

Seasonal Dynamics of Macroalgal Communities of the Northern Florida Reef Tract

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Coral communities worldwide are undergoing intense degradation in response to natural and human disturbances, and many reef systems have already experienced significant declines in live coral cover associated with an increase in macroalgal abundance. Here, we document the seasonal dynamics of the macroalgal communities of the Northern Florida Reef Tract, providing a baseline for long-term studies of coral-algal competition in the area.

Both macroalgal biomass and percent cover on reefs showed an increasing trend from January to July, when both light and temperature conditions were favorable for growth. Maximum percent cover (56.7%) was found in July and minimum levels in December (25.8%). During these peaks in algal cover, many corals were completely covered by dense mats of algae. Two genera, *Halimeda* and *Dictyota*, represented the largest proportion (77–99%) of the total algal biomass. In the summer, *Dictyota* spp. dominated the algal community, occupying up to 40% of the reef bottom with a dry biomass of up to 20 g.m⁻². In addition, two species, *Styopodium zonale* and *Trichogloea requienii*, showed a significant bloom in April 1998, covering a significant percentage of the bottom (up to 25%) at an inshore reef. Species that exhibited rapid space monopolization on Florida reefs, such as *Dictyota* spp. and *Styopodium zonale*, also showed rapid growth in microcosm and field growth studies.

No correlations were found between fish grazer abundance and algal biomass or percent cover, indicating that present grazer population abundance and composition are not adequate to prevent space monopolization and coral overgrowth by algae such as *Dictyota* spp. and *Halimeda* spp. Only a continued monitoring effort will determine whether the seasonal dynamics of the algal community may result in the decline of coral populations in the Northern Florida Reef Tract.

Introduction

Coral reef communities worldwide face serious threats from a combination of both natural and human-induced disturbances. Long-term ecological studies coincide in reporting general declines in live coral cover and a correlative increase in macroalgal abundance (Ginsburg 1993, Birkeland 1997). Thus, the fate of coral communities appears to be closely tied to that of macroalgal communities. Although macroalgae are conspicuous components of reefs within the Florida Reef Tract, only limited information is available on their growth and community dynamics. The purpose of this research is to document patterns of algal abundance, diversity, and growth, thereby providing a baseline to study the outcome of competition between corals and macroalgae.

Competition between corals and algae can be direct (i. e., overgrowth) or indirect (i. e., through the pre-emption of primary space). The presence of macroalgae has been shown to reduce coral growth (Tanner 1995, Miller and Hay 1996), as well as limit coral recruitment and juvenile survivorship (Birkeland 1977, Hughes 1989, Tomascik 1991, Wittenberg

and Hunte 1992). Algae can also cause coral tissue mortality due to shading, sediment accumulation, abrasion, and allelopathy (Potts 1977, Sammarco 1982, Lewis 1986, Chadwick 1988, Coen 1988, Coles 1988, Keats *et al.* 1997, Littler and Littler 1997a).

Examples of drastic ecosystem degradation resulting in the replacement of coral-dominated systems by macroalgal-dominated ones are plentiful (Smith *et al.* 1981, Sheppard 1988, Bell and Tomascik 1993, Steneck 1993, Hughes 1994, Littler and Littler 1997b). These studies showed that factors that favor algal growth, such as increased nutrient inputs and reduced grazing intensity, can produce long-lasting phase shifts within coral communities as corals are outcompeted by macroalgae (Done 1992).

In the recent past, considerable controversy has arisen over factors controlling algal abundance on coral reefs. Top-down (i. e., consumption) and bottom-up (i. e., resource availability) controls of algal community dynamics have been proposed as opposing hypotheses, and the relative importance of herbivory and nutrient levels is currently being debated for reefs of the Florida Keys and elsewhere (Littler and Littler 1984, Hughes 1994, Szmant and Forrester

1996, Lapointe 1997, 1999, Lapointe *et al.* 1997, Hughes *et al.* 1999). In the present study, we evaluate the relationships between the abundance of the dominant grazers, parrotfishes and surgeonfishes, and the abundance and composition of macroalgal communities on inshore patch reefs and offshore bank reefs of the Northern Florida Reef Tract.

Given their fast growth and turnover rates compared to other reef benthic components, it has been suggested that algae could be used as early-warning indicators of reef degradation (McCook *et al.* 1997). However, as with any environmental indicator, a knowledge of its distribution and variability is needed before its application (Ward 1990). To provide such baseline information for the algal communities of the Northern Florida Reef Tract, we documented: 1) the physical environment, and 2) seasonal distribution, abundances, biomass, percent cover, diversity, and growth of the dominant macroalgal groups.

Materials and Methods

Macroalgal communities were surveyed at four reefs within Biscayne National Park, on the Northern Florida Reef Tract (Fig. 1). Two inshore sites, Bache Shoals (25°29.187' N, 80°08.880' W) and Elkhorn Reef (25°21.782' N, 80°09.841' W), and two offshore sites, Triumph Reef (25°28.333' N, 80°06.704' W) and Pacific Reef (25°22.186' N, 80°08.360' W) were sampled. All surveys were done at depths of 3–5 m.

