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Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching

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Abstract

Tissue biomass (ash-free dry weight) and symbiotic dinoflagellates (density, chlorophyll *a* cell^{-1} or cm^{-2} of coral surface area) of five species of reef-building corals were monitored seasonally for up to 4 yr at three different depths in the Bahamas. The lowest values of all tissue biomass and algal symbiont parameters occurred during the late summer–fall sample periods. In contrast, the highest densities and pigment content of symbionts usually occurred during the winter, whereas tissue biomass peaked most often in the spring, the time lag implying a functional relationship between these variables. Corals living in shallow water often (but not always) had higher levels of all parameters measured compared to deeper corals, except chlorophyll *a* content, which usually displayed the opposite trend. The results show that corals from all depths exhibited bleaching (loss of symbiotic dinoflagellates and/or their pigments) every year, regardless of whether they appeared white, tan, or mottled to the human eye. We speculate that these patterns are driven by seasonal changes in light and temperature on algal and animal physiology. Furthermore, we hypothesize that all tropical reef-building corals, world-wide, exhibit similar predictable cycles in their tissue biomass and symbiotic algae.

The health of reef corals has been an issue worldwide for several years, made more prominent by incidences of bleaching, where loss of symbiotic dinoflagellates (also known by the generic term zooxanthellae), the algal pigments, or both has been linked to heat stress (Jokiel and Coles 1990; Brown 1997). Although a proposed relationship to global warming has not been firmly established (Atwood et al. 1992; Brown 1997), the prevalent concept of bleaching is that something terribly wrong is occurring during the warm season of so-called "bleaching years" that is not happening in other years. Although extreme environmental events have been linked to regional observations of bleaching in the past, including osmotic stress related to storms and tidal flow (Goreau 1964; Lang et al. 1988; Van Woesik et al. 1995), photobleaching in relation to high ultraviolet (UV) light exposure (Gleason and Wellington 1993) and elevated seawater temperatures associated with El Niño (Glynn 1993), the mechanisms of widespread seasonal thermal bleaching are apparently much more subtle.

Research projects on thermal bleaching events during the last 25 yr have historically begun *after* the first observations of discoloration of corals, making it easier to categorize these events as unusual disasters rather than in the context of the normal life of a coral (e.g., Jaap 1979, 1985; Porter et al. 1989; Szmant and Gassman 1990). Although laboratory experiments have documented decreased densities of symbiotic dinoflagellate and pigment content in corals correlated with acute increases in temperature (Coles and Jokiel 1978; Hoegh-Guldberg and Smith 1989; Fitt and Warner 1995), their relevance to the more gradual temperature changes found in nature have been difficult to establish. Two notable exceptions include Jokiel and Coles' (1977) precocious study detailing the sublethal effects of long-term exposure to temperatures only 1 or 2°C higher than the ambient mean (e.g., 28–30°C) on corals in Hawaii. In a second seminal thermal study, Glynn and D'Croz (1990) provided definitive data showing steady decreases in densities of symbiotic dinoflagellates cm^{-2} from *Pocillopora damicornis* in the Eastern Pacific at 28, 30, and 32°C over a 12-week period, with the rate of decrease being directly proportional to the increase in temperature. Even with the results of these studies providing a framework for what might be happening to corals in the field, it is interesting to note that except for the monitoring of the Caribbean 1987 bleaching event (Porter et al. 1989), recovery of corals on a Florida reef over the course of the next 2 yr (Szmant and Gassman 1990; Fitt et al. 1993), and Stimson's (1997) aggregation of data over an 8-yr period documenting high and low periods of symbiont densities in the Pacific coral *P. damicornis*, there have been few studies designed to investigate what might actually be happening to corals on the reef throughout the year.

With this goal in mind, we established a long-term coral tissue monitoring program for five species of reef corals in the Bahamas and in the Florida Keys. Results from 4 yr of seasonal sampling of coral tissue biomass and zooxanthellae densities and their pigment content from the Bahamian sites are presented here. A brief summary of this work was first reported in Science (Fitt et al. 1997; Pennisi 1998).

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Materials and methods

Study site and collection of corals—Corals were collected from four locations in the vicinity of Lee Stocking Island in the Bahamas four times during each year beginning in the Spring of 1995. *Montastrea annularis* and *Montastrea faveolata* were collected from 1–2 m deep off the southern end of Norman's Pond Cay, 3–4 m deep off Iguana Cay (Rainbow Garden Reef), and 13 m deep off the east side of Lee Stocking Island (South Perry Reef). *Acropora cervicornis* was also collected from 13 m at the latter site, as was *Montastrea franksi* starting the third year. Collections at the shallowest site (1–2 m), a fringing patch reef on the east side of the island consisting primarily of *Acropora palmata* and *A. cervicornis,* was begun at the end of the first year.

Six colonies of each species were tagged at each site at the beginning of the study to ensure subsequent collection from the same colony. The only exception was *A. cervicornis,* which was sampled from 1–6 distinct colonies from the same site every collection period, but not necessarily the same colonies each time. All samples of corals were taken from nonshaded areas at or near the tops of each coral colony. Four times a year, pieces of coral approximately 25–50 cm^2 in size were chipped from each replicate colony with a pick and rock hammer, placed in individual prelabeled plastic bags, and transported immediately to the laboratory in an insulated cooler. Collections took place in the early morning. This is an ongoing study with quarterly sampling expected to continue at least through 2003. All data are presented graphically in terms of mean ± 95% confidence intervals. Significant differences were determined by repeated measures analysis of variance (ANOVA, Statview), again at the $P < 0.05$ level of confidence.

