ELSEVIER

Journal of Experimental Marine Biology and Ecology
297 (2003) 141–159

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

The impact of *Dictyota* spp. on *Halimeda* populations of Conch Reef, Florida Keys

Kevin Beach[a,*], Linda Walters[b], Heidi Borgeas[a], Celia Smith[c], James Coyer[d], Peter Vroom[e]

[a] *Department of Biology, University of Tampa, 401 W. Kennedy Blvd., Tampa, FL 33606, USA*
[b] *Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816, USA*
[c] *Department of Botany, University of Hawai'i, 3190 Maile Way, Honolulu HI 96822, USA*
[d] *University of Groningen, Kerklaan 30 P.O. Box 14, 9750 AA Haren, The Netherlands*
[e] *Joint Institute of Marine and Atmospheric Research, University of Hawaii at Manoa, Honolulu HI 96822, USA*

Received 15 February 2003; received in revised form 3 May 2003; accepted 29 July 2003

Abstract

Species of the brown alga *Dictyota* dominate the reef tract in the Florida Keys. In surveys during summer and fall months between 1994 and 2001, *Dictyota* occupied as much as 70% of the benthos on Conch Reef. *Dictyota* spp. were found growing epiphytically on *Halimeda tuna*, *Halimeda opuntia*, *Lobophora variegata*, *Galaxura* sp., fire coral, hard corals, soft corals, bryozoans and a variety of sponges on Conch Reef. From 1994 to 2001, the percent coverage of *Halimeda* spp. declined from 15% to 3% on the same reef. In Aug. 1999, 2000 and 2001, on average, 56% of two *Halimeda* species on Conch Reef had >50% of their thalli covered by *Dictyota menstrualis* and *Dictyota pulchella*. To address the impact of *Dictyota* on *Halimeda*, short-term growth of unepiphytized and heavily epiphytized (>50% *Dictyota* cover) *H. tuna* were compared with unepiphytized *H. tuna* to which a *Dictyota* mimic was attached. The number of new segments per plant ranged from 1 to 174 over 9 days. *Halimeda* thalli with >50% *Dicytota* cover and thalli covered with *Dictyota* mimic grew significantly slower than unepiphytized thalli. A second short-term experiment addressed the impact of neighboring *Dictyota* on the growth and metabolism of unepiphytized *H. tuna*. Augmenting or clearing epilithic *Dictyota* around but not in contact with *H. tuna* had no impact on growth or metabolism of *H. tuna*. Unepiphytized and heavily epiphytized *H. tuna* were also collected for studies of metabolism. This work indicated that epiphytic *Dictyota* negatively impacts metabolic rates of *H. tuna* in part by shading *H. tuna* thalli. This negative impact was also in part chemically mediated, as exposure to *Dictyota*-

* Corresponding author. Tel.: +1-813-253-3333x3327; fax: +1-813-258-7881.
E-mail address: kbeach@ut.edu (K. Beach).

doi:10.1016/j.jembe.2003.07.003

conditioned water elevated respiration rates in the same manner as seen in the metabolic studies of naturally epiphytized *H. tuna*.

Keywords: Epiphyte; Macroalgae; Photosynthesis; Respiration; Secondary chemistry

1. Introduction

Over the last two decades, macroalgae have been the dominant benthic space occupiers in the northern and southern sections of the Florida Keys reef tract (Hanisak and Overdorf, 1998; Lirman and Biber, 2000). On these coral reefs, macroalgal cover was found to be 58% during the summer of 1998 (Lirman and Biber, 2000). Two genera, *Halimeda* and *Dictyota*, comprised 77–99% of the macroalgal biomass sampled on four reefs over the course of January, May and August samplings in 1998 (Lirman and Biber, 2000). *Dictyota* spp. cover peaked in the summer of 1998 at 40% (Lirman and Biber, 2000). *Dictyota cervicornis*, *Dictyota menstrualis* and *Dictyota pulchella* are common in the Florida Keys reef tract (Hanisak and Overdorf, 1998). These three species vary seasonally in their relative abundance (Hanisak and Overdorf, 1998). *D. menstrualis* is most abundant in September, *D. cervicornis* in March, while *D. pulchella* occurs at low levels year-round (Hanisak and Overdorf, 1998). *D. menstrualis* and *D. pulchella* are the two most common species on Conch Reef (personal observation) and they commonly occur as an entangled turf or as unattached benthic drift (tumbleweeds).

Species of *Dictyota* are frequently found growing epiphytically on many reef species (Littler and Littler, 2000). In the Florida Keys, *Dictyota* has been frequently observed to overgrow corals and other macroalgae (Lirman and Biber, 2000; Beach and Walters, 2000; Walters and Beach, 2000). Epiphytic colonization by macroalgae frequently results in whole or partial host mortality, reduced growth rates, and decreased reproductive output (e.g., Davis et al., 1989; Wahl, 1989). Attached organisms may cause an increase in weight, and thus reduce buoyancy and increase drag (Woollacott and North, 1971; Dixon et al., 1981; Cuomo et al., 1985). Flexibility of the basibiont may also be reduced, potentially increasing breakage in turbulent conditions (Dixon et al., 1981). Further, predation on the host may increase if the epiphytes are grazed upon (Bernstein and Jung, 1979; Dixon et al., 1981; Bronmark, 1985; D'Antonio, 1985). In seagrass populations, overgrowth by epiphytes has resulted in significant reductions in photon flux density (PFD) (Sand-Jensen, 1977; Bulthuis and Woelkerling, 1983). Competition for nutrients has also been postulated, with hosts receiving materials only after they have passed through an epiphytic filter (Sand-Jensen and Revsbech, 1987).

Epibiotic cover may, however, also play a beneficial role (Wahl, 1989). One advantage to the host may be a reduction in grazing pressure if the epiphyte is less palatable than the host (Feifarek, 1987; Barkai and McQuaid, 1988; Wahl and Hay, 1995; Wahl et al., 1997; Laudien and Wahl, 1999). Epiphytes can also chemically or physically camouflage their host (Stoeker, 1978; Witman and Suchanek, 1984; Feifarek, 1987). Metabolites released

by the epiphyte may benefit the host, whether passed directly or indirectly through surrounding seawater (Harlin, 1973).

Recent work suggests that secondary metabolites produced by epiphytes may significantly decrease host growth and increase mortality (Walters et al., 1996). *Dictyota* has been found to contain several secondary compounds including pachydictyol-A, dictyol-E, dictyol-B acetate and dictyodial (Cronin et al., 1995). These and related compounds leach from the alga readily into the surrounding seawater (Walters et al., 1996; Targett and Arnold, 1998) and likely contact coral and other macroalgae. Thirty-five percent of the margins of hard corals on Triumph Reef in the Upper Florida Keys were found to be in direct contact with *Dictyota* (Lirman, 2001). Contact with *Dictyota* reduced growth rates and elevated tissue mortality of the hard corals *Montastrea faveolata* and *Porities astreoides* (Lirman, 2001). Chemical defenses of *Dictyota* have been primarily shown to deter feeding by many species of fish, sea urchins and some amphipods (Hay et al., 1988; Bolser and Hay, 1996), but other roles such as alleopathy are plausible (Fletcher, 1975).

As a prominent algal genus in the Florida Keys (Hanisak and Overdorf, 1998), *Dictyota* has the potential to negatively or positively impact many host species. One common host is the calcified genus *Halimeda* (Lirman and Biber, 2000; Beach and Walters, 2000; Walters and Beach, 2000). Members of the ubiquitous tropical genus *Halimeda* (Chlorophyta, Bryopsidales) are important in many tropical and subtropical waters around the globe as primary producers, stabilizers of sediments and producers of reef sediments (Drew, 1983; Beach et al., 2003). In fact, *Halimeda* annually contributes more to reef sediments than either corals or coralline algae in the Florida Keys reef tract (Wiman and McKendree, 1975). In the upper Florida Keys, carbonate sediments range in composition from 50% to 70% *Halimeda* fragments (Wiman and McKendree, 1975). The consequences of the interaction of these two genera need to be examined, given the importance of primary production by *Halimeda* to calcium carbonate production and high levels of *Dictyota* cover in the Florida Keys.

