

Reduction of zooxanthellae density, chlorophyll *a* concentration, and tissue thickness of the coral *Montastraea faveolata* (Scleractinia) when competing with mixed turf algae

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Abstract

We evaluated the effects of competition for space between mixed turf algae (MTA) and the hermatypic coral *Montastraea faveolata* Ellis and Solander (1786) using reciprocal transplantation of 17 cm² cores and by measuring the response of some biological parameters of the coral: zooxanthellae density, mitotic index, chlorophyll *a* (Chl *a*) concentration, and tissue thickness. Mitotic index and Chl *a* zooxanthellae⁻¹ were not significantly affected by the competition, but zooxanthellae density, Chl *a* cm⁻², and tissue thickness were reduced in *M. faveolata* tissue surrounded by algae. Lower values have been reported for these three biological parameters of scleractinian corals subjected to stress conditions. Stressed *M. faveolata* surrounded by MTA were completely overgrown in 6–9 months. MTA frequently formed unattached cushions before the algae were attached to the coral skeleton. The cushions could be affecting *M. faveolata* by shading the coral tissue beneath the algae and probably causing stress to the tissue. Trapped sediments in the cushions may also be affecting *M. faveolata* by trapping sediments that cause smothering or burial of coral tissue. This is the first demonstration that algae directly stress a coral species and that MTA can be superior competitors than *M. faveolata* under experimental conditions. *M. faveolata* is sensitive to algae and bacteria, and the outlook for this coral species is poor if deleterious conditions act together in the Caribbean Sea.

Deterioration of coral reef health in several parts of the world, registered as changes in communities initially dominated by corals and their transformation to reefs dominated by algae, has emphasized the importance of studying the competition between algae and corals (Lirman 2001). Competition between these organisms is a critical process that determines their abundance and the community structure of a coral reef, especially under degradation events of the reef such as overfishing, dredging, and eutrophication (McCook 2001). Loss of reef health is becoming more frequent as a result of the use of marine resources and coastal development, particularly in the region of the Caribbean Sea, including the Mexican Caribbean (Hughes 1994; Lang et al. 1998; Gardner et al. 2003). Despite the importance of studying algal-coral competition in order to understand what might be occurring during the degradation of coral reefs, there are very few studies critically examining the nature of coral-algal interactions (McCook 2001).

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Many reefs are threatened worldwide (Hughes et al. 2003), presumably because overfishing and contamination (Hughes 1994) are exceeding the resilience capacity of coral-dinoflagellate symbiosis. Wilkinson (2002) estimated that 30% of coral reefs are already greatly damaged and around 60% may be lost by 2030. An increase in macroalgal cover has been reported for numerous individual reefs from the Caribbean basin, where coral cover has diminished from ~50% in the 1970s to ~10% in 2001 (Gardner et al. 2003).

The overgrowth of algae in reef systems has been evaluated in different forms: (1) using experiments that directly manipulate the competitors (Tanner 1995; McCook 2001; River and Edmunds 2001), the abundance of herbivores (Belliveau and Paul 2002), or both (Jompa and McCook 2002a,b); (2) establishing correlations (nonindicative of causality) between the abundance of both groups (Lapointe et al. 1997); (3) and by direct observations (Lirman 2001). Nevertheless, scant experimental evidence of the competition between algae and corals is available, and the existing information is frequently anecdotal (McCook 2001; McCook et al. 2001).

Algae can influence the growth, reproduction, and survival of coral species (Lirman 2001; Jompa and McCook 2003a,b), and hence their fitness. For example, River and Edmunds (2001) reported that the coral *Porites porites* reduced its growth when exposed to shading and abrasion by the brown alga *Sargassum hystrix*, whereas Tanner (1995) found that the fecundity of *Acropora palifera* was twice as large in colonies located in areas where algae were removed. Also, Jompa and McCook (2002a,b) observed an increment of *Porites cylindrica* mortality due to overgrowth of the brown alga *Lobophora variegata* in the basal part of the coral. Filamentous algae can certainly overgrow and kill corals (McCook et al. 2001, Jompa and McCook 2003a,b), but in some cases algae can be overgrown and displaced by corals (McCook 2001), and sometimes they have no significant

effect on corals (Jompa and McCook 2003a,b; McCook et al. 2001). In at least one case, however, macroalgae (i.e., *Halimeda opuntia*) can indirectly affect coral by hosting bacteria lethal to them (Nugues et al. 2004).