Determination of coral biomass and zooxanathellae—Freshly collected pieces of coral were preferably split into halves if large enough, or replicate pieces were collected if small (<10 cm^2) or from *A. cervicornis* and placed in petri dishes containing reef seawater until processed. The tissue covering one piece from each colony was removed with a recirculating Waterpik® containing distilled water. The tops of pieces of *Montastrea* species, the entire branch of *A. cervicornis* at least 1 cm away from the tip, and approximately equal areas covering both sun and shade sides of *A. palmata* were waterpiked. The "blastate" was immediately frozen (−20°C) and later lyophilized prior to dry weight analysis. Dry weight was determined for three replicate subsamples of lyophilized homogenate before ashing in a Fisher Scientific muffle furnace for 4 h at 500°C. Ash-free dry weight was calculated from the difference between dry weight and ash weight.

The other half-piece of coral was waterpiked with filtered seawater (0.45 μm), the resulting homogenized slurry was subsampled twice (15 ml) for chlorophyll *a* (Chl *a*) determinations, and a small aliquot (ca. 1 ml) was preserved with formalin for zooxanthellae counts. Chlorophyll samples were centrifuged (1,500 rpm, 3–5 min) to pellet the algae, then frozen at least overnight to help break open the cells. Acetone was added to the frozen pellet, and the resulting mixture was homogenized in a small glass tissue grinder (90% final concentration), allowed to develop overnight at −20°C, and centrifuged, and absorbances were read on a spectrophotometer. Chl *a* content was calculated using equations of Jeffery and Humphrey (1975). Densities of symbiotic dinoflagellates were calculated from replicate (n = 8–10) hemocytometer counts and surface area determinations by correlations between weight and surface area of aluminum foil.

Temperature measurements—Ambient seawater temperatures were recorded at each site with HOBO Temperature Loggers (±0.1°C), with data points taken automatically every 1 h and daily averages calculated and plotted.

Statistical analyses—Initially all data sets were tested for assumptions of normality and homogeneity of variance, and if necessary, data were transformed to maintain normality in subsequent ANOVA. Significance of variables measured over the length of the study were determined by repeated measures ANOVA, with depth the between-factor with species occurring at more than one depth. Interspecific differences were investigated by a one-factor (coral species) and two-factor (coral species and depth) repeated measures ANOVA. Significant differences between main effects (coral species or depth) were further analyzed by Scheffe post hoc analysis for significance at the $P < 0.05$ level.

Results

Density of symbiotic dinoflagellates—Every year the lowest densities of zooxanthellae occurred in the late summer or early fall (Fig. 1). Algal density increased rapidly in the late fall to peak levels in the winter and/or spring, decreasing again during the next summer period. These seasonal fluctuations were significant over time ($P < 0.05$) for all species of corals studied, except for the shallow (1–2 m) staghorn coral, *A. cervicornis,* where the number of colonies available for sampling (n = 2–3) was too small for statistical analysis.

There was significantly lower ($P < 0.0001$) symbiont density within *M. faveolata* in the deeper corals (14 m) compared to the other two depths (1–2 and 3–4 m), but in *M. annularis,* these differences were not significant ($P > 0.05$). However, both species of coral showed a significant interactive effect between time and depth ($P < 0.0001$), with many time points showing greater fluctuations in symbiont density in corals collected at the intermediate and deeper depths compared to the shallow site. Density of zooxanthellae in *A. cervicornis* collected from 1–2 and 13 m were not significantly different.

Pigment content—Concentrations of Chl *a* per zooxanthella were also significantly higher in winter than summer for all species of corals ($P < 0.05$), except in deep (13 m) colonies of *A. cervicornis,* where algal cells maintained more uniform levels of pigment at significantly ($P < 0.05$) higher levels than *A. cervicornis* in shallow water (Fig. 2). Symbiotic dinoflagellates in *M. annularis* from 14 m had significantly higher cellular chlorophyll content compared to the same species at the shallower depths ($P < 0.0001$), whereas there was no significant difference ($P > 0.05$) in Chl *a* content in symbionts from *M. faveolata* between depths. How-

