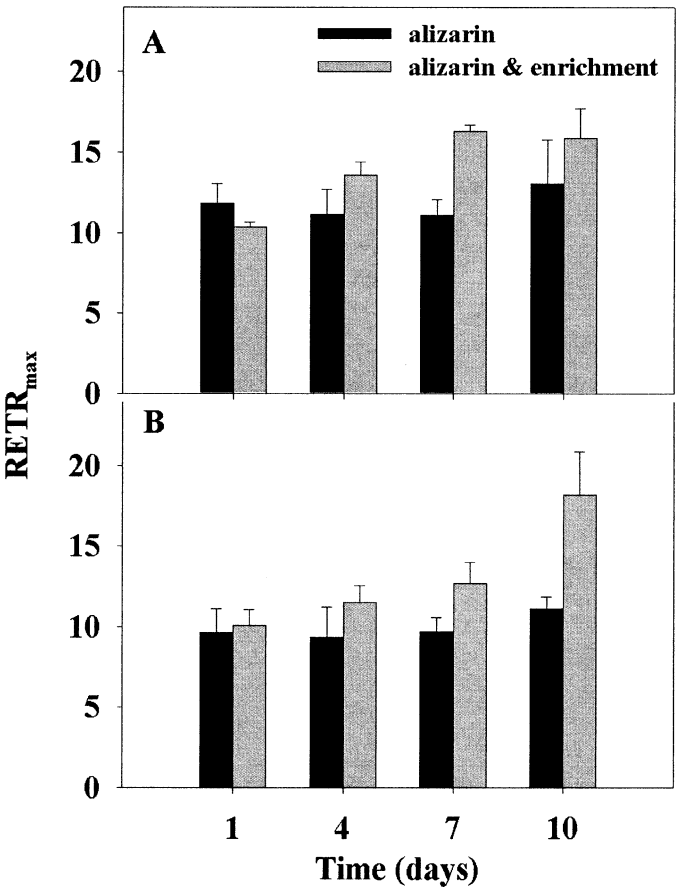

Fig. 10. Changes in $RETR_{max}$ as calculated from rapid light curves for alizarin- and alizarin and nutrient–enriched *H. tuna* samples from the SC and PIN sites over time.

rates, lower efficiency, and lower Chl *a*, *b*, and carotenoid (siphonein and siphonaxanthin) concentrations. Deeper samples however, had higher growth rates and larger stature than shallow samples. The lower net growth rates in the shallow population may be explained by several interacting factors in addition to nutrient limitation, including photoinhibition, removal of tissue by grazers, and the manipulation of algal tissue by amphipods (Vroom et al. 2003). Walters et al. (2002) and Vroom et al. (2003) showed a significant but roughly equivalent amount of grazing and amphipod habitation on *H. tuna* at both sites, which suggests that these factors are not contributing to the between-site differences in net biomass accumulation reported here.

The shallow population of *H. tuna* showed a greater decline in electron transport rates at high irradiances (beta, Fig. 9) than the deep populations; this trend became more pronounced over time. Because in situ fluorescence measurements were taken on these samples during midday, it seems likely that the shallow populations were naturally experiencing photodamage associated with higher ambient light environments (Fig. 2) and, when examined with saturating pulses from PAM fluorometer, they were less able to cope with the high actinic irradiances that are standard for this measurement. These results are possibly linked to differenc-

Table 6. ANOVA results for photosynthetic parameters estimated by PAM fluorescence every 3 d in the field ($n = 3$); treatment, alizarin or alizarin and nutrients; site, SC or PIN. Statistically significant values are given in boldface.

	$RETR_{max}$		Alpha		I_k		Beta	
Factor	$F_{1,3,1,3,1,3,3}$	p	$F_{1,3,1,3,1,3,3}$	p	$F_{1,3,1,3,1,3,3}$	p	$F_{1,3,1,3,1,3,3}$	p
Treatment	10.09	**0.003**	0.52	0.475	10.47	**0.002**	2.24	0.141
Site	5.98	**0.018**	2.50	**0.051**	8.97	**0.004**	3.95	**0.050**
Time	1.84	0.153	0.45	0.721	0.88	0.459	3.99	**0.013**
Trt × site	0.13	0.718	15.35	**0.001**	10.27	**0.002**	1.66	0.204
Trt × time	3.01	**0.039**	1.08	0.368	4.22	**0.010**	0.23	0.874
Site × time	0.48	0.701	0.62	0.603	0.39	0.757	0.24	0.865
Trt × site × time	0.84	0.481	2.07	0.116	0.49	0.691	1.38	0.259

Table 7. Summary of general patterns observed in growth and photosynthetic parameters for *H. tuna* in the study from Shallow Conch and Pinnacle, with and without nutrient enrichment. Different letters indicate significant differences in *F* tests (see ''Results''), with A and B indicating site differences and C and D treatment differences; higher letters represent greater values of the given parameter.