Hermatypic corals undergo changes in some biological parameters involved in their growth and maintenance in a coral ecosystem when subjected to stress. Thus, under normal conditions the coral's symbiotic dinoflagellate density is relatively constant, averaging approximately $1.0\text{--}2.5 \times 10^6 \text{ cm}^{-2}$ (Jones and Yellowlees 1997, but see Fagoonee et al. 1999 for seasonal changes in density values). However, a reduction in zooxanthellae density and in Chl *a* concentration was found in *Porites porites* colonies after exposure to copper (Jones 1997). Similarly, Cervino et al. (2003) registered a decrease in zooxanthellae density when they exposed several hermatypic corals to cyanide. Ruiz-Zárte et al. (2000) recorded a reduction of zooxanthellae density in stressed *Manicina areolata* colonies transplanted to an area with a high density of the seagrass *Thalassia testudinum*, where a reduction in light occurred. Jones (1997) mentioned the potential of using the loss of zooxanthellae to assess stress in zooxanthellated corals. Also, Barnes and Lough (1999) suggested that tissue thickness is reduced when environmental conditions are less favorable for corals, and Mendes and Woodley (2002) reported that *Montastraea annularis* underwent a reduction in tissue depth during the first months after the onset of an environmental stress (bleaching) event. Although some biological parameters have been measured in corals subjected to stress, we did not find any work that evaluates biological parameters of corals in response to competition with algae.

The hermatypic coral *M. faveolata* is part of a complex of three sibling species (*Montastraea annularis*, *Montastraea faveolata*, and *Montastraea franksi*) distributed throughout the Caribbean Sea and the Gulf of Mexico (Knowlton et al. 1992). These species are of high ecological importance in the northeastern Atlantic, being one of the most important reef builders in the central-southern region of Quintana Roo (Ruiz-Zárte et al. 2003). A mixture of turf (mainly filamentous) algae grows on the three *Montastraea* and other coral species inhabiting the Mexican Caribbean (Ruiz-Zárte et al. 2003 pers. obs.). Turf algae are the dominant flora on both intertidal and subtidal shores of many tropical and temperate zones (Airoldi 1998). Filamentous turf algae are commonly associated with relatively pristine reef systems and are a major contributor to their high productivity (Klump and McKinnon 1989). Nonetheless, a consistent correlation between algal turf abundance, sediment load, and reduced reef resilience was found by Birrell et al. (2005) in the Great Barrier Reef. It is generally accepted that turf algae do not out-compete healthy adult coral colonies, but rather colonize stressed or dead coral surfaces (Diaz-Pulido and McCook 2002; Jompa and McCook 2003a,b).

The purpose of this study was to evaluate the effect on the biological parameters and cover change of coral tissue of *M. faveolata* when this species competes for space with mixed turf algae (MTA). The biological parameters measured were zooxanthellae density, mitotic index, Chl *a* cm^{-2} , Chl *a* zooxanthellae $^{-1}$, and tissue thickness. Competition is defined as the interaction between coral and algae that can

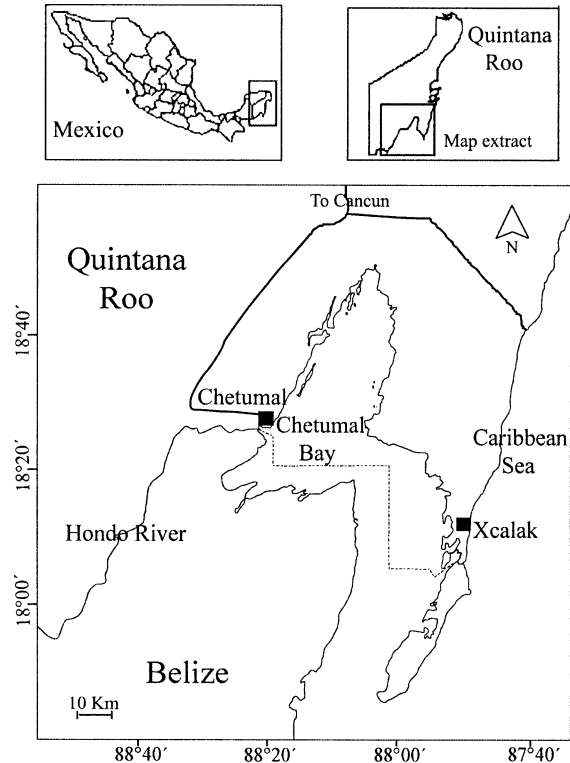


Fig. 1. Study site (Xcalak) in the southern Mexican Caribbean.

result in the growth of one over the other organism when both are experimentally placed side by side.

Materials and methods

Study area—Xcalak is located in the southern part of Quintana Roo ($18^{\circ}15'N$, $87^{\circ}50'W$, Fig. 1). A protected ecological zone called Santuario del Manatí is found on its western side, and its southern part is bordered (5.5 km away) by the Belizean National Park and Marine Reserve Bacalar Chico. The study site is restricted to fishing and located within the National Park Arrecifes de Xcalak, where only small-scale tourism is allowed. The distance between the coastline and the reef crest is approximately 1,000 m. Maximal bottom depth of the study site, in the rear part of the reef, is 2.0 m.