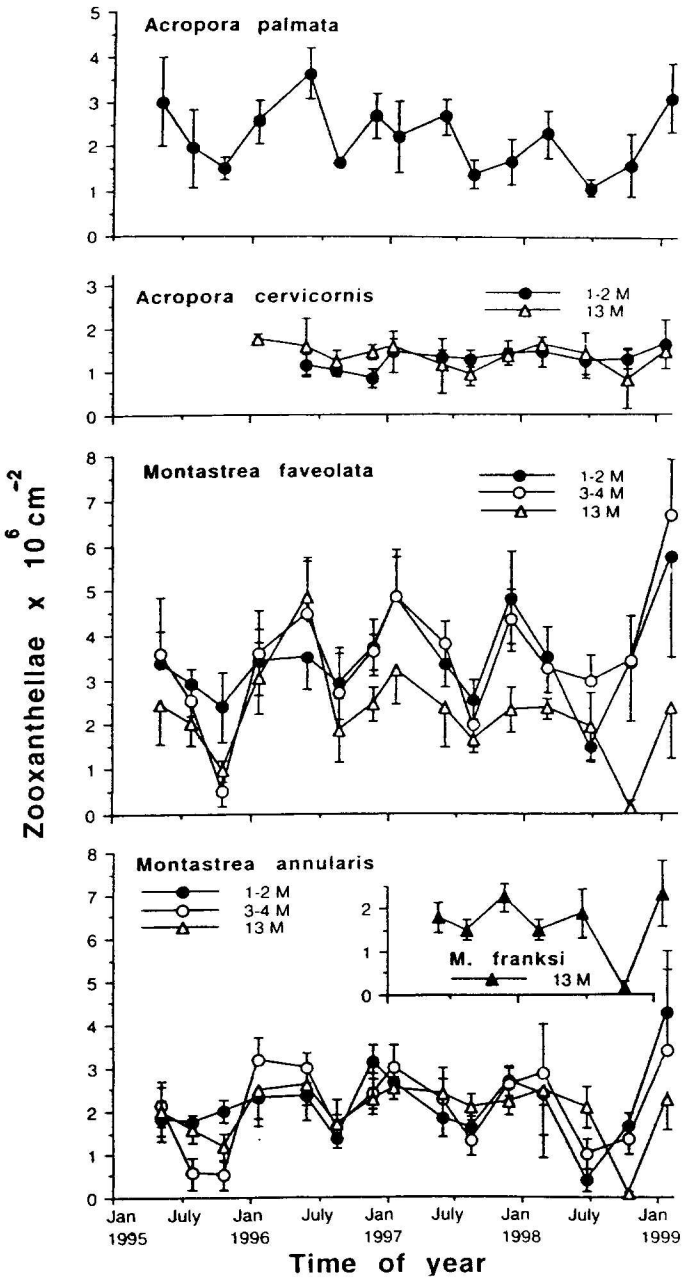

Fig. 1. Density of zooxanthellae in relation to time of year. Coral species and depths are noted on each graph. The *x*-axis is marked by calendar date (tick marks at 1 January and 1 July). Data are expressed as mean ± 95% confidence interval; some error bars are too small to see.

ever, there were interactive effects with time and depth for *M. faveolata* ($P = 0.001$) and *M. annularis* ($P = 0.06$), which indicates that there were differences in the rates of seasonal increase and decrease in pigment content in zooxanthellae from corals at different depths, probably reflecting the differences in seasonal variation in photon flux density (PFD) at the different depths.

With both density of symbionts and pigment content decreasing during the summer, it is not surprising that Chl *a* cm^{-2} was also lowest then (Fig. 3). All species of corals

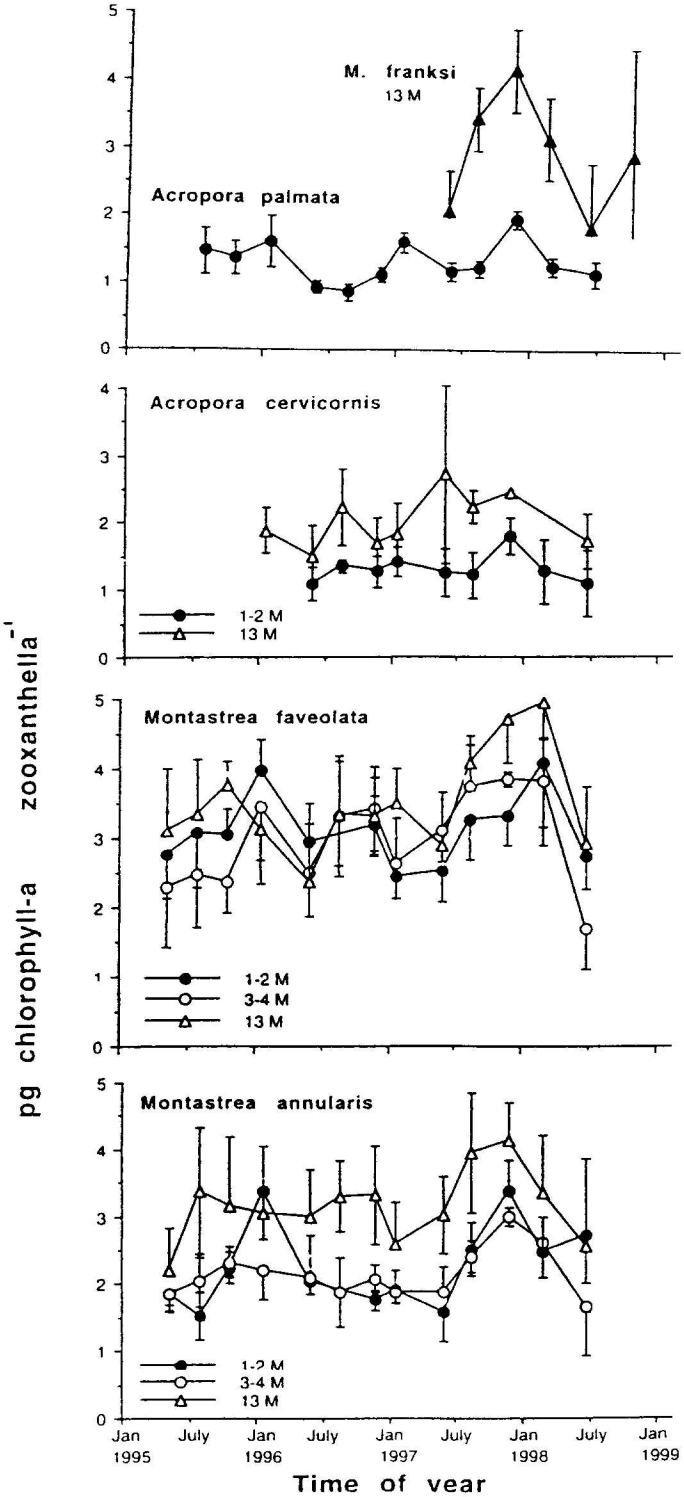

Fig. 2. Chl *a* content of zooxanthellae in relation to time of year. Coral species and depths are noted on each graph. The *x*-axis is marked by calendar date (tick marks at 1 January and 1 July). Data are expressed as mean ± 95% confidence interval; some error bars are too small to see.