	Site		Treatment	
Parameter	Shallow Conch	Pinnacle	Control	Nutrient
Growth				
Number of segments	A	B	C	C
Weight	A	B	C	D
Segment size				
Length	A	B	C	D
Width	A	B	C	C
Circumference	A	B	C	D
Pigments				
Chl *a*	A	A	C	D
Chl *b*	A	A	C	C
Carotenoids	A	A	C	D
Tissue nutrients				
Nitrogen	A	B	C	D
Phosphorus	A	A	C	D
Photosynthetic parameters				
RETR	A	B	C	D
Alpha	B	A	C	C
Beta	A	B	C	C
I_k	B	A	C	D

es in photoacclimation between the populations and/or possibly nutrient stress. Photoinhibition has previously been documented in shallow populations of *H. tuna* from both the SC site (Beach et al. 2003) and the Mediterranean (Hader et al. 1996). More research is needed to understand how photoinhibition and nutrient limitation interact and the subsequent consequences to resource allocation, growth, and physiology in tropical marine algae.

Although both populations of *H. tuna* at Conch Reef did show nutrient limitation, the PIN population was less nutrient limited than the SC population, as evidenced by higher tissue nitrogen, faster overall growth rates, larger stature, and lower or no responses to enrichment (Turpin 1991). On the basis of tissue nutrient data, both populations appeared to be phosphorous limited (TP increased with enrichment at both sites). Maximum electron transport rates increased in both populations with the addition of nutrients, but there was no significant change in efficiency. Littler et al. (1988) showed a significant positive relationship between nutrient pulses and photosynthetic rates in several species of *Halimeda* and suggested that these species are adapted to take advantage of short nutrient pulses. Scheffelke (1998) also showed rapid increases in photosynthesis with the addition of nutrients in the tropical alga *Sargassum baccularia.* Clearly, some species of tropical macroalgae are able to readily use transient nutrient sources.

Relationship between Halimeda tuna *and tidal bores*—Wolanski et al. (1988) suggested that deep (30–45 m) *Halimeda* meadows at Ribbon Reef in the northern portion of the Great Barrier Reef are supported by nutrient upwelling associated with tidal jets. These researchers documented tidal jet patterns and processes in the Ribbon Reef network, including associated reduced temperatures and increased nitrate concentrations but did not make any direct links to the biology or physiology of the *Halimeda* populations that dominate the region. On the basis of estimated densities (685 g m^{-2}), rates of productivity (Drew 1983) and tissue nitrogen levels (0.24% N) (Atkinson and Smith 1983), they determined the amount of nitrogen required to support such a population. It was estimated that 0.26 μmol nitrate moving at 0.5 m s^{-1} would deliver 786 kg of N d^{-1} to the *Halimeda* banks. Tidal jets and associated upwelling events may therefore have provided the physical conditions conducive to *Halimeda* growth in this area for much of the Holocene period.

Leicther et al. (1996, 2003) documented physical conditions similar to Ribbon Reef on Conch Reef. Changes in nitrate concentration from 0.1 to 4.0 μmol (but concentrations up to 15 μmol nitrate have been reported seaward of the southern Florida Keys [Lee et al. 1994]), reduced temperatures (decreases of 5–9°C in 20 min; Leichter and Miller 1999), increased flow speed (up to 25 cm s^{-1}), and, potentially, increases in extinction coefficients correspond with the arrival of a tidal bore. Leichter et al. (1998) documented dynamic responses of the planktonic community to internal waves, but the effects of these events on benthic community structure and productivity in the tropics have remained elusive.