Such an examination will enhance our understanding of how overgrowth of coral reefs by specific algal species has the capacity to impact community processes. In the following research, we examine the relationship of *Dictyota* and *Halimeda* by addressing three questions: (1) How has abundance of *Halimeda* changed on Conch Reef from 1994 to 2001? (2) How does *Dictyota* impact *Halimeda* growth and metabolism when it grows on or near *Halimeda*? (3) Can any impact of *Dictyota* be attributed solely to shading or is the interaction more complex?

2. Methods and materials

2.1. Study area and benthic surveys

All surveys and experiments were conducted on Conch Reef (24°57′ 00″N; 80°27′ 13″ W) at 21 and 7 m field sites from Oct. 1994 to Aug. 2001. Benthic encrusting and upright organisms on 7 and 21 m sites on Conch Reef were surveyed via a modified band transect approach called the random point contact method (RPC) (Coyer et al., 1999). RPC surveys were conducted in Oct. 1994, June 1997, Sept. 1997, July 1998, Sept. 1998,

Aug. 1999, Aug. 2000, Sept. 2000 and Aug. 2001. At each station, divers recorded the organism contacted by each of 40 randomly located knots on strings attached at both ends to a length of 1.5 m PVC pipe. When stretched taut, there was only one possible location for each knot. Ten randomly chosen stations (subsamples) were positioned along each of three transect lines (samples) within a permanent 100 m^2 area sampled at each date at each depth. Permanent transect locations were re-visited upon each sample period. Ten stations along each transect were randomly selected for each sample period. Macroalgae were identified to at least the genus level and other organisms were identified to the lowest recognizable taxon. In Aug. 1999, 2000 and 2001, the hosts for epiphytic *Dictyota* were recorded.

During sample periods in Aug. 1999, 2000 and 2001, the population densities of *Halimeda* species were also determined along randomly placed transects within the RPC sampling region at both 7 and 21 m sites. In 30 randomly placed 1.0 m^2 quadrats at each depth, the number of *H. tuna* thalli and *Halimeda opuntia* clumps were counted and the percent cover of epiphytic *Dictyota* spp. on each was visually estimated in 25% increments.

In an adjacent region at each depth, *Dictyota* biomass was collected in 15–20 haphazardly placed 0.25 m^2 quadrats during Aug. 1999, 2000 and 2001. All *Dictyota* individuals and hosts within each quadrat were collected and transported to the laboratory. *Dictyota* was removed from its algal hosts and the wet weights of all epilithic and epiphytic *Dictyota* were recorded to species.

2.2. Impact of Dictyota epiphytes on Halimeda tuna metabolism

2.2.1. Photosynthetic Performance

The field setting at Conch Reef provides a natural experiment to examine the impact of epiphytic *Dictyota* on *Halimeda* metabolism and growth over a depth gradient with decreased PFD. Unepiphytized and heavily epiphytized individuals (>50% cover) of *H. tuna* were collected from 7 and 21 m sites in Aug. 1999 and their photosynthetic performance evaluated. Twelve specimens of each depth–epiphyte load combination were assayed. Samples were collected from Conch Reef, stored in seawater filled coolers and transferred to the laboratory within 6 h. In the laboratory, two to three segment pieces from *Halimeda* individuals were excised in seawater using a razor blade. Segments were consistently sampled from a basipetal region, two segments behind the apical-most, fully expanded segment. This procedure insured the use of similarly aged segments, as changes in photosynthetic performance and pigment content per unit fresh weight (fw) are age-dependant (Multer, 1988). Epiphytic *Dictyota* was removed from the surface of excised segments of *H. tuna* using jeweler's forceps. These cleaned samples were then placed in mesh bags in a flow-through seawater system to allow for wound recovery (24 h). In pretreatment trials, respiration rates of excised segments of *H. tuna* were elevated for 12 h (data not shown).

Photosynthetic performance of *H. tuna* was assessed by measuring the rate of O_2 evolution in response to increasing PFD (Beach et al., 1995). In brief, net photosynthesis was measured as oxygen exchange using a water-jacketed Clark-type oxygen

electrode (Rank Brothers, Cambridge, UK). Temperatures were maintained at sample collection temperature ± 1 °C via a Neslab RTE-110 temperature-controlled water bath. Illumination was provided by a Kodak Ektagraphic III E slide projector with 300 W tungsten halogen lamp. Photon flux density was varied from 0 to 2000 μmol quanta m^{-2} s^{-1} with neutral density filters calibrated with Hansitech Quantitherm sensor. To minimize carbon limitation, filtered seawater was augmented to 20 mM $NaHCO_3^-$ above ambient levels. The physiological parameters: dark respiration (R_d), compensation irradiance (I_c), saturation irradiance (I_k), quantum efficiency (α) and maximum rate of net photosynthesis (P_{max}) were obtained via nonlinear regression using the hyperbolic tangent model of Jassby and Platt (1976): (i) $P = P_{max}\tanh(\alpha I/P_{max}) + R_d$; (ii) $I_c = R_d/\alpha$; (iii) $I_k = P_{max}/\alpha$.

2.2.2. Pigmentation

Chlorophyll *a* (Chl *a*), *b* (Chl *b*) 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 relative carotenoid content was determined by the use of equations suggested by Henley and Dunton (1995). All pigment contents were normalized to tissue fw.

2.3. H. tuna growth experiment I: impact of epiphytic Dictyota

Alazarin Red-S histochemically stains calcium carbonate of many organisms, including *Halimeda* (Multer, 1988; Vroom and Smith, 2001). In Aug. 1999, individuals were covered with ca. 4 l plastic bags in situ. Bags were secured to the alga's primary axis with a rubber band placed securely around the base of each *H. tuna*. One milliliter of a 1% dye solution, initially placed in 1.5 ml Eppendorf tubes, was then dispersed in the bags. After 24 h, the bags were removed and the existing segments were stained red. By retrieving tagged-stained individuals after 9 days, growth over time was measured.

Fifty to fifty-five replicates were stained for each of three treatments: (1) >50% *Dictyota* cover of *Halimeda*, (2) < 25% *Dictyota* cover of *Halimeda* and (3) addition of *Dictyota* mimic. The addition of *Dictyota* mimic was achieved by cable-tying a 10 × 20 cm piece of brown plastic which had vertical slits cut through it every 1.0 cm to unepiphytized *H. tuna* individuals. The *Dictyota* mimic treatment was designed to simulate the shading impact of the naturally occurring epiphyte without the presence of the secondary metabolites that are known to be released from *Dictyota* species. Transmittance of irradiance through *Dictyota* mimics was compared with freshly collected, entangled *Dictyota* by placing mimics and *Dictyota* over a cosine-corrected irradiance sensor in a 10-gal aquarium (data not shown) at solar noon. The range of irradiances passing though mimics was similar to *Dictyota* (40–50%). The addition of *Dictyota* mimic was imposed after the Alazarin Red-S staining. After beginning the experimental treatments, *H. tuna* individuals grew in the field for 9 days before harvesting. A total of 51, 41 and 42 individuals were recovered from treatments 1 to 3, respectively. After harvesting, individuals were soaked in a 0.5% bleach solution for

10 min, and the number of new segments (white) was recorded and separated from old-growth (red). The wet weight of the old and new segments was then determined for each thallus.