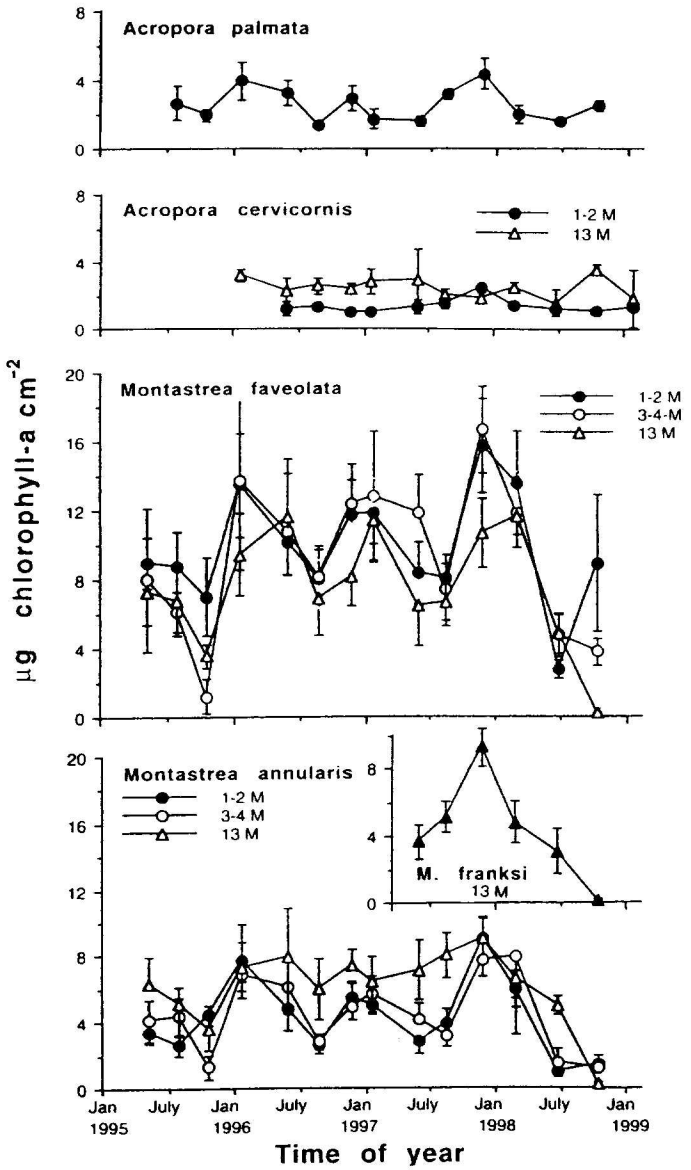

Fig. 3. Chl *a* content of coral tissue expressed on a surface area basis in relation to time of year. Coral species and depths are noted on each graph. The *x*-axis is marked by calendar date (tick marks at 1 January and 1 July). Data are expressed as mean ± 95% confidence interval; some error bars are too small to see.

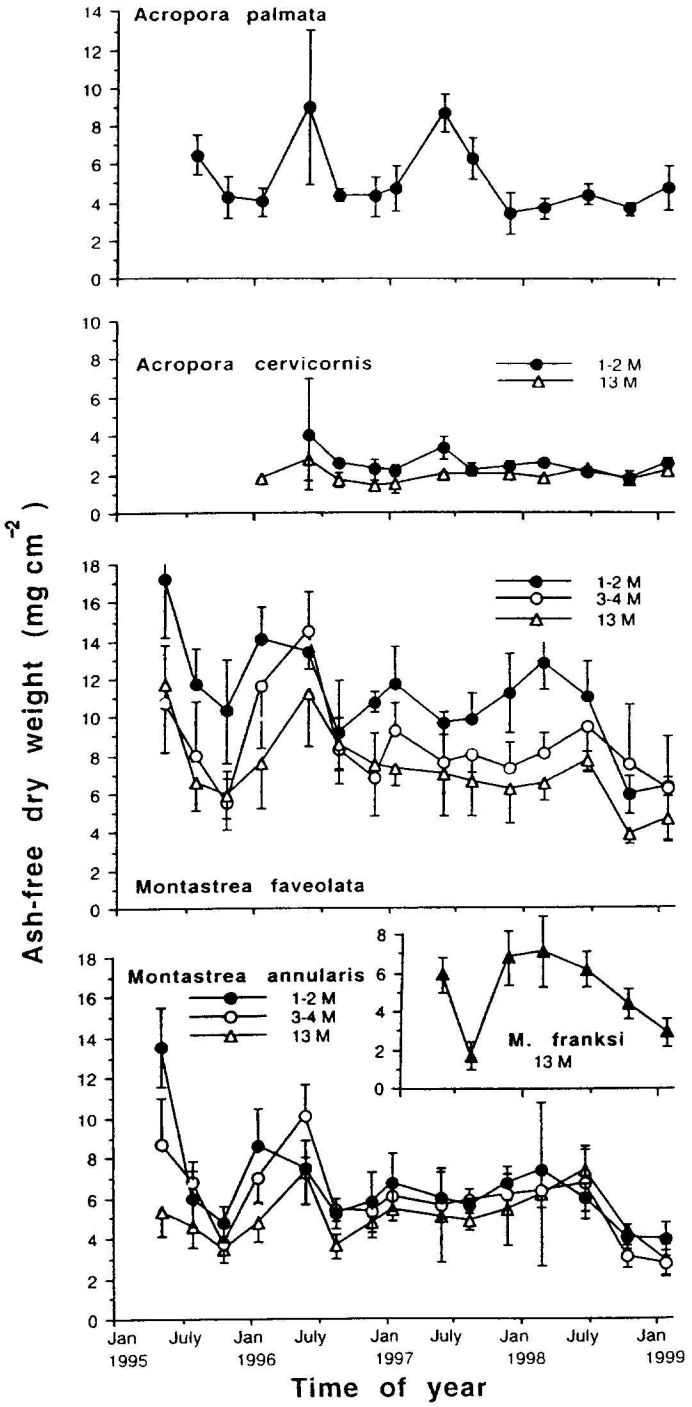

Fig. 4. Coral tissue weight (ash-free dry weight) expressed per unit surface area in relation to time of year. Coral species and depths are noted on each graph. The *x*-axis is marked by calendar date (tick marks at 1 January and 1 July). Data are expressed as mean ± 95% confidence interval; some error bars are too small to see.