Schmitter-Soto et al. (1997) reported 176 fish species for the study area, the most frequently occurring being *Thalassoma bifasciatum*, *Acanthurus coeruleus*,* *Halichoeres garnoti*, *Chromis cyanea*, *Stegastes partitus*, *Sparisoma aurorenatum*,* and *Scarus taeniopterus** (those marked with an asterisk feed on algae and seagrasses; Sierra et al. 1994). The Huache and Santa Rosa lagoons are found in the posterior part of Xcalak, and both have an open interaction with the sea, originating import and export of organic matter, nutrients, and sediment (Carranza-Sánchez et al. 1996). The sedimentation rate at a site located approximately 50 km from the study site was $422.2 \text{ mg cm}^{-2} \text{ month}^{-1}$ (Cruz-Piñón et al. 2003).

Experimental design—Reciprocal transplantation and controls of healthy *M. faveolata* and MTA growing on dead

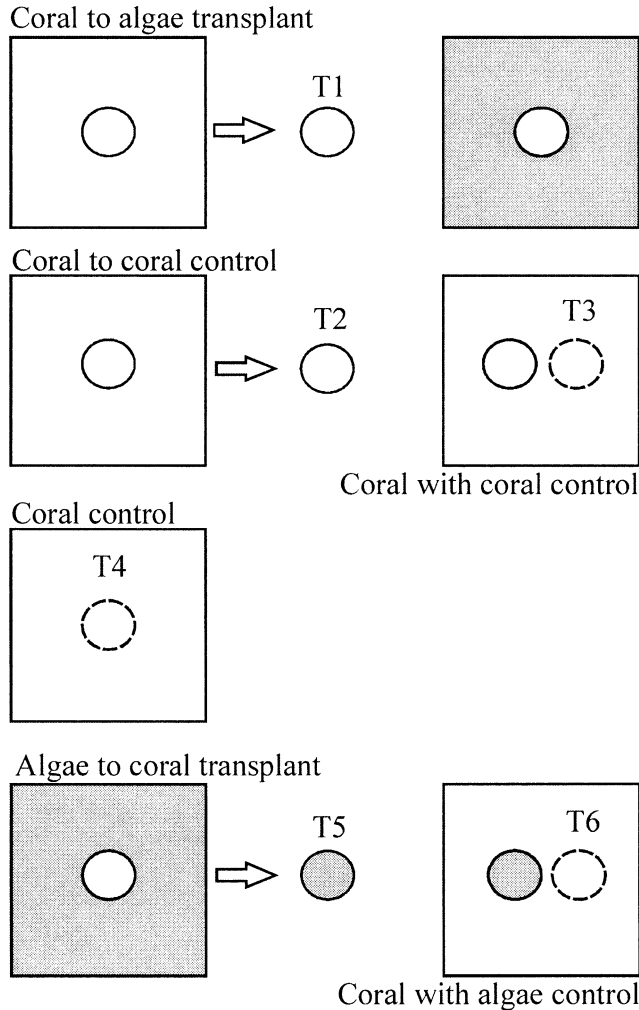


Fig. 2. Graphic representation of the six treatments carried out in this study, including coral colonies (squares) and coral cores (circles; dashed circles represent unmanipulated cores). Healthy corals are represented by open squares and circles, whereas MTA growing on dead corals are represented by filled squares and circles. Treatments: T1 = coral to alga transplant; T2, T3, and T4 = controls of T1; T5 = alga to coral transplant; and T6 = control of T5. See text for details.

corals were conducted to evaluate the effects on *M. faveolata* biological parameters and cover change of coral tissue resulting from the competition with MTA.

Coral to alga transplants—In November 2003 we transplanted cores of healthy coral tissue into dead coral colonies covered by MTA (treatment 1 [T1] in Fig. 2). The cores measured 5 cm in diameter (16.8 cm²), approximately 2 cm in depth, and were extracted with a pneumatic drill. The cores were cemented with marine epoxy glue in a hole previously made with the pneumatic drill in the coral colony hosting the transplants. Each core was identified with a steel rectangle (15 × 55 mm) marked with letters and consecutive numbers. The steel marker was nailed to a dead part of the hosting colony. Three controls were carried out for these transplants. The first control consisted of cores of healthy

corals transplanted into healthy coral colonies (Fig. 2, T2) to test if the biological parameters of the coral were affected by the transplant manipulation. The second control consisted of healthy coral cores collected next to the cores used as the first control (Fig. 2, T3) to test if coral colonies were affected by receiving the transplanted coral cores. The third control consisted of cores obtained from unmanipulated healthy corals (Fig. 2, T4). These were extracted on the two sampling dates, in May 2004 (T4m) and August 2004 (T4a), and at the beginning of the experiment (T4i, in November 2003) to record the biological performance of *M. faveolata* under “natural,” unmanipulated environmental conditions during the course of the experiment and at the beginning of the experiment.