Macroalgae in this study were identified using keys by Taylor (1960) and Littler and Littler (1997c). Abundant algae were grouped by genus (e. g., *Halimeda* and *Dictyota*) or by functional group (Littler and Littler 1980, Steneck and Dethier 1994). The

functional groups used are: turf algae (filamentous forms of algae with canopy < 1 cm), filaments (FIL, canopy > 1 cm), corticated terete algae (CTA, e. g., *Laurencia* spp., *Acanthophora* spp.), articulated calcareous algae (ACA, e. g., *Amphiroa* spp., *Jania* spp.), and crustose coralline algae (CCA).

Physical environment

Temperature and surface irradiance values for 1998 were obtained from the NOAA C-MAN weather station at Molasses Reef (Fig. 1). Hourly readings of water temperature were averaged to obtain a daily mean value. Light readings in the 400 to 700 nm wave band were recorded at hourly intervals at 35 m above sea level by LI-COR sensors. Values from 10:00 and 17:00 were averaged to obtain daily means.

Algal biomass and species composition

Macroalgae were collected in May and August 1998 within 0.25 m² PVC quadrats placed haphazardly over the bottom. Within each quadrat, all visible macroalgae were collected by hand during a 5-minute interval. A total of 15 such quadrats were sampled per reef. Algal biomass was also collected in the back-reef area of Elkhorn Reef to provide a within-reef comparison. Samples were sorted by species or functional group. Algal tissue was dried to constant weight at 70 °C. Sample specimens were preserved to determine species composition within sites.

Percent cover and relative algal abundance

Close-up photographs of the reef benthos were taken haphazardly to estimate the percent cover and seasonal composition of the algal community. Each photo-quadrat encompassed an area of 15 × 20 cm and 35 such quadrats were surveyed per reef. Percent cover of the different algal groups was determined by the point-quadrat method (Stoddart and Johannes 1978). A piece of acetate paper with randomly-placed dots was placed over each photograph and the identity of the algal group directly under each dot was determined. A preliminary analysis of photographs using 25 and 50 random points showed that percent cover estimates did not change significantly when the number of random points was doubled. Accordingly, a total of 25 points were surveyed for each photograph.

Given the limitations of the hand collection method used here which precludes the collection of small filaments and encrusting species, the seasonal composition of the algal community was also assessed from photographs. The relative cover of each species was determined as the number of points occupied by a given group divided by the total number of points within each photograph occupied by macroal-

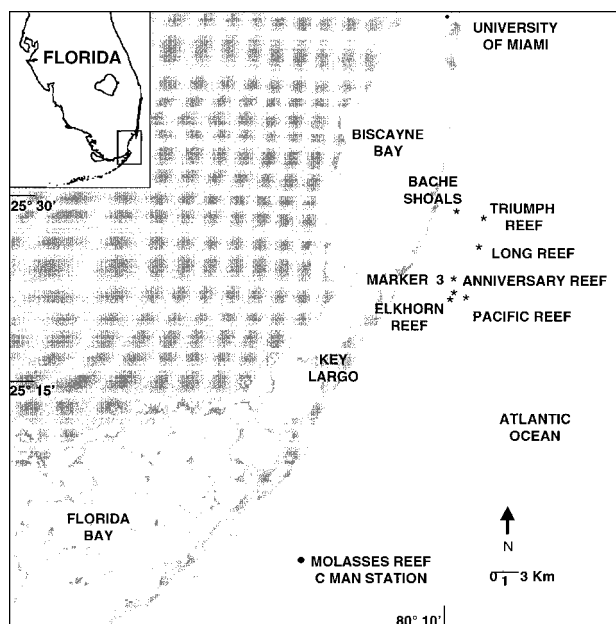


Fig. 1. Map of the Northern Florida Reef Tract with the location of study sites.

gae. Values for each group were averaged for all photographs taken at the same site.

Algal growth

Microcosm and field studies were performed to determine the growth rates of abundant macroalgal species. In June–July 1998, tissue from 12 species of abundant macroalgae was collected from Bache Shoals and Triumph Reef and transported back to the outdoor microcosm facilities at the University of Miami within 3 hours of collection. For each species, 15 thalli (2–3 gr, wet weights) were placed inside 9.4-L aquaria filled with seawater collected at the same time as the algal tissue to provide water quality parameters similar to those found in the field. The aquaria (used as static growth chambers) were placed inside 120-L tanks set up in a flow-through system for temperature control. Air stones were placed inside each aquarium for aeration. Temperature was maintained between 28 and 30 °C for the duration of the growth study. Thalli were weighed initially and at the end of the growth study (2–3 days).