showed significant seasonality in Chl *a* cm^{-2} ($P < 0.0005$). Both *M. annularis* and *M. faveolata* had significant interactive effects in their pigmentation per unit surface area between time and depth ($P < 0.0001$), indicating that the rates of Chl *a* accumulation in winter and loss during summer were not the same for each depth. In spite of these yearly cycles in pigmentation, only *M. annularis* and *M. faveolata* collected during October 1995 from the 3–4- and 13-m sites and most of the *Montastrea* spp. collected during late summer and fall of 1998 appeared visibly lighter in color to the observer; no other corals appeared white, mottled, or otherwise bleached to the human eye during this 4-yr period.

Coral tissue biomass—The tissue biomass of all corals expressed as ash-free dry weight also varied significantly seasonally ($P = 0.02$), with the lowest values again in the summer and fall (Fig. 4). Peak tissue biomass typically occurred in the spring, usually lagging one sample period be-

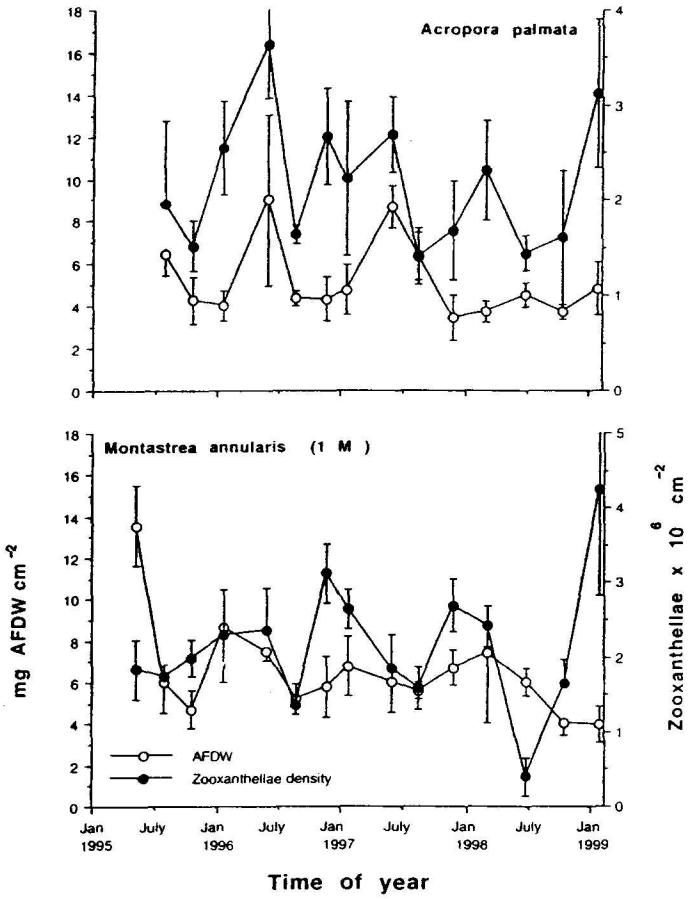

Fig. 5. A typical representation of the relationship between coral tissue weight (ash-free dry weight) in relation to density of zooxanthellae, both expressed per unit surface area. The *x*-axis is marked by calendar date (tick marks at 1 January and 1 July). Data are expressed as mean ± 95% confidence interval; some error bars are too small to see.

hind the initial peaks of zooxanthellae density (i.e., Fig. 5). Tissue weight of *M. annularis* and *M. faveolata* were significantly ($P = 0.02$ and 0.007, respectively) higher in shallow corals compared to deeper corals of the same species at 14 m (Fig. 4). There was no significant effect for depth for *A. cervicornis*. Both *M. annularis* and *M. faveolata* had significant interactive effects for time and depth ($P < 0.02$) for ash-free dry weight, indicating that the seasonal rise and fall in tissue weight differed depending on depth. *A. cervicornis* also showed a significant interactive effect for time and depth ($P < 0.001$), as corals at the deeper site demonstrated greater degrees of fluctuation in biomass over time relative to the shallow site.

Species differences—Densities of symbiotic dinoflagellates in *M. faveolata*, as well as tissue biomass, were significantly higher than those in *M. annularis* at the shallow and intermediate depths. However at the deepest site (13 m), there were no significant differences ($P > 0.05$) in symbiont density between any of the three species of *Montastrea*. Densities of symbionts in *A. palmata* varied seasonally between 1.5 and 3.5 × 10^6 cells cm^{-2}, significantly higher ($P <$ 0.0001) than *A. cervicornis* at any depth, which contained ca. 50% fewer symbionts in summer compared to winter. There was no interactive effect for time–*Montastrea* species–depth ($P = 0.28$), indicating that for each site, *Montastrea* species showed similar fluctuations in cell density over the course of the study.