2.3.1. In situ PFD

Throughout the duration of the growth experiment (see above), instantaneous PFD from 400 to 700 nm was measured and recorded every 5 min at both 7 and 21 sites using LiCor 4π underwater quantum sensors attached to Licor LI-1400 data loggers. Data loggers and quantum sensors were deployed continuously throughout the experiment 0.25 m above the benthos through the use of custom underwater housings (The Sexton Company, Salem, OR, USA).

2.4. Impact of Dictyota exudates on metabolism of H. tuna

To test the impact of secondary chemicals from *Dictyota* spp. on *H. tuna*, each was collected between 8 and 11 Aug. 2000 at the 21 m site. Unepiphytized *H. tuna* were prepared for photosynthetic and respiration measurements as described above. Two grams of *Dictyota* spp. thalli was placed in 500 ml of filtered seawater at ambient temperature, 20% surface irradiance and continuously aerated for 12 h. After 12 h, the *Dictyota* was removed and the water was coarse-filtered with a glass fiber filter. Dark respiration rates and P_{max} of *H. tuna* were determined first in 0.2 μm filtered seawater (fsw) with 10 min exposures to darkness and then to saturating irradiance. After these measurements in fsw, the fsw in the oxygen electrode was replaced with an equal volume of water conditioned with *Dictyota* (see above). *H. tuna* ($n=28$) was acclimated in darkness for 10 min in *Dictyota*-water and then R_d and P_{max} were measured a second time. Further, oxygen consumption–production rate of *Dictyota*-water alone was determined after each *H. tuna* trial in order to control for any changes in oxygen levels from constituents of the *Dictyota*-water. The same transfer procedure was also run with *H. tuna* ($n=12$), replacing fsw with new fsw and examining changes in metabolic performance induced simply by handling.

2.5. H. tuna growth experiment II: impact of neighboring Dictyota

In Aug. 2001, eighty 0.25 m^2 areas were haphazardly selected at 21 m by placing 0.25 m^2 quadrats around areas of the reef that contained at least two unepiphytized *H. tuna* individuals. Twenty quadrats were randomly assigned to each of four treatments. The first treatment (control) was left unaltered. The second treatment had artificially elevated levels of *Dictyota*. *Dictyota* levels were increased by placing fist-sized clumps (ca. 2 g) of freshly collected *Dictyota* into 0.3 m^2 mesh bags and securing the mesh bags on the perimeter of each of the sides of the 0.25 m^2 quadrat. This addition approximated the average amount of *Dictyota* that naturally occurred per unit area on Conch Reef, thereby doubling the *Dictyota* biomass. A third treatment controlled for any shading effects that might occur. On the four sides of these quadrats were placed mesh bags containing a brown plastic, similar in the surface area to *Dictyota* used in the

Dictyota addition treatment. In the fourth treatment, all *Dictyota* present in quadrats was manually removed. In each quadrat, one *H. tuna* was stained with Alazarin Red-S for estimates of growth as described above. A second *H. tuna* was harvested at the end of the study (14 days) for analysis of P_{max} and R_d as described above.

2.6. Statistical comparisons

Two-way ANOVA was used to differentiate relative percent cover of *Halimeda* spp. over the duration of the study (factor 1 = time) at the 7 and 21 m survey depths (factor 2 = depth). Normality of the residuals was tested with the equivalent of a Shapiro–Wilk test with an α of 0.05. Pearson correlation coefficient and a *Z*-test for nonzero correlation were used to examine the relationship between percent cover of *Dictyota* and *Halimeda* over the course of this study. Two-way ANOVAs were used to differentiate pigment levels and physiological parameters of epiphytized versus unepiphytized *H. tuna* (factor 1 = epiphyte load) from the two sample depths (factor 2 = depth). In order to minimize the probability of making a type 1 error statistical comparisons were not run on I_k, I_c or P/R ratio because their calculation uses other parameters that were examined with statistical tests. On account of a lack of normality of the residuals, a Kruskal–Wallis one-way ANOVA on ranks was used to differentiate growth rates of unepiphytized, heavily epiphytized *H. tuna* and *H. tuna* with mimic epiphyte loads. Pairwise *t*-tests were used to compare metabolic rates of *H. tuna* before and after exposure to *Dictyota*-water if the distribution of differences was normal. If the test for normality failed, a pairwise Wilcoxon signed rank test was used to compare metabolic rates of *H. tuna* before and after exposure to *Dictyota*-water.

Lastly, one-way ANOVAs were performed to gauge the impact of neighboring *Dictyota* on *H. tuna* growth and metabolism. If data were not normally distributed, a Kruskal–Wallis one-way ANOVA on ranks was used to analyze the impact of neighboring *Dictyota* on *H. tuna*. In the cases showing significant differences, the Dunn's method multi-comparison post hoc test versus the control group was used to elucidate which group(s) differed from the control.

3. Results

3.1. Benthic surveys

On average, the brown algae *Dictyota* spp. (*D. pulchella* and *D. menstrualis* combined) was the most abundant benthic organism category at both sites on Conch Reef, followed by turf algae and then the green algae *Halimeda* (*H. tuna*, *H. opuntia*, *Halimeda goreaui*) (Fig. 1). Percent cover of hard corals, soft corals, crustose coralline algae and sponges were all greater at 21 versus 7 m (Fig. 1).

The overall percent cover of *Halimeda* spp. changed over the course of the study. *Halimeda* spp. cover decreased steadily from 15% in Oct. 1994 to 3% in Aug. 2001 ($p < 0.0001$) (Fig. 2). There was no significant impact of depth on the percent cover of

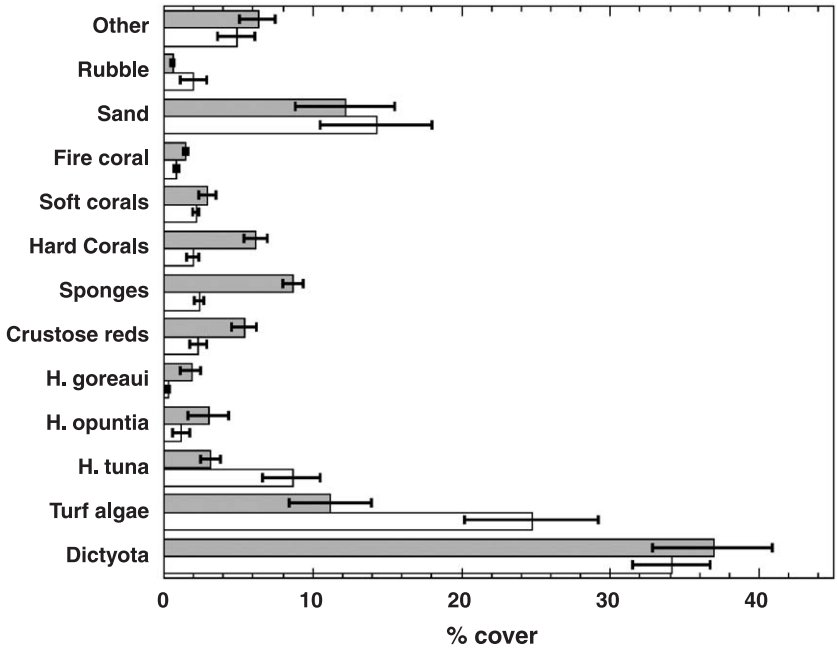

Fig. 1. Relative percent cover (mean ± S.E.M.) of sessile benthic organisms at 7 (white bars) and 21 m (gray bars) on Conch Reef, Florida Keys. Means were calculated from eight surveys between Oct. 1994 and Aug. 2001.