In July–August 1999, growth rates were estimated *in situ* for four macroalgal species, *Dictyota pulchella* Hörning *et* Schmetter, *D. cervicornis* Kützinger, *Laurencia poiteaui* Lamouroux, and *Halimeda goreauii* Taylor. Algal tissue was collected and placed inside 1-L clear plastic containers. The plastic containers, which had holes punched through the sides to allow for water circulation, were attached to a mooring line at a distance of 50 cm from the bottom. For each species, 15 thalli were placed at one inshore (Bache Shoals) and one offshore (Triumph Reef) site. Thalli were weighed initially and at the end of the growth study (5 days).

For the growth studies, growth was recorded as percent weight change per day using the following formula:

$$\%change = [(wt_{t1} - wt_{t0})/wt_{t0}]/t,$$

where

w_{t0} = initial weight

w_{t1} = final weight

t = time

Grazer abundance and grazing rates

Swimming surveys of the main fish grazers, parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), were performed within 50 m² belt transects in July 1998 (n = 6 transects per site). Moving at a slow pace, each transect (2 × 25 m) was surveyed in approximately 3 minutes. All parrotfishes and surgeonfishes found immediately ahead of the moving diver were counted.

In July 1999, fish surveys were carried out in the four initial study sites (Bache Shoals, Elkhorn Reef,

Pacific Reef, and Triumph Reef) as well as in three additional sites:

Marker 3 Reef (25°22.408' N 80°09.667' W),
Anniversary Reef (25°23.306' N 80°09.913' W), and
Long Reef (25°26.690' N 80°07.150' W) (Fig. 1).

Grazing assays using the seagrass *Thalassia testudinum* Banks *ex* König and the macrophyte *Laurencia poiteaui* were done to compare the intensity of fish grazing among sites (Hay 1981). Freshly collected blades of *Thalassia* were cut into 5 cm-long sections and woven into one end of 3-strand nylon rope sections (30 cm long). Pre-weighed sections of *Laurencia poiteaui* were woven into the opposite end of the ropes. Thirty such ropes were placed on the bottom and were collected after 2 hours. The remaining seagrass blades were measured and the ungrazed algal tissue was weighed. Control ropes were also placed on the reefs at the same time to determine the potential changes in algal or seagrass biomass due exclusively to growth or handling. Five control ropes, similar to those ropes used for determining grazing rates, were placed on the bottom inside clear plastic bags to prevent grazing during the assays. Grazing assays were performed in April and August 1998.

The data were examined for conformity to the assumptions of each statistical test prior to analysis. Normality was tested with the Shapiro-Wilk test and homoscedasticity was tested with the Bartlett's test. When assumptions were not met, non-parametric tests were used instead (Sokal and Rohlf 1981).

Results

Physical environment

Seasonal trends in light and temperature are shown in Figure 2. Mean daily temperatures in the Northern Florida Reef Tract commonly reach minimum values between February and March and maximum values between July and September. In 1998, mean water temperatures exceeded 30 °C on 57 days between July and September, and the maximum water temperature

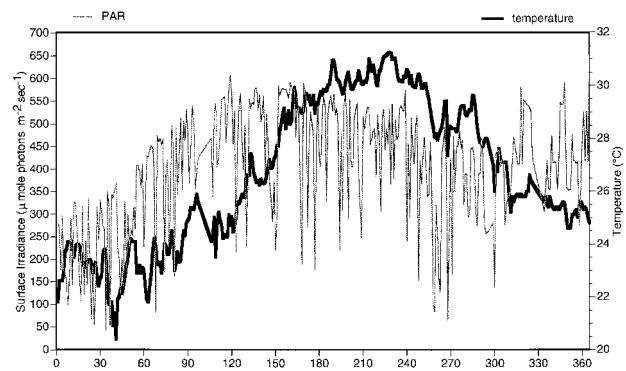


Fig. 2. Mean daily surface irradiance and sea temperatures from the NOAA C-MAN weather station at Molasses Reef, Florida for 1998.

was 31.3 °C. Maximum values of surface irradiance were recorded between May and August, while lowest values were obtained in January and February.

Algal biomass and species composition

Two genera, *Halimeda* and *Dictyota*, represented the largest proportion (77–99%) of the algal biomass within the reefs sampled (Table I). An exception to this pattern was seen at Elkhorn Reef on May 1998 when two species, *Styopodium zonale* (Lamouroux) Papenfuss and *Trichogloea requienii* (Montagne) Kützing, underwent a significant bloom. The presence of these species was first detected in April 1998 and within a short period of time they monopolized a significant percentage of the bottom (up to 25% cover in May 1998), and represented up to 70% of the total algal biomass within Elkhorn Reef. These species had disappeared by the time of the following biomass survey in August 1998. Similar blooms of *Styopodium zonale* have been observed on a yearly basis on this reef since 1993 (Lirman, per. obs.).