Symbiotic dinoflagellates in *M. faveolata* contained significantly more Chl *a* per cell ($P < 0.05$) than those in either *M. franksii* or *M. annularis* at all depths, except in comparisons with the latter species at 13 m. Deeper (13 m) *A. cervicornis* had higher Chl *a* content per cell than either *A. palmata* or *A. cervicornis* in shallow water (1–2 m). The significant interactive effect for time–coral species–depth ($P = 0.0265$) indicates that cellular chlorophyll was changing at different rates between the different coral species.

Comparisons of Chl *a* per unit surface area yielded similar results to those seen per cellular unit, with *M. faveolata* exhibiting greater pigmentation than *M. annularis* at all depths ($P < 0.0005$). At the deepest site (13 m), *M. annularis* and *M. faveolata* both had higher pigmentation than *M. franksi*. Chl *a* per unit of surface area for *A. palmata* and deeper *A. cervicornis* were both significantly higher ($P = 0.0016$) than pigmentation of shallow *A. cervicornis*. There was a significant interactive effect with time–coral species–depth for this variable ($P < 0.0004$).

Interspecific comparisons of ash-free dry weight showed tissue biomass of *M. faveolata* was significantly greater than tissue biomass of *M. annularis* at all depths ($P < 0.0001$). However, because of the limited sampling period of *M. franksi*, comparisons of the three species at 13 m over only seven collection dates (through January 1999) show little difference ($P > 0.05$), even though it is clear that *M. franksi* more closely resembles *M. annularis* than *M. faveolata* in terms of other variables measured here. There was significantly higher ($P < 0.0001$) biomass of *A. palmata* than that of *A. cervicornis* at either depth. Not surprisingly, there were significant interactive effects between time–coral species–depth ($P < 0.0016$), indicating that biomass did not change equally for each species over time.

Seasonal seawater temperature—Mean daily seawater temperatures ranged from 22–33°C, with lowest temperatures recorded on the backreef during the winter and highest temperatures from the shallowest backreef site during the summer (Fig. 6). The deepest site (13 m) was on a forereef that experienced the least fluctuation in seawater temperature. The summers of 1995 and 1998 had higher seawater temperatures in general, including more days with temperatures over 30°C and 31°C at the shallower sites, compared to 1996 and 1997 (Fig. 6).

Discussion

The results of up to 4 yr of monitoring five framework species of Caribbean reef corals in the Bahamas clearly showed seasonal cycles in their tissue biomass and the symbiotic dinoflagellates living therein. Densities of zooxanthellae were highest during the coldest part of the year, generally preceding peaks in coral tissue biomass in the spring. Both parameters declined through the summer and reached

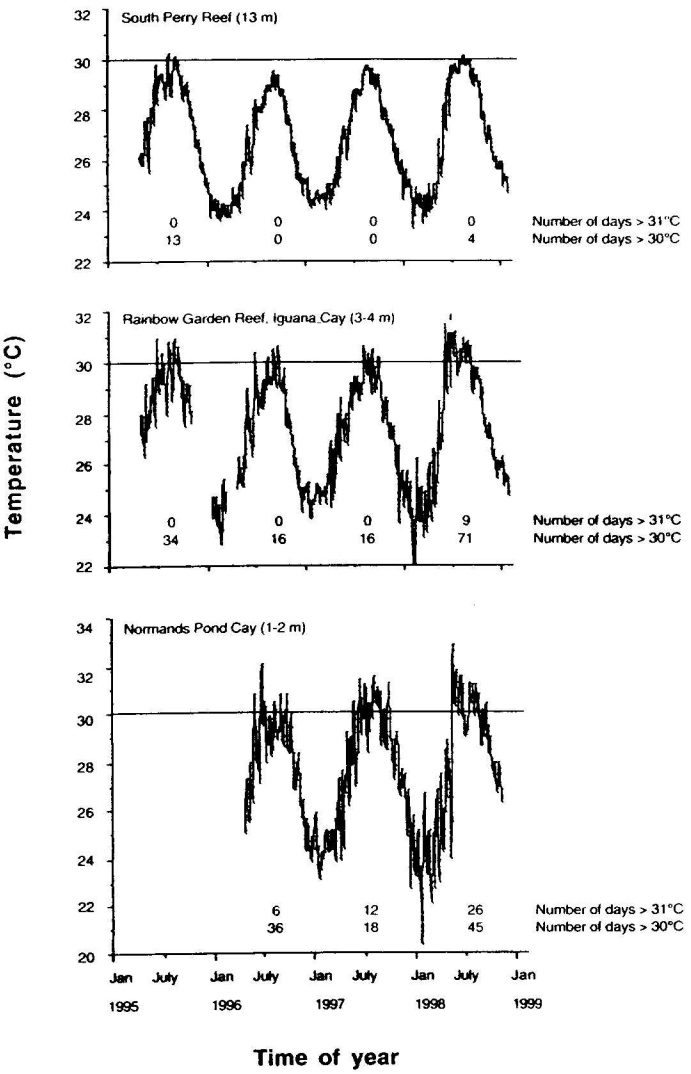

Fig. 6. Seawater temperatures recorded off Lee Stocking Island in the Bahamas with Hobo-Temp® recorders between 1995 and 1999. (A) South Perry Reef, (B) Rainbow Garden Reef, and (C) Normans Pond Cay. Line denotes 30°C.

low levels during the late summer or fall, depending on the year and sampling time. These patterns were seen for every coral sampled at all depths (except for symbiont density in shallow *A. cervicornis*) and every year in the Bahamas. In addition, these same cycles were also found for the same five species of corals sampled at three depths and four sites in the Florida Keys (Fitt in prep.). Based on the data, showing 15–90% yearly decreases in zooxanthellae density depending on the species, depth, site and year, and less dramatic pigment decreases, it is clear that all of the colonies sampled experience bleaching (=loss of zooxanthellae and/or photosynthetic pigments) every year, regardless of whether colonies actually appeared lighter in color to the human observer. In fact, during this study, corals appeared visibly bleached by divers only during the summers of 1995 and 1998.