Halimeda spp. at 7 versus 21 m ($p = 0.08$). There was no significant interaction of depth and time on the percent cover of *Halimeda* spp. ($p = 0.09$). Changes in *Halimeda* spp. cover on Conch Reef were significantly correlated with changes in *Dictyota* cover ($p = 0.001$). Changes in levels of *Dictyota* cover explained 25% ($r = -0.49$) of the variation in cover of *Halimeda* spp. (Fig. 3).

In Aug. 1999, 2000 and 2001, *Dictyota* spp. was found growing epiphytically on *H. tuna*, *H. opuntia*, *H. goreaui*, *Rhipocephalus phoenix* (Chlorophytes), *Galaxura* sp., crustose coralline algae (Rhodophytes), *Lobophora variegata* (Phaeophyte), encrusting and upright sponges, hard and soft corals, *Millepora alcicornis* (fire coral), and *Canda simplex* (bryozoan). The majority of *Dictyota* spp. growing at both survey depths on Conch Reef was epilithic but >50% of the individuals of *H. tuna* and *H. opuntia* were found to be heavily epiphytized (>50% cover) by *Dictyota* spp. (Figs. 4 and 5). The extent of *Dictyota* epiphytism was greatest on *H. tuna* at 7 m (Fig. 4).

Overall, in Aug. 1999, 2000 and 2001, the total biomass of *Dictyota* spp. ranged from a mean of 29.6 g m^{-2} at the 7 m site to 30.1 g m^{-2} at the 21 m site (Fig. 5). The ratio of the biomass of epilithic to epiphytic (on *Halimeda* spp.) *Dictyota* ranged from 3.0 at 7 m to 8.0 at 21 m (Fig. 5). The ratio of epilithic to epiphytic *Dictyota* was larger on a biomass basis than on a percent cover basis (2.0 at 7 m to 5.0 at 21 m). In Aug. 1999, 2000 and 2001, on average, 84% of the *Dictyota* biomass consisted of *D. menstrualis*, while the remaining 16% was *D. pulchella* (7 and 21 m combined). Based on percent cover

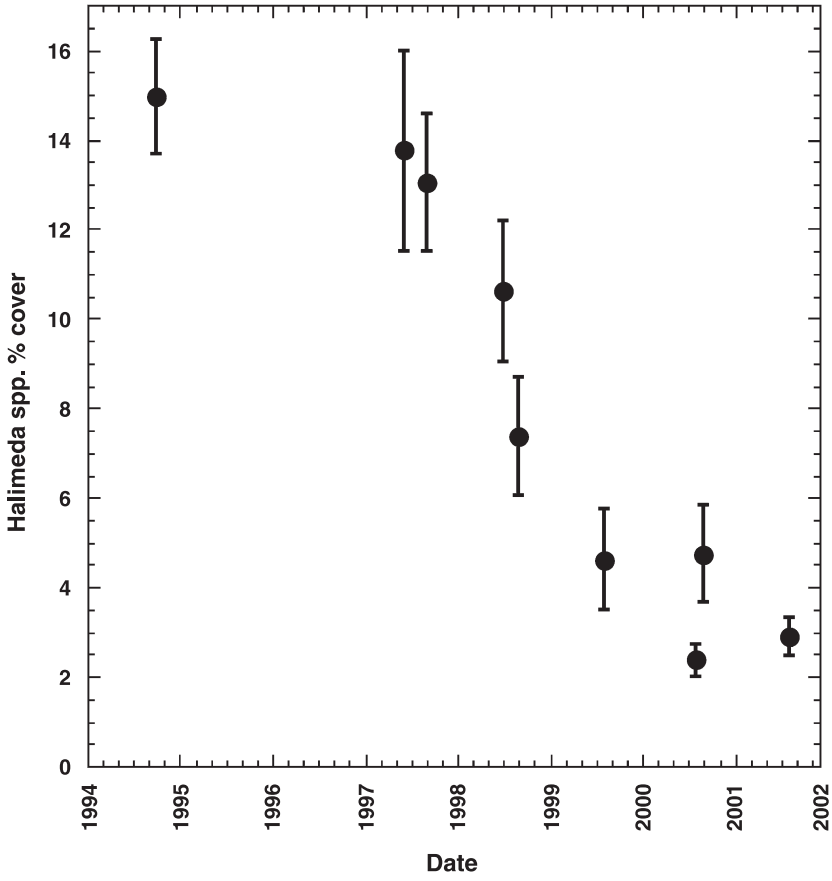

Fig. 2. Relative percent cover (mean ± S.E.M.) of *Halimeda* spp. at on Conch Reef (7 and 21 m sites combined on account of no significant difference due to depth; $p = 0.08$, two-way ANOVA) between Oct. 1994 and Aug. 2001.

measured during the same time period, 77% of *Dictyota* surveyed was *D. menstrualis* and 23% was *D. pulchella* (Fig. 6).

3.2. Impact of Dictyota epiphytes on H. tuna metabolism

3.2.1. A photosynthesis

Photosynthetic performance differed markedly based on depth and epiphyte load (Table 1). Both P_{max} and R_d changed significantly in response to these factors (Table 1). P_{max} was significantly higher in 7 m samples than in 21 m samples of *H. tuna* ($p = 0.03$). P_{max} was significantly lower in epiphytized compared with unepiphytized individuals of *H. tuna* ($p = 0.03$). There was no significant interaction of depth and epiphyte load on P_{max} ($p = 0.80$). As seen with P_{max}, R_d was significantly higher in 7 m samples than in 21 m samples of *H. tuna* ($p = 0.02$). Unlike P_{max}, R_d was

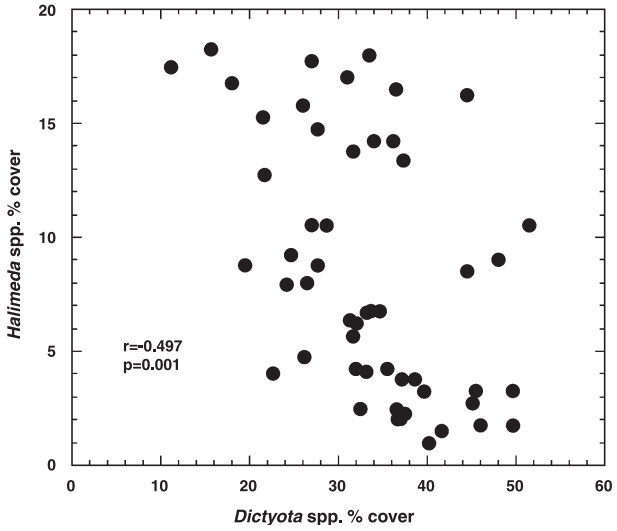

Fig. 3. Correlation of *Dictyota* spp. and *Halimeda* spp. percent cover from Oct. 1994 to Aug. 2001. Each point represents the average cover value from one of three transects at each depth from each of nine survey dates ($n = 54$).

significantly higher in epiphytized compared with unepiphytized *H. tuna* ($p < 0.001$) (Table 1). No significant interaction between depth and epiphyte load was found for R_d ($p = 0.90$). As a result of the direction and magnitude of the changes in P_{max} and R_d, the P/R ratio was lower in epiphytized individuals than in unepiphytized individuals of

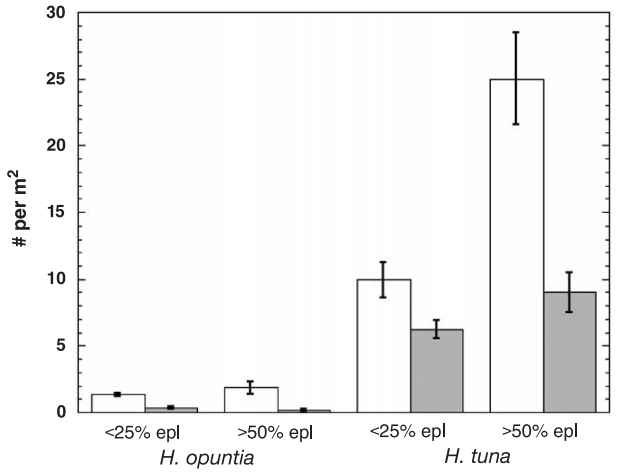

Fig. 4. Population densities (mean ± S.E.M.) of epiphytized (>50% cover by *Dictyota*) versus unepiphytized (< 25% cover by *Dictyota*) *H. tuna* and *H. opuntia* at 7 (white bars) and 21 m (gray bars) on Conch Reef in Aug. 1999–2001.