A general increase in biomass for most algal groups was observed between May and August 1998. However, differences between dates were only significant for a few groups (Table I, Mann Whitney U-test, $p < 0.05$). No significant differences in total algal biomass were found among reefs in May 1998 (Kruskal-Wallis, $p > 0.1$). In August 1998, Pacific Reef had a significantly lower algal biomass compared to the other reefs (Kruskal-Wallis, $p < 0.05$). A power analysis revealed very low power (0.1–0.3) for those comparisons that were not significantly different.

Significant differences in biomass between offshore and inshore reefs were detected only for *Dictyota* spp. in May (higher biomass in offshore reefs), and CTA, ACA and filaments in both May and August (higher biomass in inshore reefs, Kruskal-Wallis, $p < 0.05$, Tukey-Kramer comparisons).

Although there was a general increase in the number of species between the January-May and August surveys, species composition did not differ considerably among sites or season, and no clear inshore-offshore patterns were detected. Species in several genera (i. e., *Halimeda*, *Dictyota*, *Amphiroa*, *Gelidiella*, *Gelidiopsis*, and *Galaxaura*) showed seasonal persistence, and more than half of the species found in the initial surveys were found in subsequent surveys (Table II).

Percent cover

The percent cover of macroalgae showed an increasing trend from January to July, followed by a subsequent decrease (Fig. 3). Maximum cover for all reefs was observed in July (56.7%, S. E. = 4.6) and minimum levels were observed in December (25.8%, S. E. = 2.6). Significant differences in algal cover were detected between July-October and December (ANOVA, $p > 0.1$, Tukey-Kramer comparisons). When data were grouped by reef type, inshore reefs showed higher, non-significant, percent cover of algae at all times (t-tests, $p > 0.1$).

Macroalgal communities were dominated by turf forms, *Dictyota* spp., *Halimeda* spp., and CCA but the relative cover of algal groups varied throughout the year (Fig. 4). Both turf forms and *Halimeda* spp. showed an inverse relationship with *Dictyota* spp. On all four reefs, the algal community was dominated by turf forms throughout the year, except during the summer, when *Dictyota* spp. became dominant. Filaments, CTA, and ACA groups were minor components of the algal communities in terms of relative bottom cover throughout the year.

Algal growth

The growth rates of 12 species of macroalgae collected from the Northern Florida Reef Tract and kept

Table I. Mean biomass (gr dry weight/m² ± 1 S. E.) of the most abundant macroalgal species or groups within the northern Florida Reef Tract. BS = Bache Schoals, ER = Elkhorn Reef, ER (BR) = Back Reef area on Elkhorn Reef, TR = Triumph Reef, PR = Pacific Reef. CTA = Corticated Terete Algae, ACA = Articulated Calcareous Algae. * = significant differences in mean biomass between dates with the same reef (Mann-Whitney U-tests, $p < 0.05$). n = 15.

Reef	Date	<i>Halimeda</i> spp.	<i>Dictyota</i> spp.	CTA	ACA	Filaments	<i>Styopodium</i> <i>zonale</i>	<i>Trichogloea</i> <i>requienii</i>	Total
BS	Jan	47.4 (9.7)	0.3 (0.1)	0.64 (0.16)	0.37 (0.16)	0.24 (0.15)	0	0	47.3 (8.6)
BS	Aug	194.7 (89.6)*	12.2 (2.2)*	0.78 (0.26)	0.64 (0.25)	0.03 (0.01)	0	0	206.3 (99.2)*
ER	May	35.3 (7.3)	7.5 (2.3)	0.21 (0.05)	2.30 (9.75)	1.25 (0.63)	46.8 (20.0)	0	90.3 (22.2)
ER	Aug	33.9 (14.8)	8.2 (2.6)	1.99 (1.03)	2.74 (0.78)	0.53 (0.50)	0	0	44.2 (13.1)*
ER(BR)	May	33.9 (15.3)	5.1 (1.6)	0.37 (0.20)	0.07 (0.07)	0.14 (0.05)	13.0 (6.3)	23.7 (9.4)	43.2 (24.3)
ER(BR)	Aug	185.1 (32.5)*	2.4 (2.0)	0.20 (0.10)	0.18 (0.14)	0.68 (0.55)	0	0	186.7 (32.6)
TR	May	142.4 (59.6)	8.3 (1.3)	0.33 (0.20)	0.12 (0.05)	0.21 (0.07)	0	0	153.4 (59.1)
TR	Aug	258.6 (92.9)	19.7 (5.2)*	0.41 (0.12)	0.34 (0.12)	0	0	0	284.3 (95.3)
PR	May	47.2 (16.0)	9.7 (1.9)	0.33 (0.05)	0.23 (0.04)	0.09 (0.05)	0	0	56.3 (17.5)
PR	Aug	17.5 (17.5)	20.4 (1.4)*	0.10 (0.05)*	0.45 (0.34)	0.02 (0.02)	0	0	38.2 (18.2)

in 9.4-L aquaria at the microcosm facility at the University of Miami ranged from 0.6% to 5.6% (% daily change in biomass, Table III). Brown algae, including *Styopodium zonale* (5.65%) and *Dictyota* spp. (3.1–4.9%), had the fastest growth rates. Among the red algae, *Champia parvula* (Agardh) Harvey had the fastest growth rates (5.0%).