There are several interpretations as to the driving force for the cycles observed. The first obvious explanation for the reductions in coral tissue biomass from the spring highs through the late summer–fall lows involves steadily increasing seawater temperatures and their effect on increasing respiratory metabolism and decreasing energy reserves in the coral tissue. Wintertime minimum temperatures reach as low as 20°C in January and February, depending on location in the Caribbean (e.g., Shinn 1966), rising steadily through the spring with broad summertime peaks near 30°C for a month or more (e.g., Fig. 6). Respiratory rates would hypothetically double over this temperature range, assuming a Q_{10} of 2. In fact, respiration rates measured from *M. annularis* between winter and summer off Key Largo, Florida, in 1992 nearly doubled (Q_{10} = 1.8) (Porter and Szmant unpubl. data). Similarly, respiration rates of the anemone *Aiptasia pulchella* in Hawaii were twice as high in July as they were in October (Muller-Parker 1987), and those of the symbiotic jellyfish *Cassiopea xamachana* were a third higher in September (29.9°C) than in January (24.2°C) in the Florida Keys (Verde and McCloskey 1998).

Densities of symbiotic dinoflagellates may also be influenced by the effects of seawater temperature on algal physiology in at least three different ways. First, optimum growth and photosynthetic rates of zooxanthellae vary with the particular type of *Symbiodinium* sp., with some species growing at maximum rates between 26 and 32°C, while others grow fastest at 26°C, slower at 30°C, and not at all at 32°C (Warner, Schmidt, Fitt, in prep.). Unfortunately, the symbionts living in Acroporid corals from the Caribbean, as well as those from species of *Montastrea,* have not been cultured, and it is not clear if these particular dinoflagellates grow in their host during all seasons of the year. However, two studies suggest that symbiotic dinoflagellates grow faster in their host during the fall and winter when water temperatures are cooler than in the summer. Growth rates of symbionts living in bleached *M. annularis* on the reef increased significantly the winter following the 1987 summertime bleaching event in the Florida Keys (Fitt et al. 1993), and symbionts in the anemone *A. pulchella* from Hawaii grew four times faster and exhibited 33% higher photosynthesis rates in the fall compared to summer (Muller-Parker 1987). In addition, Stimson (1997) found that the density of zooxanthellae in the tissues of the Hawaiian coral *P. damicornis* taken from sporadic field collections over a 5-yr period was about twice as high in winter as in summer, correlating negatively with average sunlight and positively with dissolved nitrate content and temperature of the seawater (see also Fagoonee et al. 1999). In contrast, Muller-Parker (1987), working on *A. pulchella* at the same Hawaiian location, concluded that growth of zooxanthellae in these anemones was independent of ambient irradiance. More recently, Brown et al. (in press) correlated rising sea surface temperature (SST) and increasing photosynthetically active radiation (PAR) dose during the dry season with relatively lower symbiont density and increased algal densities and pigments when SST and PAR were lower during the wet season for four species of shallow-water corals in Thailand.

A second form of influence of temperature on algal physiology involves heat stress. Symbiotic dinoflagellates in *M. annularis* maintained in aquaria for 24 h at 32°C exhibited classic symptoms of heat stress indicative of irreversible

photosystem damage, also known as "chronic" photoinhibition (Fitt and Warner 1995; Warner et al. 1996). When seawater temperatures in the Florida Keys in the summer of 1997 rose to 30–31°C (1°C higher than average highs in the previous 5 yr), the same irreversible photosystem damage was documented for the first time in zooxanthellate corals living on the reef (Warner et al. 1999).

Third, carbon fixation by symbiotic dinoflagellates may be reduced during periods of high light due to reversible down-regulation of photosynthesis, also known as dynamic photoinhibition. Recent work on IndoPacific corals living in shallow water shows that such a pathway functions in symbiotic dinoflagellates, whereby cycling of specific carotenoids diverts harmful "extra" photons away from chlorophyll reaction centers, which may subsequently lower photosynthetic output during the brightest time of day (Brown et al. 1999). This phenomenon may explain the results of some diel studies showing midday reductions in maximum photosynthesis of intact shallow-water corals (e.g., Chalker and Taylor 1978; Battey and Porter 1988).

Symbiotic dinoflagellates contribute much of their photosynthate to their host, which the host can use for respiration, growth, and reproduction (Muscatine 1990). The fact that zooxanthellae densities increased late in the year *before* the seasonal increase in coral tissue biomass suggests a functional relationship between these two parameters. With respiratory carbon demand from intact coral potentially doubling in the summer, coupled with both dynamic and chronic photoinhibition of photosynthesis of symbionts (Warner et al. 1999), it is not surprising that tissue biomass of corals decreases in summer and fall months.