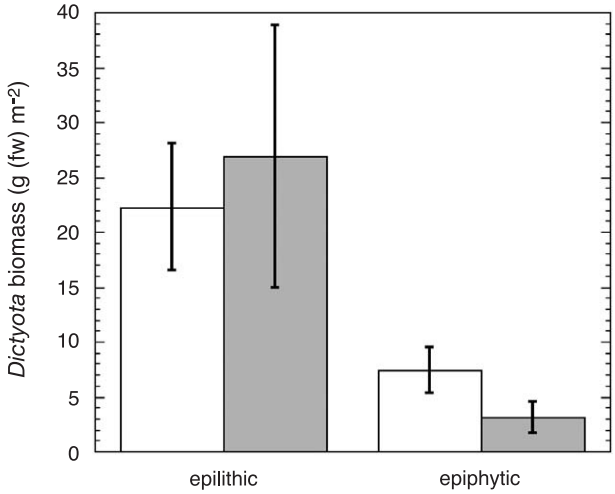

Fig. 5. Epilithic and epiphytic *Dictyota* spp. biomass (g m^{-2}) (mean ± S.E.M.) at 7 (white bars) and 21 m (gray bars) on Conch Reef averaged from Aug. 1999, 2000 and 2001 ($n = 50$ per depth).

H. tuna at both depths (Table 1). Quantum efficiency was the only photosynthetic parameter that was constant over depth ($p = 0.86$) and not impacted by epiphyte load ($p = 0.46$). No significant interaction of depth and epiphyte load was detected on α ($p = 0.14$).

3.2.2. Pigmentation

Chlorophyll *a* and *b* concentrations in *H. tuna* did not differ based on sampling depth (Chl *a*: $p = 0.22$; Chl *b*: $p = 0.99$) or degree of epiphytization (Chl *a*: $p = 0.10$; Chl *b*:

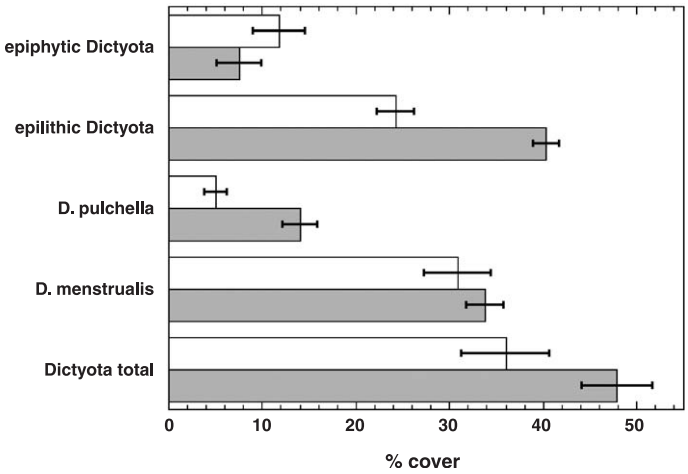

Fig. 6. Relative percent cover (mean ± S.E.M.) of *Dictyota* at 7 (white bars) and 21 m (gray bars) on Conch Reef by substrate type and species averaged from Aug. 1999–2001 ($n = 9$ per depth).

Table 1
Mean (± S.E.M.) pigment and physiological parameters for unepiphytized and epiphytized *H. tuna* over depth

	7 m, Unepiphytized	7 m, Epiphytized	21 m, Unepiphytized	21 m, Epiphytized
Chl *a* (mg/g fw)	0.275 (0.030) A	0.325 (0.020) A	0.251 (0.020) A	0.287 (0.024) A
Chl *b* (mg/g fw)	0.241 (0.023) A	0.266 (0.016) A	0.241 (0.017) A	0.266 (0.020) A
Total caro. (mg/g fw)	0.106 (0.014) A	0.136 (0.008) B	0.097 (0.010) A	0.112 (0.011) B
P_{max} (μmol O_2 g $(fw)^{-1}$ min^{-1})	0.156 (0.012) A	0.129 (0.010) B	0.129 (0.010) B	0.107 (0.010) C
α (μmol O_2 g $(fw)^{-1}$ min^{-1}/μmol quanta m^{-2} s^{-1})	0.003 (0.0003) A	0.003 (0.001) A	0.004 (0.001) A	0.002 (0.0004) A
R_d (μmol O_2 g $(fw)^{-1}$ min^{-1})	0.072 (0.003) A	0.088 (0.006) B	0.061 (0.004) C	0.078 (0.004) D
I_k (μmol quanta m^{-2} s^{-1})	70.74 (15.60)	52.81 (6.84)	48.02 (8.37)	49.72 (6.50)
I_c (μmol quanta m^{-2} s^{-1})	30.33 (4.25)	36.07 (4.87)	20.54 (2.39)	37.92 (5.05)
P_{max}/R_d ratio	2.24 (0.22)	1.47 (0.05)	2.20 (0.16)	1.38 (0.11)

$N = 12$ for each depth–epiphyte combination. Statistical comparisons via two-way ANOVA. Different letter designations indicate differences among categories at $p > 0.05$ as judged by post hoc comparisons. Statistical comparisons were not performed on ratios of parameters in order to minimize type 1 error rate.
Caro.: carotenoids.
Chl: chlorophyll.
P_{max}: net maximum photosynthetic rate.
R_d: dark respiration.
I_c: compensation irradiance.
I_k: saturation irradiance.
fw: fresh weight.

$p = 0.20$) (Table 1). Total carotenoid concentration was significantly higher ($p = 0.04$) in epiphytized than in unepiphytized individuals of *H. tuna* (Table 1). Depth (7 vs. 21 m) did not have an effect on carotenoid concentrations in *H. tuna* ($p = 0.16$). No significant interaction of depth and epiphyte load was detected on pigment concentrations (Chl *a*: $p = 0.76$; Chl *b*: $p = 0.99$; carotenoids: $p = 0.53$).