The growth rates measured *in situ* for *Dictyota pulchella*, *D. cervicornis*, *Laurencia poiteau*, and *Hal-*

Table II. Macroalgal species present within 0.25 m² quadrats sampled on four Florida reefs at two different times of the year (n = 15 quadrats per site). Bache Shoals was sampled in February 1998 and all other reefs in May 1998. All reefs were sampled in August 1998. ● = present in survey.

Macroalgal species	Feb– May	Au- gust
Green algae		
<i>Halimeda goreauii</i> Taylor	●	●
<i>Halimeda tuna</i> (Ellis et Solander) Lamouroux	●	●
<i>Halimeda opuntia</i> (Linnaeus) Lamouroux	●	●
<i>Halimeda opuntia f. triloba</i> (Decaisne) Barton	●	●
<i>Halimeda discoidea</i> Decaisne		●
<i>Halimeda simulans</i> Howe		●
<i>Caulerpa</i> sp.		●
<i>Cladophora</i> sp.	●	
Red algae		
<i>Amphiroa fragilissima</i> (Linnaeus) Lamouroux	●	●
<i>Amphiroa tribulus</i> (Ellis et Solander) Lamouroux	●	●
<i>Amphiroa rigida f. antillana</i> Børgesen	●	●
<i>Gelidiopsis intricata</i> (Agardh) Vickers	●	●
<i>Gelidiopsis variabilis</i> (Agardh) Schmitz		●
<i>Gelidiella acerosa</i> (Forsskål) Feldmann et Hamel	●	●
<i>Gelidium floridanum</i> Taylor	●	
<i>Laurencia poiteau</i> (Lamouroux) Howe	●	●
<i>Laurencia corallopsis</i> (Montagne) Howe		●
<i>Laurencia</i> sp.		●
<i>Hypnea spinella</i> (Agardh) Kützing	●	●
<i>Botryocladia pyriformis</i> (Børgesen) Kylin	●	●
<i>Champia parvula</i> (Agardh) Harvey	●	●
<i>Jania adhaerens</i> Lamouroux	●	●
<i>Trichogloea requienii</i> (Montagne) Kützing	●	●
<i>Acanthophora spicifera</i> (Vahl) Børgesen		●
<i>Polysiphonia</i> sp.		●
<i>Galaxaura obtusata</i> (Ellis et Solander) Lamouroux		●
<i>Liagora farinosa</i> Lamouroux		●
<i>Murrayella pericladis</i> (Agardh) Schmitz		●
<i>Centrocerus</i> sp.		●
Brown algae		
<i>Dictyota pulchella</i> Hörning et Schnetter	●	●
<i>Dictyota bartayresiana</i> Lamouroux	●	●
<i>Dictyopteris deliculata</i> Lamouroux	●	●
<i>Dictyota cervicornis</i> Kützing	●	●
<i>Styopodium zonale</i> (Lamouroux) Papenfuss		●

imeda goreauii compared favorably with those measured for the same species in the microcosm growth studies as no significant differences between growth rates were found (t-tests, $p > 0.05$, Table III). Moreover, no significant differences in growth rates were found between thalli of the same species placed at inshore and offshore reefs (t-tests, $p > 0.1$).

Grazer abundance

Significant differences in the mean abundance of herbivorous fishes were detected (Table IV). In 1998 and 1999, offshore reefs had a significantly higher abundance of surgeonfishes compared to inshore reefs (ANOVA, $p < 0.05$, Tukey-Kramer comparisons). In 1999, the mean abundance of parrotfishes was significantly higher on inshore reefs compared to offshore reefs (ANOVA, $p < 0.05$, Tukey-Kramer comparisons). Whereas the mean abundance of surgeonfishes did not show any significant changes between 1998 and 1999, the mean abundance of parrotfishes showed significant increases between 1998 and 1999, reaching a maximum mean abundance of 72 individuals.m⁻¹ on Bache Shoals (Table IV). The abundance of the sea urchin *Diadema antillarum* Philippi was extremely low in the area surveyed. Only 2 juveniles (< 3 cm in test diameter) were found on Elkhorn Reef in 1998, and no other individuals were found on any of the other reefs.

No significant correlations were found between percent cover of macroalgae and mean fish grazer abundance in 1998 ($r = -0.03$, $p > 0.1$) or 1999 ($r = -0.3$, $p > 0.1$). Moreover, in reefs such as Bache Shoals and Elkhorn Reef, no significant changes in mean algal cover were detected between 1998 and 1999 (t-test, $p > 0.1$) even when the mean abundance of herbivorous fishes in 1999 was more than double what was recorded in 1998 (Table IV).