Sometime in the fall, water temperatures begin to decrease in South Florida and the Caribbean Sea. The timing of this decline in temperature varies every year, usually "stepping" down in response to continental cold fronts moving south into the Caribbean (Fig. 6, Fitt and Costley 1998). So-called bleaching years have occurred in the past when these cold fronts stalled north of the Florida Keys and seawater temperatures remained near their summertime highs for prolonged periods of time, well into the fall. For instance during the Caribbean-wide bleaching event of 1987, seawater temperatures in South Florida remained at (*not* above) their summertime mean average of 29–30°C through November (Attwood et al. 1992; Fitt et al. 1993). Continuation of the summertime decline in algal symbionts into November and December would soon result in densities less than 0.5×10^6 zooxanthellae cm^{-2} for most of the *Montastrea* species, a density at which the corals look tan or white. It is important to note that in the 1987 event, even pure-white *M. annularis* had 10–25% of their complement of zooxanthellae (Porter et al. 1989; Fitt et al. 1993). However, it is not hard to imagine complete loss of symbionts if the warm water were to remain even longer. Such was apparently the case during the 1982–1983 El Niño when Glynn (1983) documented the total absence of symbiotic dinoflagellates in tissues of corals in the Eastern Pacific off Panama; those corals apparently did not regain symbionts and experienced devastating (up to 97%) mortality (Glynn and D'Croz 1990). In a related scenario, seawater temperatures *higher* than the average mean, such as those experienced by corals on the Florida Reef Tract during the summer of 1997, would induce a more rapid decline in symbiont density, as clearly illustrated in laboratory experiments (Glynn and D'Croz 1990).

Spawning occurs in both Acroporids and species of *Montastrea* in the summer and, depending on the fecundity of the coral, could account for significant reductions in tissue biomass, especially lipids (Battey et al. 1998). Sampling in August in the current study was designed to precede these spawning events in the *Montastreas,* such that any effect of spawning would be seen following the August collection date. Unfortunately samples were taken only four times a year; more frequent sampling might better distinguish the effects of events such as spawning. Constant reduction of coral tissue biomass from late spring through the summer, documented here, seems counterintuitive to the long-held belief that summertime is when corals build up biomass for reproduction, which most often occurs in the late summer and fall (Szmant 1996). However, Szmant and Gassman (1990) found no evidence of spawning in bleached corals during 1987 and 1988 spawning periods, implying that spawning success varies yearly depending on the factors responsible for driving the tissue biomass lower at different rates during different years. All of these data strongly suggest that corals spawn only if they still have enough energy stores left when spawning time arrives.

Depth gradients of densities of symbiotic dinoflagellates and coral tissue biomass as seen here have been known for years (e.g., McCloskey and Muscatine 1984; Battey and Porter 1988). Some authors have proposed that the decrease in symbiont density with depth is a response to decreased PFD, even as symbiotic algae acclimate through increased algal pigments and apparent avoidance of self-shading (e.g., Dubinsky et al. 1984). Decreased photosynthate translocated from the symbiotic dinoflagellates is thus thought to result in lower coral tissue biomass with depth. Perhaps the reason so many corals at depth in the Bahamas and the Florida Keys appeared lighter in color before shallower corals during both 1987 and 1997 is because, although they may exhibit the same rate of symbiont decrease, they started out with lower densities of symbionts and thinner coral tissue than their shallow-water counterparts. Similar arguments could be used to explain the decreased percent cover of corals on a reef; longer periods of warm water and more frequent episodes of higher than normal summertime temperatures might result in skinnier and more vulnerable corals the next year.

In contrast, corals at the Rainbow Garden site (3–4 m) lost most of their symbionts (to ca. 0.5×10^6 cells cm^{-2}) during the summer of 1995, similar to the high-saline and thermal bleaching patterns described by Lang et al. (1988) at the same site. The high densities of symbionts found at 13 and 3–4 m in *M. annularis* and *M. faveolata* following the summer of 1995 is reminiscent of the recovery patterns of bleached *M. annularis* collected from the Florida Keys following the 1987 bleaching event (Fitt et al. 1993), where spectacular growth rates of symbionts were documented within corals containing low densities of symbionts. We speculated at the time that higher than normal levels of intracellular nutrients might have been available for algal growth in the corals containing low densities of symbionts, which might result in transient higher than normal densities

of zooxanthellae, as seen in the present study. In fact, it was clear from measurements taken during our October 1995 collection that the 13 and 3–4 m *Montastrea* spp. corals were in recovery phase, with normal levels of photosynthetic efficiency and chlorophyll content from the remaining symbionts recorded.

Dissolved inorganic nutrients also influence densities of symbiotic dinoflagellates in corals, as well as their pigmentation (Muscatine et al. 1989; Hoegh-Guldberg 1994; Muller-Parker et al. 1994). Stimson (1994) correlated density of symbionts from *P. damicornis* with dissolved nitrate concentration in seawater in Hawaii (cf. Fagoonee et al. 1999), although it is not clear if these symbiotic dinoflagellates would take up nitrate with ammonium available in the seawater. There is little data on seasonal variation of dissolved inorganic nitrogen or dissolved inorganic phosphorus on Caribbean reefs that might correlate with and contribute to the cycles observed (e.g., Szmant and Forrester 1996).

On the basis of results of this study, we hypothesize that all reef corals worldwide exhibit similar seasonal cycles (1) with lowest coral tissue biomass and densities of symbiotic dinoflagellates at the end of the season with the warmest seawater temperatures, (2) with rapid regrowth of symbionts only after seawater temperatures decrease, and (3) preceding a somewhat slower recovery of coral tissue biomass relative to the recovery rates of symbionts. Obviously the longer ocean temperatures remain at the average summertime maximum, the lower the densities of symbiotic dinoflagellates will go. Furthermore, years with higher than normal average seawater temperatures (e.g., El Niño years) will be associated with steeper downward slopes in symbiont density and coral tissue biomass over time, possibly resulting in the visibly tan or white corals characteristic of past bleaching years if the conditions persist long enough for the densities of symbionts to fall below 0.5 million symbionts cm^{-2}. Lower densities of symbiotic dinoflagellates during consecutive summers may not allow coral tissue biomass to fully recover by spring, possible leading to tissue and colony death.

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