3.3. H. tuna growth experiment I: impact of epiphytic Dictyota

Individuals of *H. tuna* with a <25% epiphyte load had a median growth rate that was significantly higher ($p = 0.001$) than that of both heavily epiphytized (>50%) *H. tuna* and *H. tuna* with the addition of a *Dictyota* mimic (Fig. 7). Median growth rates were reduced by 39% in *H. tuna* heavily epiphytized by *Dictyota* and by 49% with the addition of a *Dictyota* mimic when compared to unpeiphytized *H. tuna* (Fig. 7). To judge if differences in growth were attributable to the age or size of individuals in treatments, the initial number of segments and the initial biomass (remaining tissue stained red by dye) were compared among treatments with a Kruskal–Wallis one-way ANOVA on ranks. There was no significant difference in the number of initial segments among treatments ($p = 0.388$), nor was there a difference in initial biomass ($p = 0.248$). From this, we concluded that there was no difference in the size or approximate age of

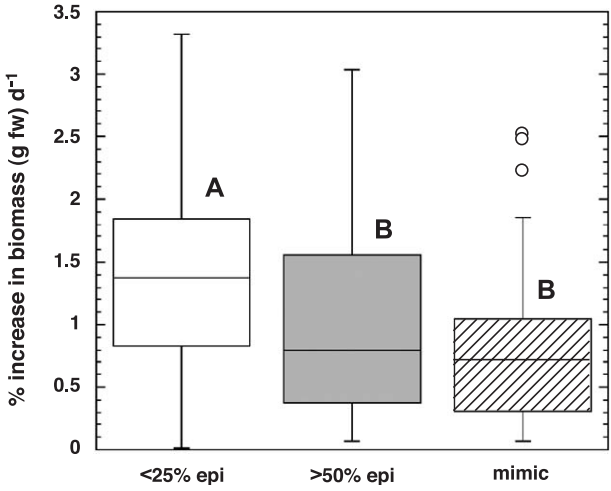

Fig. 7. Box plots (midline = median, box = ± 25% of distribution, whiskers = entire range of data set excluding outliers) of growth rates of *H. tuna* during growth experiment at 7 m on Conch Reef from 3 to 12 Aug. 1999. Treatments included low epiphyte load (< 25% epi), epiphytized (>50% epi) and the addition of a *Dictyota* mimic (mimic) to unepiphytized *H. tuna*. Common letters indicate no significant difference versus control (< 25% epi) at $p = 0.05$ as judged by Kruskal–Wallis one-way ANOVA and post hoc tests. O = outliers.

the samples within each treatment and that any differences detected were attributable to the naturally occurring epiphyte load (>50% epiphyte cover) or experimentally imposed treatments (addition of mimic).

3.3.1. In situ PFD

From 3 to 12 Aug. 1999, the 21 m site received 35% of PFD that reached the 7 m site (data not shown). Photon flux densities at 7 and 21 m sites at solar noon were on average 20.4 and 8.9 times in excess of that required to saturate photosynthesis (I_k), respectively (Table 1). During the 9 days of consecutive PFD measurements, the 21 m population of *H. tuna* was exposed to an average of 10.6 h of saturating irradiance each day (H_{sat}) whereas the 7 m population was exposed to 11.5 h H_{sat}.

3.4. Impact of Dictyota exudates on H. tuna metabolism

Respiration rates were significantly elevated in *H. tuna*, with exposure to *Dictyota*-conditioned water when compared to fsw ($p < 0.001$). Respiration rates of *H. tuna* were on average 200% higher after exposure to *Dictyota*-water than in fsw after compensating for control corrections (Fig. 8). Gross P_{max} was not impacted by exposure of tissue to *Dictyota*-water ($p = 0.056$) as judged by pairwise Wilcoxon signed rank test (Fig. 8). The combination of these changes reduced the P/R ratio from 2.47(± 0.59 S.D.) for *H. tuna* in fsw to 1.05 (± 0.34 S.D.) for *H. tuna* in *Dictyota*-conditioned water.

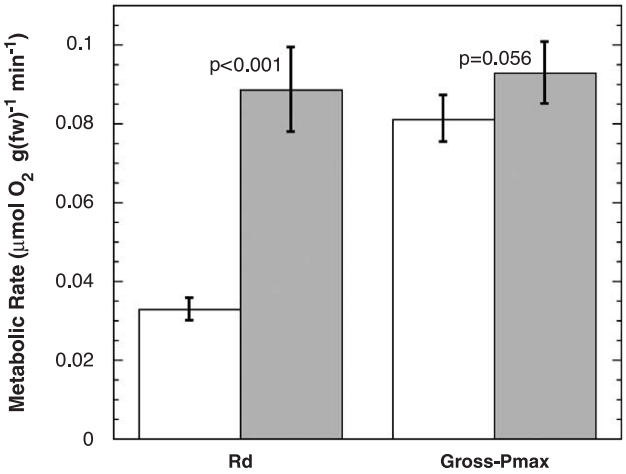

Fig. 8. Maximum gross photosynthetic and respiration rates (mean ± S.E.M.) of *H. tuna* before (white bars) and after (gray bars) exposure to *Dictyota*-conditioned water ($n = 28$). Common letters indicate no significant difference among samples at $p = 0.05$ as judged by pairwise *t*-test (gross P_{max}) or Wilcoxon signed rank test (R_d).

3.5. H. tuna growth experiment II: impact of neighboring Dictyota

Neighboring *Dictyota* had no meaningful, statistically significant impact on *H. tuna* growth or metabolism. No significant differences were found among treatments for growth rates of *H. tuna* when based on the number of new segments per day ($p = 0.995$) or grams of new growth per day ($p = 0.990$). Respiration rates did not differ among treatments ($p = 0.663$, Kruskal–Wallis one-way ANOVA). However, for P_{max}, the experimental removal of *Dictyota* had significant impact ($p = 0.027$). A Tukey test showed a difference between the unmanipulated control and the treatment cleared of *Dictyota* ($p < 0.05$). The control had a greater P_{max} (0.987 (μmol O_2 g $(fw)^{-1}$ min^{-1}) than the treatment cleared of *Dictyota* (0.698 (μmol O_2 g $(fw)^{-1}$ min^{-1}). Comparisons among all other treatments showed no significant differences ($p > 0.05$) among estimates of P_{max}.

4. Discussion

Like much of the Florida Keys reef tract, Conch Reef is an algal dominated ecosystem. From Oct. 1994 to Aug. 2001, *Dictyota* spp., turf algae, *Halimeda* spp. and crustose red algae comprised 72% of the cover at 7 m and 58% of the cover at 21 m. On average, *Dictyota* spp. occupied 36% of the benthos at 7 and 21 m during this time period. *Dictyota* has a negative impact on reef biota, not only by taking up much of the available free space but by growing as an epiphyte. Greater than half of the *Halimeda* spp. community on Conch Reef was heavily epiphytized by *Dictyota* in our surveys. Epiphytic *Dictyota*

negatively impacted short-term metabolism (minutes), long-term growth (days), and possibly longer-term percent cover (years) of *H. tuna*.

Dictyota on Conch Reef grows both as epilithic individuals and on a variety of hosts on Conch Reef including stony corals, soft corals, sponges, fire coral and *Halimeda* spp. Even though the majority of *Dictyota* grew as epilithic individuals, the degree of epiphytism by *Dictyota* has the potential to markedly impact reef biota as 56% of the *H. tuna*, 10% of the *H. opuntia*, 8.4% of sponges, 10% of fire coral, and 3.3% of soft and stony corals on Conch Reef had *Dictyota* growing on their tissues.

Epiphytic *Dictyota* negatively impacted growth of *H. tuna*. Both epiphytized *H. tuna* and *H. tuna* with a *Dictyota* mimic had significantly lowered growth rates relative to unepiphytized *H. tuna*. Epibiotic shading of photosynthetic surfaces has been reported to reduce incoming light in marine systems by up to 80% (Bulthuis and Woelkerling, 1983; Sand-Jensen and Revsbech, 1987; Cebrián et al., 1999). In seagrass populations, this has resulted in PFD reduction below the compensation point to the extent that a negative carbon budget resulted (Sand-Jensen, 1977; Bulthuis and Woelkerling, 1983). Reduction in PFD on *H. tuna* by epiphytic *Dictyota* spp. did not result in a negative carbon budget for *H. tuna* at 7 m, since heavily epiphytized individuals continued to grow in our growth experiment. Instead, *H. tuna* acclimated to the reduced PFD as evidenced by physiological differences observed between epiphytized and unepiphytized individuals.