Because the arrival of a tidal bore is coupled with both increased nutrient concentrations and increased flow rates, nutrient flux across benthic boundary layers could be quite high and ideal for nutrient uptake by upright macroalgal species (Hurd et al. 1996; Fong et al. 2001). However, reductions in temperature also accompany these events, and re-

duced temperature often reduce metabolic rates in tropical algae; therefore, these effects may overshadow increases in photosynthesis that are associated with nutrient increases (Abel and Drew 1985). Algae may also take up and store nutrients during an upwelling event for later use. Although our data represent the first experimental evidence indirectly linking natural upwelling on a coral reef to the growth, photosynthesis, and morphology of a common tropical macroalgae clearly, more research is needed to understand the interactions of temperature, nutrient concentrations, flow, and light regimes with tropical algal physiology.

On Conch Reef, lessened nutrient limitation and higher growth rates of *H. tuna* at the PIN site imply that this location is exposed to a source of nutrients that is absent or reduced at the SC site. The delivery of nutrient rich subthermocline water to the deeper reef slope community via internal tides is likely the cause of such patterns (Leichter et al. 2003). The dramatic change in bathymetry between the SC and PIN sites (Fig. 1), coupled with the rapid mixing that occurs as these tidal bores move into shallow water, creates a gradient in temperature and nutrient concentration with depth. Furthermore, because of the high frequency of internal tides (Leichter and Miller 1999), the deeper reef slope community receives much higher nutrient flux than the SC site. Published values for nutrient concentrations associated with internal tide events in the Florida Keys are as much as 10–40-fold higher than background nutrient concentrations ranging 1.0–4.0 μmol NO_3 and 0.1–0.3 μmol for SRP (Leichter et al. 2003). Elevated levels of phytoplankton productivity have been observed in the water column in conjunction with internal tide events (Leichter et al. 1998), and tissue nutrient concentrations of deep water *C. isthmocladum* on Conch Reef also correspond to nutrient enrichment along a depth gradient (Leichter et al. 2003); our study presents the first experimental evidence of differential nutrient status for a common benthic reef organism.

A number of other recent studies have suggested that internal tide events may contribute significantly to benthic productivity in the Florida Keys. Miller et al. (1999) did not find a significant response by the algal community after a nutrient-enrichment experiment at a location ~6 km from our site. The authors offered several possible explanations for their findings. Among these was that periodic upwelling coupled with excess uptake allowed seaweeds to remain nutrient saturated for the 4 months of their study. Szmant and Forrester (1996) examined water-column and sediment nitrogen and phosphorous distribution patterns throughout the Florida Keys. They discussed a mesoscale oceanographic gyre system that could potentially deliver up to 40 times the amount of nutrient to the Florida Keys than from all anthropogenic sources combined (as identified by the US Environmental Protection Agency). Finally, Leichter et al. (2003) estimated that inputs of nitrogen and phosphorous from internal tidal bores to the Florida Keys were indeed much higher than estimates of inputs from waste and storm-water runoff. Although it is now clear that these dynamic physical events can naturally deliver nutrients onto deep reefs in the Florida Keys, more experimental research is needed on a broader spatial scale to link biological processes to the physical environment in other tropical reef systems.

The results of the present study and those of Leichter et al. (2003) underscore the extent to which nutrient dynamics on tropical reefs can be more complex than was previously thought. Future research needs to incorporate spatially and temporally rigorous nutrient sampling to fully account for these episodic pulses and other unaccounted-for nutrient sources. Many studies have documented the presence of highly productive deep-water algal communities in the tropics, but few studies have attempted to link large-scale oceanographic processes to their persistence. Biological and physiological parameters of some species of macroalgae can reflect both the short- and long-term nutrient environment on reefs (Umezawa et al. 2002) and should be used in conjunction with field-based experimentation to link physical processes to biological patterns in the tropics. Large-scale physical events, such as internal tides may be an important source of externally derived nutrients for tropical reefs and may be contributing significantly to the diversity and productivity of benthic coral reef communities.

References

ABEL, K. M., AND A. DREW. 1985. Response of *Halimeda* metabolism to various environmental parameters. Proc. Int. Coral Reef Symp. **5:** 21–26.

ANDREWS, J. C., AND P. GENTIEN. 1982. Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: A solution to Darwin's question? Mar. Ecol. Prog. Ser. **8:** 257–269.