Grazing rates

A comparison of the biomass of *Thalassia* and *Laurencia* on control ropes before and after the graz-

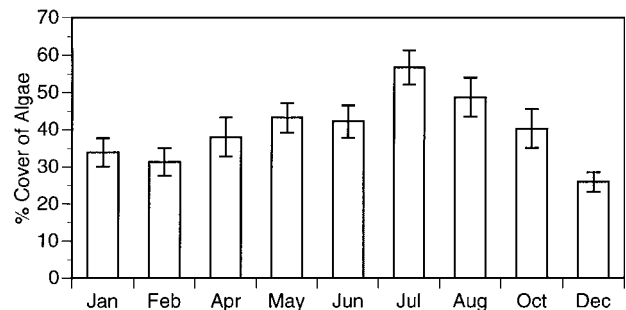


Fig. 3. Mean percent cover of macroalgae (\pm S.E.) on reefs of the Northern Florida Reef Tract. Only Bache Shoals was sampled in January and February. Only Triumph and Elkhorn Reefs were sampled in April and October. All four reefs were sampled in all remaining times. n = 35 photo-quadrats per site.

ing assays showed that changes due to handling or growth were not significant (t-tests, $p > 0.1$). Grazing rates, as estimated by the grazing assays, were significantly different among reefs and between seasons (2-Way ANOVA, $p < 0.05$, Table V). Consumption of *Thalassia* and *Laurencia* was significantly higher on offshore reefs compared to inshore reefs. Although season had a significant effect on consumption rates, *Thalassia* and *Laurencia* assays exhibited different seasonal responses. Whereas consumption of *Thalassia* was significantly higher in August than in April, the opposite results were obtained for *Laurencia*, which registered higher losses due to grazing in April than in August. No significant interactions were found between reef type and season ($p > 0.05$). The highest consumption rates for both species were found on Pacific Reef in April 1998 (ANOVA, $p < 0.05$, Tukey-Kramer comparisons). No significant correlation was found between consumption rates and biomass of *L. poiteaui* on reefs in August ($r = 0.18$, $p > 0.05$). Lastly, a significant correlation was only found between *Thalassia* grazing rates and the abundance of surgeonfishes in Summer 1998 ($r = 0.95$, $p < 0.05$).

Discussion

The macroalgal communities of the Northern Florida Reef Tract showed marked seasonal dynamics; algal biomass and percent cover, which were at their lowest levels in winter, increased as both water temperature and light levels increased. Peak abundance and biomass, specially of *Dictyota* spp., were found between July and August when it reached 56.7% cover, followed by subsequent declines. The decline that took place in the later part of the year was correlated with high temperatures that exceeded 30 °C as well as a decline in light availability. Negative effects of high temperatures on Florida macrophytes were previously reported by Dawes *et al.* (1976), Josselyn (1977), and Mathieson and Dawes (1986).

Different algal groups dominated the algal communities at different times of the year. *Dictyota* spp. exhibited highest relative abundance during the summer months when they were found growing not only on the bottom but overtopping corals and other types of algae such as *Halimeda* spp. as well. Similar space monopolization was observed during the bloom of two algal species (*Styopodium zonale* and *Trichog-*