For example, one shade acclimation mechanism may involve light harvesting carotenoids. Siphonein and siphonoxanthin are the principle carotenoids in *H. tuna* (Rowan, 1989) and they function as accessory pigments, harvesting light for photosynthesis (Kageyama et al., 1977). Levels of this class of pigments were elevated in epiphytized compared with unepiphytized *H. tuna*, allowing for increased absorption of incident PFD. Secondly, P_{max} and I_k were depressed in epiphytized compared with unepiphytized individuals as is typical in a shift from a sun to shade acclimation states (Boardman, 1977). Thus, physiological shifts permit photosynthesis to operate at an optimum level under conditions of limiting PFD (Boardman, 1977; Beach and Smith, 1996).

Even with physiological acclimation to shade, epiphytism of *H. tuna* by *Dictyota* had a marked impact on daily carbon gain (DCG) over the depth gradient in this study. Daily carbon gain for unepiphytized *H. tuna* at 7 m was 0.65 mg C g $(fw)^{-1}$ day^{-1}, whereas epiphytized individuals at 7 m had an estimated DCG of 0.35 mg C g $(fw)^{-1}$ day^{-1} (calculations based on the measurement that the epiphytes absorb 40% of incident irradiance (data not shown) and Dennison and Alberte 1982). At the 7 m site, epiphyte load on *H. tuna* led to a 45% reduction in DCG. At the 21 m site, where irradiance levels are lower overall and H_{sat} is reduced, epiphyte load on *H. tuna* led to an 85% reduction in DCG from 0.39 mg C g $(fw)^{-1}$ day^{-1} to 0.006 mg C g $(fw)^{-1}$ day^{-1}. Clearly, epiphytic cover of *Dictyota* on primary producers such as *H. tuna* has negative implications on growth and may impact the lower limit of distribution and productivity by this species at depth.

Acclimation to a shade state accounts for several but not all of the observed physiological changes in unepiphytized versus epiphytized *H. tuna*. R_d and I_c are typically depressed in a manner similar to P_{max} and I_k during photoacclimation from sun to shade

(Beach and Smith, 1996). R_d was elevated in epiphytized *H. tuna*, thereby elevating I_c and depressing the *P*/*R* ratio by 36%. This is strikingly similar to the 39% reduction in growth measured for heavily epiphytized versus unepiphytized *H. tuna*. An elevated rate of respiration is not consistent with a shade acclimation response, which typically maintains a constant *P*/*R* ratio in both sun and shade states (Boardman, 1977; Beach and Smith, 1996). There are two possible explanations in addition to the impact of shading for the negative impact epiphytic *Dictyota* has on *H. tuna*. We cannot discount the role of epiphytes limiting nutrients to the host (Sand-Jensen and Revsbech, 1987). However, work with four species of *Halimeda* from the Bahamas by Littler et al. (1988) showed an elevation in respiration rates with nutrient pulses. Elevated nutrient levels have been shown to promote growth and synthesis of respiratory and photosynthetic machinery in primary producers, thereby elevating respiration rates (Syrett, 1953; Lapointe et al., 1984). If *Dictyota* was acting as a nutrient filter while epiphytic on *Halimeda*, then it is unlikely that nutrient limitation by the epiphyte is responsible for the elevated respiration rates we observed in epiphytized *H. tuna*.

Alternately, chemicals released by *Dictyota* appear to negatively impact *H. tuna* over time. The potential for accumulation of secondary metabolites from the large biomass of epiphytic *Dictyota* in *Halimeda* tissues may increase *Halimeda*'s overall exposure to these secondary chemicals to levels well above those found in the water column at any one time. In a similar manner, tide pools accumulate secondary metabolites from *Fucus vesiculosus* that inhibits fouling of tide pool macroalgae (Fletcher, 1975). When *H. tuna* was exposed for 10 min to water conditioned with *Dictyota*, respiration rates of *H. tuna* were significantly elevated, depressing the *P*/*R* ratio by 58%. Epiphyte loads of *Dictyota* could lead to substantial release of secondary chemicals into hosts that may be associated with long-term changes in abundance and productivity of *H. tuna* and other reef flora and fauna in the Florida Keys reef tract. Decreased growth by corals with *Dictyota* on their margins may also be a result of the apparent alleopathic effects of what are thought to be largely antiherbivore and antifouling metabolites (Cronin et al., 1995; Walters et al., 1996; Lirman, 2001; Walters et al., in press). In contrast, secondary metabolites released by neighboring *Dictyota* do not appear to have an impact on *H. tuna* growth and metabolism.

4.1. Conclusion

In conclusion, two species of *Dictyota* dominated Conch Reef as judged by percent cover from 1994 to 2001 in summer and fall surveys. *Dictyota* not only occupies space on the reef but it also grows on a variety of reef flora and fauna, including members of the algal genus *Halimeda*. Growth of *Dictyota* on *H. tuna* reduced growth rates of this host by 39% and has the potential to limit its vertical distribution by negatively impacting DCG with increased light limitation. The negative impact on *H. tuna* appears to be due to a combination of shading of the host and elevated respiration rates potentially caused by exposure to the secondary metabolites released by *Dictyota*. Consequently, as cover of *Dictyota* persists, calcium carbonate production by *Halimeda* is decreased. Although *H. tuna* mediates the impact by physiological acclimation, the long-term effect of *Dictyota* on coral reef dynamics remains to be determined.

Acknowledgements

We sincerely thank the following without whom this research would not have been possible: G. Bernardi, M. Burns, D. Byron, E. Calvert, N. Crane, K. DeAngelis, A. Di Girolamo, C. Dominik, J. Heine, C. Hunter, R. Kagan, A. Kahn, E. Klohn, B. Konar, J. Liss, K. Mobley, A. Patka, D. Pence, R. Okano, C. Roberts, D. Steller, L. Wall, L. Wick, S. Whittaker, M. Woo, J. Zamzow, the staff at NURC: G. Buck, K. Boykin, C. Cooper, K. Foreman, W. Fox, K. Johns, D. Kesling, S. Miller, F. O'Leary, B. Person, O. Rutten, M. Van Every, D. Ward, and the Aquarius support team. Funding was provided through the NURC, UNCW, grants #9814, #9925, #9927, #2001-09 to CS, LW, KB and JC, Dana and Delo grants from UT to KB, Florida Sea Grant and UCF to LW. For National Marine Sanctuary Authorization FKNMS-99-065, our thanks to B. Haskell, FKNMS. [**SS**]

References

Barkai, A., McQuaid, C., 1988. Predator–prey role reversal in a benthic ecosystem. Science 242, 62–64.

Beach, K.S., Smith, C.M., 1996. Ecophysiology of tropical rhodophytes: II. Microscale acclimation in photosynthesis. J. Phycol. 32, 710–718.

Beach, K.S., Walters, L.J., 2000. *Dictyota* bloom in FKNMS: fragments and fouling. Proceeding of AAUS 20th Annual Symposium. American Academy of Underwater Sciences, Nahant, Massachusetts, USA, pp. 61–63.

Beach, K.S., Smith, C.M., Michael, T.M., Shin, H.W., 1995. Photosynthesis in reproductive unicells of *Ulva fasciata* and *Enteromorpha flexuosa*: implications for ecological success. Mar. Ecol. Prog. Ser. 125, 129–137.

Beach, K., Walters, L., Vroom, P., Smith, C., Coyer, J., Hunter, C., 2003. Variability in the ecophysiology of *Halimeda spp*. on Conch Reef, Florida Keys. J. Phycol. 39, 1–12.

Bernstein, B.B., Jung, N., 1979. Selective pressures and coevolution in a kelp canopy community in Southern California. Ecol. Monogr. 49, 335–355.

Boardman, K., 1977. Comparative photosynthesis of sun and shade plants. Annu. Rev. Plant Physiol. 28, 355–377.