ARONSON, R. B., AND W. F. PRECHT. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. Limnol. Oceangr. **45:** 251–255.

ATKINSON, M. J., AND S. V. SMITH. 1983. C : N : P ratios of benthic marine plants. Limnol. Oceanogr. **28:** 568–574.

BEACH, K., L. WALTERS, P. VROOM, C. SMITH, J. COYER, AND C. HUNTER. 2003. Variability in the ecophysiology of *Halimeda* spp. on Conch Reef, Florida Keys, USA. J. Phycol. **39:** 1–12.

BELL, P. R. F. 1992. Eutrophication and coral reefs: Some examples in the Great Barrier Reef lagoon. Wat. Res. **26:** 553–568.

DELGADO, O., AND B. E. LAPOINTE. 1994. Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. Coral Reefs **13:** 151–159.

DODGE, R. E. 1984. Coral calcification rates by the buoyant technique: Effects of alizarin staining. J. Exp. Mar. Biol. Ecol. **75:** 217–232.

DREW, E. A. 1983. *Halimeda* biomass, growth rates and sediment generation on reefs in the central Great Barrier Reef Province. Coral Reefs **2:** 101–110.

FALKOWSKI, P. G., AND J. LAROCHE. 1991. Acclimation to spectral irradiance in algae. J Phycol. **27:** 8–14.

FONG P., K. KAMER, AND K. E. BOYER. 2001. Nutrient content of macroalgae with differing morphologies may indicate sources of nutrients for tropical marine systems. Mar. Ecol. Prog. Ser. **220:** 137–152.

FRENETTE, J. J., S. DEMERS, L. LEGENDRE, AND J. DODSON. 1993. Lack of agreement among models for estimating the photosynthetic parameters. Limnol. Oceanogr. **38:** 679–687.

FUJITA, R. M. 1985. The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. J. Exp. Mar. Biol. Ecol. **92:** 283–301.

———, P. A. WHEELER, AND R. L. EDWARDS. 1989. Assessment of macroalgal nitrogen limitation in a seasonal upwelling region. Mar. Ecol. Prog. Ser. **53:** 293–303.

FURNAS, M. J., AND A. W. MITCHELL. 1996. Nutrient inputs into

the central Great Barrier Reef (Australia) from subsurface intrusions of Coral Sea waters: A two-dimensional displacement model. Cont. Shelf Res. **16:** 1127–1148.

GLYNN, P. W. 1977. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. J. Mar. Res. **35:** 567–585.

HADER, D.-P., M. PORST, H. HERRMANN, J. SCHAFER, AND R. SANTAS. 1996. Photoinhibition in the green algae *Halimeda tuna* Ellis et Sol measured in situ. Photochem. Photobiol. **64:** 428-424.

HAINES, K. C., AND P. A. WHEELER. 1978. Ammonium and nitrate uptake by the marine macrophytes *Hypnea musciformis* and *Macrocystis pyrifera.* J. Phycol. **14:** 319–324.

HATCHER, B. G. 1997. Coral reef ecosystems: How much greater is the whole than the sum of the parts? Coral Reefs **16:** 77–91.

———, AND A. W. D. LARKUM. 1983. An experimental analysis of the factors controlling the standing crop of the epilithic algal community on a coral reef. J. Exp. Mar. Biol. Ecol. **69:** 61–84.

HAY M. E., V. J. PAUL, AND S. LEWIS. 1988. Can tropical seaweeds reduce herbivory by growing at night—diel patterns of growth, nitrogen-content, herbivory, and chemical versus morphological defenses. Oecologia **75:** 233–245.

HENLEY, W. J., AND K. H. DUNTON. 1995. A seasonal comparison of carbon, nitrogen and pigment content in *Laminaria solidungula* and *L. saccharina* (Laminariales, Phaeophyta) in the Alaskan Arctic. J. Phycol. **31:** 325–331.

HUGHES, T. 1994 Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. Science **265:** 1547–1551.

———, AND J. H. CONNELL. 1999. Multiple stressors on coral reefs: A long-term prospective. Limnol. Oceanogr. **44:** 932–940.

———, A. M. SZMANT, R. STENECK, R. CARPENTER, AND S. MILLER. 1999. Algal blooms on coral reefs: What are the causes? Limnol. Oceanogr. **44:** 1583–1586.