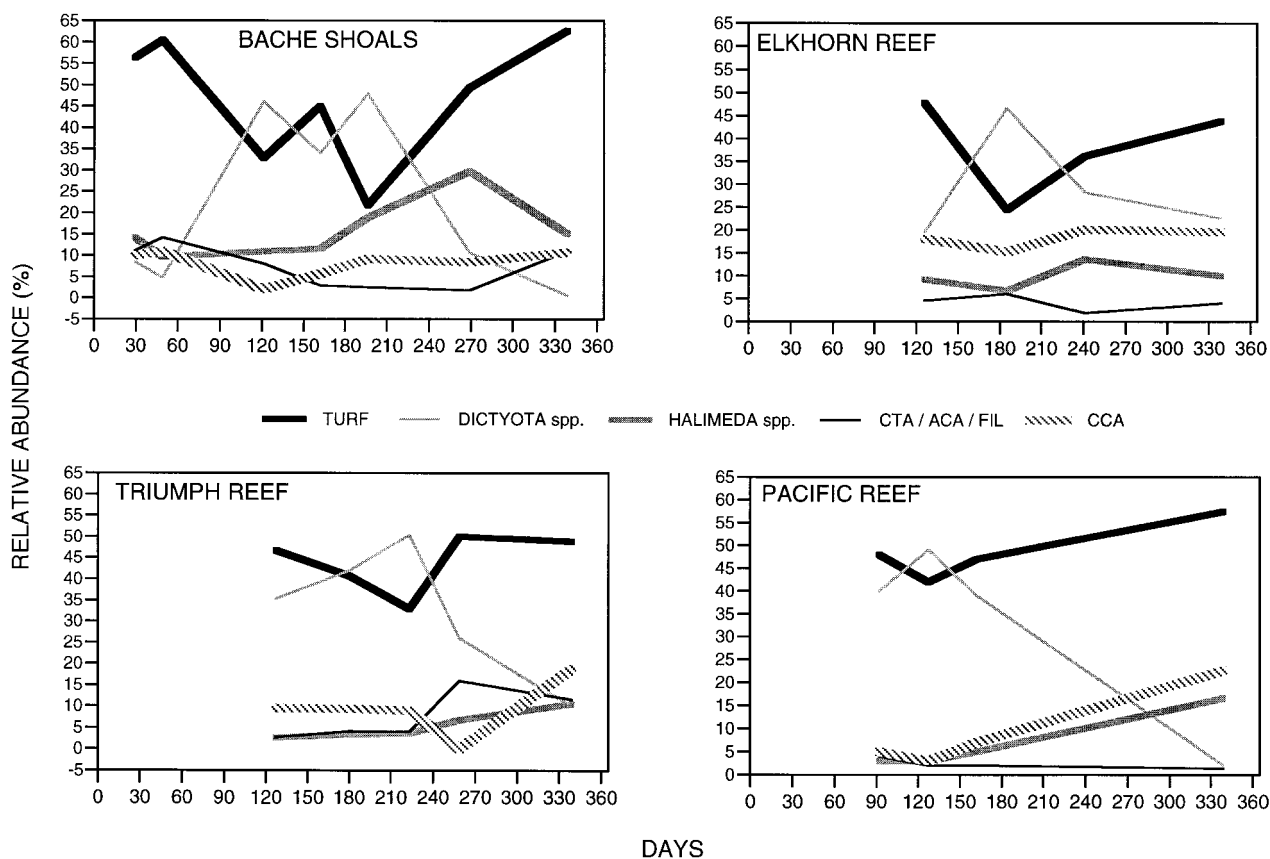


Fig. 4. Seasonal abundance of different macroalgal groups expressed as mean relative percent cover (i. e., number of points occupied by a given group divided by the total number of points within each photograph occupied by macroalgae). TURF = filamentous forms of algae with canopy < 1 cm, FIL = filaments with canopy > 1 cm, CTA = corticated terete algae (e. g., *Laurencia* spp., *Acanthophora* spp.), ACA = articulated calcareous algae (e. g., *Amphiroa* spp., *Jania* spp.), and CCA = crustose coralline algae. $n = 35$ photo-quadrats were surveyed from each site.

loea requienii) that lasted three months and completely covered small corals. The species that exhibited rapid space monopolization on Florida reefs,

Table III. Growth rates (\pm S.E.) of dominant macroalgae from the northern Florida Reef Tract expressed as % increase in weight per day. n = 15.

Macroalgal species	Growth (% per day)	
	Micro- cosms	Field
Brown algae		
<i>Styopodium zonale</i>	5.6 (0.6)	
<i>Dictyota pulchella</i>	4.9 (1.5)	4.0 (1.0)
<i>Dictyota bartayresiana</i>	3.7 (0.9)	
<i>Dictyota cervicornis</i>	3.1 (0.5)	3.8 (1.1)
<i>Sargassum platycarpum</i> Montagne	0.8 (0.2)	
Red algae		
<i>Champia parvula</i>	5.0 (0.3)	
<i>Laurencia poiteaui</i>	2.8 (0.5)	3.4 (0.7)
<i>Laurencia papillosa</i> (Agardh) Greville	1.7 (0.3)	
<i>Trichogloea requienii</i>	1.1 (0.3)	
<i>Hypnea spinella</i>	0.8 (0.3)	
<i>Galaxaura obtusata</i>	0.6 (0.1)	
Green algae		
<i>Halimeda goreauii</i>	1.3 (0.4)	1.5 (0.5)

such as *Dictyota* spp. and *Styopodium zonale*, also showed rapid growth in microcosm and field growth studies. Summer blooms were reported previously for another species, *Codium isthmocladum* Vickers, on Florida reefs where it reached up to 100% cover over large areas (Lapointe 1997).

Numerous studies of herbivory on reefs have documented that macrograzers (i. e., fishes and urchins) can have an overriding influence on the abundance and composition of algal communities (Wanders 1977, Littler and Littler 1984, Hay 1985, Lewis 1986, Carpenter 1986, Lessios 1988, Morrison 1988, Hughes 1994, Hixon and Brostoff 1996). In this study, however, several lines of evidence indicate a less influential role of herbivorous fishes at the present time. These findings include: a) a general lack of correlation between algal community attributes (i. e., biomass and percent cover) and abundance and consumption rates of fish grazers, b) peaks in algal biomass and percent cover at a time of the year when fish grazing rates are commonly highest (Schmitt 1997), and c) no significant differences in algal cover between 1998 and 1999, even when the number of fish grazers nearly doubled. A similar lack of correlation between herbivorous fish abundance and percent cover of different algal groups was reported by Schmitt (1997) for the Florida Keys.