Bolser, R.C., Hay, M.E., 1996. Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. Ecology 77, 2269–2286.

Bronmark, C., 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. Oikos 45, 26–30.

Bulthuis, D.A., Woelkerling, W.J., 1983. Biomass accumulation and shading effects of epiphytes on leaves of seagrass, *Heterzostera tasmanica*, in Victoria, Australia. Aquat. Bot. 16, 137–148.

Cebrián, J., Enríquez, S., Fortes, M., Agawin, N., Vermaat, J.E., Duarte, C.M., 1999. Epiphyte accrual on *Posidonia oceanica* (L.) Delile leaves: implications for light absorption. Bot. Mar. 42, 123–128.

Coyer, J., Steller, D., Witman, J., 1999. A Guide to Methods in Underwater Research: The Underwater Catalog. Shoals Marine Laboratory, Ithaca, NY.

Cronin, G., Lindquist, N., Hay, M.E., Fenical, W., 1995. Effects of storage and extraction procedures on yields of lipophylic metabolites from the brown seaweeds *Dictyota cilioata* and *D. menstrualis*. Mar. Ecol. Prog. Ser. 119, 265–273.

Cuomo, Y., Vanzanella, F., Fresi, E., Cinelli, F., Mazzella, L., 1985. Fungal flora of *Posidonia oceanica* and its ecological significance. Trans. Br. Mycol. Soc. 84, 35–40.

D'Antonio, C., 1985. Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores? J. Exp. Mar. Biol. Ecol. 86, 197–218.

Davis, A.R., Targett, N.M., McConnell, O.J., Young, C.M., 1989. Epibiosis of marine algae and benthic invertebrates: natural products chemistry and other mechanisms inhibiting settlement and overgrowth. In: Scheuer, P.J. (Ed.), Bioorganic Marine Chemistry, vol. 3. Springer-Verlag, Berlin, pp. 85–114.

Dennison, W.C., Alberte, R.S., 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. Oecologia 55, 137–144.

Dixon, J., Schroeter, S.C., Kastendiek, J., 1981. Effects of the encrusting bryozoan *Membranipora membranacea*, on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). J. Phycol. 17, 341–345.

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.

Feifarek, B.P., 1987. Spines and epibionts as antipredator defenses in the thorny oyster *Spondylus americanus* Hermann. J. Exp. Mar. Biol. Ecol. 105, 39–56.

Fletcher, R., 1975. Heteroantangonism observed in mixed algal cultures. Nature 253, 534–535.

Hanisak, M.D., Overdorf, L.S., 1998. Spatial and temporal variability in the abundance of coral reef algae in the Florida Keys. J. Phycol. 34S, 52.

Harlin, M.M., 1973. Transfer of products between epiphytic marine algae and host plants. J. Phycol. 9, 243–248.

Hay, M.E., Paul, V.J., Lewis, S.M., Gustafson, K., Tucker, J., Trindell, R.N., 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., Dunton, K.H., 1995. A seasonal comparison of carbon, nitrogen, and pigment content in *Laminaria solidungula* and *L. saccharina* (Phaeophyta) in the Alaskan Artic. J. Phycol. 31, 325–331.

Jassby, A.D., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21, 540–547.

Kageyama, A., Yokohama, Y., Shimura, S., Ikawa, T., 1977. An efficient energy transfer from a carotenoid siphonoxanthin, to chlorophyll a observed in a deep-water species of Chlorophycean seaweed. Plant Cell Physiol. 18, 477–480.

Lapointe, B.E., Tenore, K.R., Dawes, C.J., 1984. Interaction between light and temperature of the physiological ecology of *Gracilaria tikvahiae* (Gigartinales: Rhodophyta): I. Gross photosynthesis and respiration. Mar. Biol. 80, 161–170.

Laudien, J., Wahl, M., 1999. Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. Mar. Ecol. 20, 35–47.

Lirman, D., 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19, 392–399.

Lirman, D., Biber, P., 2000. Seasonal dynamics of macroalgal communities of the northern Florida reef tract. Bot. Mar. 43, 305–314.

Littler, D.S., Littler, M.M., 2000. Caribbean Reef Plants. Offshore Graphics, Washington, DC.

Littler, M.M., Littler, D.S., Lapointe, B.E., 1988. A comparison of nutrient- and light limited photosynthesis in psammophytic versus saxicolous forms of *Halimeda* (Caulerpales, Halimediaceae) from the Bahamas. Coral Reefs 6, 219–225.

Moran, R., Porath, D., 1980. Chlorophyll determination in intact tissue using *N*,*N*-dimethylformamide. Plant Physiol. 65, 478–479.

Multer, H.G., 1988. Growth rate, ultrastructure and sediment contribution of *Halimeda incrassata* and *Halimeda monile*, Nonsuch and Falmouth Bays, Antigua, W.I. Coral Reefs 6, 179–186.

Porra, R.J., Thompson, W.A., Kriedemann, P.E., 1989. Determination of accurate extinction coefficients and simultaneous equation for assaying chlorophylls *a* and *b* extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic spectroscopy. Biochim. Biophys. Acta 975, 384–394.

Rowan, K.S., 1989. Photosynthetic Pigments of Algae. Cambridge Univ. Press, Cambridge, UK.

Sand-Jensen, K., 1977. Effect of epiphytes on eelgrass photosynthesis. Aquat. Bot. 3, 55–63.

Sand-Jensen, K., Revsbech, N.P., 1987. Photosynthesis and light adaptation in epiphyte–macrophyte associations measured by oxygen microelectrodes. Limnol. Oceanogr. 32, 452–457.

Stoeker, D., 1978. Resistance of a tunicate to fouling. Biol. Bull. 155, 615–626.

Syrett, P.J., 1953. The assimilation of ammonia by nitrogen starved cells of *Chlorella vulgaris*: I. A correlation of assimilation with respiration. Ann. Bot. (Lond.) 17, 1–19.

Targett, N.M., Arnold, T.M., 1998. Predicting the effects of brown algal phlorotannins on marine herbivores in tropical and temperate oceans. J. Phycol. 34, 195–205.

Vroom, P.S., Smith, C.M., 2001. The challenge of siphonous green algae. Am. Sci. 89, 524–531.
Wahl, M., 1989. Marine epibiosis: I. Fouling and antifouling: some basic aspects. Mar. Ecol. Prog. Ser. 58, 175–189.
Wahl, M., Hay, M.E., 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. Oecologia 102, 329–340.
Wahl, M., Hay, M.E., Enderlein, P., 1997. Effects of epibiosis on consumer–prey interactions. Hydrobiologia 355, 49–59.
Walters, L.J., Beach, K.S., 2000. Algal bloom in the Florida Keys. Underwater Nat. 25, 27–29.
Walters, L.J., Hadfield, M.G., Smith, C.M., 1996. Waterborne chemical compounds in tropical macroalgae: positive and negative cues for larval settlement. Mar. Biol. 126, 383–393.
Walters, L.J., Smith, C.M., Hadfield, M.G., in press. Recruitment of sessile marine invertebrates on Hawaiian macrophytes: do pre-settlement or post-settlement processes keep plants free from fouling? Bull. Mar. Sci.
Wiman, S.K., McKendree, W.G., 1975. Distribution of *Halimeda* plants and sediments on and around a patch reef near Old Rhodes Key, Florida. J. Sediment. Petrol. 45, 415–421.
Witman, J.D., Suchanek, T.H., 1984. Mussels in flow: drag and dislodgment by epizoans. Mar. Ecol. Prog. Ser. 16, 259–268.
Woollacott, R.M., North, W.J., 1971. Bryozoans of California and North Mexico kelp beds. Nova Hedwig. 32, 455–479.