HURD, C. L., P. J. HARRISON, AND L. D. DRUEHL. 1996. Effect of seawater velocity on inorganic nitrogen uptake by morphologically distinct forms of *Macrocystis integrifolia* from wave-sheltered and exposed sites. Mar. Biol. **126:** 205–214.

KIIRIKKI, M., AND J. BLOMSTER. 1996. Wind induced upwelling as a possible explanation for mass occurrences of epiphytic *Ectocarpus siliculosus* in the northern Baltic proper. Mar. Biol. **127:** 353–358.

KUDELA, R. M., W. P. COCHLAN, AND R. C. DUGDALE. 1997. Carbon and nitrogen uptake response to light by phytoplankton during an upwelling event. J. Plankton Res. **19:** 609–630.

LAPOINTE, B. E. 1985. Strategies for pulsed nutrient supply to *Gracilaria* cultures in the Florida Keys: Interactions between concentration and frequency of nutrient pulses. J. Exp. Mar. Biol. Ecol. **93:** 211–222.

———. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms in Jamaica and southeast Florida. Limnol. Oceangr. **42:** 1119–1131.

LARNED, S. T. 1998. Nitrogen versus phosphorus limited growth and sources of nutrients for coral reef macroalgae. Mar. Biol. **132:** 409–421.

LEE, T. N., M. E. CLARKE, E. WILLIAMS, A. M. SZMANT, AND T. BERGER. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull. Mar. Sci. **54:** 621–646.

LEICHTER, J. J., AND S. L. MILLER. 1999. Predicting high-frequency upwelling: Spatial and temporal patterns of temperature anomalies on a Florida coral reef. Cont. Shel. Res. **19:** 911–928.

———, G. SHELLENBARGER, S. J. GENOVESE AND S. R. WING. 1998. Breaking internal waves on a Florida (USA) coral reef: A plankton pump at work? Mar. Ecol. Prog. Ser. **166:** 83–97.

———, H. L. STEWART, AND S. L. MILLER. 2003. Episodic nutrient transport to Florida coral reefs. Limnol. Oceanogr. **48:** 1394–1407.

———, S. R. WING, S. R. MILLER, AND M. W. DENNY. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnol. Oceanogr. **41:** 1490–1501.

LERMAN, D., AND P. BIBER. 2000. Seasonal dynamics of macroalgal communities of the northern Florida reef tract. Bot. Mar. **43:** 305–314.

LITTLER, M. M., AND D. S. LITTLER. 1984. Models of tropical reef biogenesis: The contribution of algae. Progr. Phycol. Res. **3:** 323–364.

———, ———, AND B. E. LAPOINTE. 1988. A comparison of nutrient- and light-limited photosynthesis in psammophytic versus epilithic forms of *Halimeda* from the Bahamas. Coral Reefs **6:** 219–225.

———, ———, AND E. A. TITLYANOV. 1991. Comparisons of N- and P- limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: A test of the relative-dominance paradigm. Coral Reefs **10:** 199–209.

MARANON, E., AND E. FERNANDEZ. 1995. Changes in phytoplankton ecophysiology across a coastal upwelling front. J. Plankton Res. **17:** 1999–2008.

MCCOOK, L. J. 1996. Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: Cross-shelf transplants. Mar. Ecol. Prog. Ser. **139:** 179–192.

———. 1999. Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. Coral Reefs **18:** 357–367.

———. 2001. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs **19:** 419–425.

———, J. JOMPA, AND G. DIAZ-PULIDO. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. Coral Reefs **19:** 400–417.

MILLER, M. W., M. E. HAY, S. L. MILLER, D. MALONE, E. E. SOTKA, AND A. M. SZMANT. 1999. Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. Limnol. Oceanogr. **44:** 1847–1861.

MORAN, R., AND D. PORATH. 1980. Chlorophyll determination in intact tissues using *N,N*-dimethylformamide. Plant Physiol. **65:** 478–479.

ODUM, H. T., AND E. P. ODUM. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. **25:** 291–320.

ORMOND, R. F. G., AND S. A. BANAIMOON. 1994. Ecology of intertidal macroalgal assemblages on the Hadramount coast of Southern Yemen, an area of seasonal upwelling. Mar. Ecol. Prog. Ser. **105:** 105–120.