These findings suggest that present grazing levels are insufficient to offset algal growth and prevent macroalgal space monopolization. This space mo-

Table IV. Mean abundance (\pm 1 S.E.) of herbivorous fishes determined by swimming visual counts within 50-m² belt transects. n = 6 transects per site. nd = no data available.

Study sites		July 1998		July 1999	
		Parrotfishes	Surgeonfishes	Parrotfishes	Surgeonfishes
Inshore	Bache Shoals	36.0 (6.6)	9.2 (1.3)	72.0 (9.05)	6.2 (1.5)
	Anniversary Reef	nd	nd	55.2 (7.5)	7.8 (3.5)
	Marker 3 Reef	nd	nd	54.5 (1.0)	10.0 (1.4)
	Elkhorn Reef	13.2 (2.6)	9.5 (1.2)	40.0 (1.0)	8.2 (1.6)
Offshore	Triumph Reef	11.3 (2.6)	14.2 (1.3)	19.5 (3.6)	12.2 (1.9)
	Long Reef	nd	nd	13.6 (2.1)	17.2 (2.3)
	Pacific Reef	14.0 (1.6)	15.2 (1.7)	30.6 (5.3)	15.4 (3.3)

Table V. Mean proportion (\pm 1 S.E.) of *Thalassia testudinum* and *Laurencia poiteaui* consumed by herbivorous fishes during 2-hour assays. n = 30.

Reefs	<i>Thalassia</i>		<i>Laurencia</i>	
	Apr-98	Aug-98	Apr-98	Aug-98
Bache Shoals	0.33 (0.02)	0.61 (0.09)	0.33 (0.05)	0.12 (0.06)
Elkhorn	0.18 (0.06)	0.64 (0.15)	0.42 (0.06)	0.45 (0.10)
Triumph	0.49 (0.11)	0.98 (0.01)	0.20 (0.05)	0.41 (0.06)
Pacific	0.85 (0.07)	0.91 (0.04)	0.69 (0.05)	0.44 (0.07)
All Reefs	0.45 (0.05)	0.80 (0.07)	0.39 (0.03)	0.33 (0.06)

nopolization is especially evident for algae such as *Dictyota* spp., *Styopodium zonale*, *Trichogloea requienii*, and *Halimeda* spp. that contain structural and chemical defenses documented to deter fish grazing (Littler *et al.* 1983, Hay 1992, 1997, Paul 1992). In contrast, biomass and percent cover of other algal types commonly consumed by fish grazers such as filamentous or corticated terete algae (CTA) were low throughout the year (Hay 1981, 1984, Littler *et al.* 1983, Paul and Hay 1986). Although historical data are lacking for the area, several studies have documented that, unlike parrotfishes and surgeonfishes, the sea urchin *Diadema antillarum*, which experienced a region-wide decline starting in 1983, readily consumed *Dictyota* and *Halimeda*, the two genera that now reach high abundance and biomass on Florida Reefs (Hay and Taylor 1985, Lessios 1988, Morrison 1988). Hay and Taylor (1985) also arrived to the similar conclusion that herbivorous fishes are not able to control erect macroalgal abundance in the absence of *Diadema*.

Corals are in continuous contact with macroalgae along colony margins as they grow side by side on Florida reefs. The outcome of competition between these two dissimilar groups will be determined by their growth characteristics as well as their competitive abilities. Given the fast growth rates of algae documented in this study, this group can prove a superior competitor for space on Florida reefs under favorable environmental conditions. Although grazers have controlled algal abundance historically, the ma-

ior changes that have taken place over the last two decades may have limited their influence. The regional demise of the sea urchin *Diadema antillarum*, as well as potential increased nutrient inputs from human activities, may have resulted in the present conditions of algal overgrowth that may be threatening reef communities of the Florida Reef Tract (Carpenter 1990, Lapointe and Clark 1992, Hughes 1994, Szmant and Forrester 1996, Lapointe 1997, Bryant *et al.* 1998). In 1998, *Dictyota* spp. and *Halimeda* spp. exhibited a summer peak in biomass and percent cover that resulted in many corals being overtopped by dense algal mats. Given the lack of historical data for the region, it is extremely important to determine whether the documented seasonal dynamics are regular events, and to evaluate their potential effects on the long-term persistence of these reef communities.

Acknowledgements

This research was funded by NOAA Coastal Ocean Program awards #NA37RJ0200 and #NA37RJ0149 to the University of Miami. Biscayne National Park provided field support. We thank B. Orlando, S. Maciá, T. Jones, S. Tosini, and Richard Curry for their help. This manuscript benefited from comments by W. Cropper Jr., P. Fong, M. Miller, and two anonymous reviewers.

Accepted 27 January 2000.

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