PAYRI, C. E. 1988. *Halimeda* contribution to organic and inorganic production in a Tahitian reef system. Coral Reefs **6:** 251–262.

PINEDA, J. 1994. Internal tidal bores in the nearshore: Warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. J. Mar. Res. **52:** 427–458.

PORRA, R. J., W. A. THOMSON, AND P. E. KRIEDEMANN. 1989. Determination of accurate extinction coefficient and simultaneous equations for essaying chlorophyll a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochim. Biophys. Acta **975:** 384–394.

ROSENBERG, G., AND T. A. PROBYN. 1984. Nutrient uptake and growth kinetics in brown seaweeds: Response to continuous and single additions of ammonium. J. Exp. Mar. Biol. Ecol. **80:** 125–146.

ROUGERIE, F., J. A. FAGERSTROM, AND C. ANDRIE. 1992. Geother-

mal endo-upwelling: A solution to the reef nutrient paradox? Cont. Shelf Res. **12:** 785–798.

SCHAFFELKE, B. 1999. Short-term nutrient pulses to assess responses of coral reef macroalgae to enhanced nutrient availability. Mar. Ecol. Prog. Ser. **182:** 305–310.

———, AND D. W. KLUMPP. 1998*a*. Nutrient-limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. Mar. Ecol. Prog. Ser. **164:** 199–211.

———, AND ———. 1998*b*. Short-term nutrient pulses enhance growth and photosynthesis of the coral reef macroalga *Sargassum baccularia*. Mar. Ecol. Prog. Ser. **170:** 95–105.

SMITH, J. E., C. L. HUNTER, AND C. M. SMITH. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in Hawaii. Pac. Sci. **56:** 299–315.

———, C. M. SMITH, AND C. L. HUNTER. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs **19:** 332–342.

SMITH, S. V. 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr. **29:** 1149–1160.

STIMSON, J., S. T. LARNED, AND E. CONKLIN. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. Coral Reefs **19:** 343–357.

SZMANT, A. M., AND A. FORESTER. 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. Coral Reefs **15:** 21–41.

THACKER, R. W., D.W. GINSBURG, AND V. J. PAUL. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs **19:** 318–329.

TURPIN, D. H. 1991. Effects of inorganic N availability on algal photosynthesis and carbon metabolism. J. Phycol. **27:** 14–20.

UMEZAWA, Y., T. MIYAJIMA, M. YAMAMURO, H. KAYANNE, AND I. KOIKE. 2002. Fine scale mapping of land-derived nitrogen in coral reefs by δ^{15}N in macroalgae. Limnol. Oceanogr. **47:** 1405–1416.

VROOM, P., C. SMITH, J. COYER, L. WALTERS, C. HUNTER, K. BEACH, AND J. SMITH. 2003. Field biology of *Halimeda tuna* across a depth gradient: Comparative growth, survivorship, recruitment and reproduction. Hydrobiologia **501:** 149–166.

WALTERS, L. J., C. M. SMITH, J. A. COYER, C. L. HUNTER, K. S. BEACH, AND P. S. VROOM. 2002. Asexual propagation in the coral reef macroalga *Halimeda*: Production dispersal and attachment of small fragments. J. Exp. Mar. Biol. Ecol. **278:** 47–65.

WHITE, A. J., AND C. CRITCHLEY. 1999. Rapid light curves: A new fluorescence method to assess the state of the photosynthetic apparatus. Photosynth. Res. **59:** 63–72.

WILLIAMS, I. D., AND N. V. C. POLUNIN. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs **19:** 358–366.

WOLANSKI, E., AND B. DELESALLE. 1993. Upwelling by internal waves, Tahiti, French Polynesia. Cont. Shelf Res. **15:** 357–368.

———, E. DREW, K. M. ABEL, AND J. O'BRIEN. 1988. Tidal jets, nutrient upwelling and their influence on the productivity of the alga *Halimeda* in the ribbon reefs, Great Barrier Reef. Estuar. Coast. Shelf Sci. **26:** 169–201.

———, AND W. M. HAMMNER. 1988. Topographically controlled fronts in the ocean and their biological significance. Science **241:** 177–181.

ZIMMERMAN, R. C., AND J. C. KREMER. 1984. Episodic nutrient supply to a kelp forest ecosystem in southern California. J. Mar. Res. **42:** 591–604.

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