Alga to coral transplants—In November 2003 we also transplanted cores with MTA growing on dead corals into healthy *M. faveolata* colonies (Fig. 2, T5), similar to the transplants described above. The T5 cores were used to calculate the change of coral tissue cover surrounding the MTA. The number of controls established for these transplants was the same as in the coral to alga transplants. However, only one of these controls is given here because the rest are related to the strategies adopted by the algae when competing with *M. faveolata* and will be reported elsewhere. Coral controls for this transplantation consisted of healthy coral cores collected next to the alga transplants (Fig. 2, T6). They were used to test if healthy coral colonies were affected by receiving the algae in transplanted cores.

Before initiating the experiment, we placed the 14 cores used in T1, T2, and T5 inside the upper releasable part of two-part PVC tubes. The lower part of the tubes was cemented into 50 × 42 × 10 cm concrete blocks. The cores in the tubes were left next to the experimental coral colonies for 3 weeks to allow regeneration of coral tissue in its damaged edges. Only complete and well-cut cores were used as transplants. Six to seven replicates of each treatment were extracted in May 2004, and the others in August 2004. In order to evaluate the biological responses of *M. faveolata* under T1–T4 and T6, we measured zooxanthellae density and Chl *a* concentration (as in Carricart-Ganivet 1993), mitotic index (as in Wilkerson et al. 1988), and living tissue thickness (as in Cruz-Piñón et al. 2003).

Changes in coral and algal cover—In addition to the biological measurements of *M. faveolata*, we registered the gains or losses in coral tissue and algal cover in cores of T1 (coral to alga transplant), T5 (alga to coral transplant), and T2 (control of T1) in order to evaluate the course of space competition when both organisms were placed side by side. Monthly digital photos of the cores in experimental colonies were taken from November 2003 to August 2004. A 2.5-cm diameter coin was placed beside the core when taking the photos to later obtain the area occupied by the organisms. The area of healthy coral tissue and MTA was obtained by analyzing the photos in the Scion Image program, release 4.02 for Windows (Scion). Cover change in terms of coral tissue area is reported as negative values because mean coral cover in our experimental treatments always decreased because of MTA.

Table 1. Mean values (\pm standard deviation) of zooxanthellae density, mitotic index, Chl *a* cm^{-2} , Chl *a* zooxanthellae $^{-1}$, and tissue thickness of coral cores in each sampling date and experimental treatment. Raw data. See Fig. 2 and text for details.

Date	Treatment	Zooxanthellae density (10 cm^{-2}) $\times 10^6$	Mitotic index	Chl <i>a</i> ($\mu\text{g cm}^{-2}$)	Chl <i>a</i> ($\mu\text{g Zoox}^{-1}$) $\times 10^{-6}$	Tissue thickness (mm)
Nov	T4i	1.8 \pm 0.6	3.7 \pm 1.1	23.0 \pm 5.0	25.5 \pm 0.0	0.26 \pm 0.01
May	T1	0.9 \pm 0.3	6.3 \pm 1.9	14.1 \pm 6.5	17.0 \pm 7.6	0.23 \pm 0.01
	T2	1.2 \pm 0.2	6.1 \pm 1.0	21.9 \pm 4.7	19.0 \pm 5.1	0.23 \pm 0.03
	T3	1.2 \pm 0.2	7.0 \pm 1.4	17.1 \pm 6.2	14.9 \pm 6.3	0.23 \pm 0.01
	T4m	1.4 \pm 0.3	6.9 \pm 1.1	21.3 \pm 11.1	16.1 \pm 9.7	0.24 \pm 0.02
	T6	1.1 \pm 0.2	7.4 \pm 2.0	19.3 \pm 6.5	18.5 \pm 7.6	0.24 \pm 0.01
Aug	T1	2.9 \pm 0.5	7.9 \pm 1.5	4.6 \pm 3.2	1.8 \pm 1.1	0.20 \pm 0.01
	T2	4.5 \pm 0.7	8.8 \pm 2.3	11.3 \pm 2.4	2.7 \pm 0.6	0.25 \pm 0.01
	T3	3.4 \pm 0.1	7.8 \pm 1.6	11.4 \pm 3.0	3.4 \pm 0.6	0.26 \pm 0.02
	T4a	4.1 \pm 0.1	8.1 \pm 0.6	12.0 \pm 4.1	3.1 \pm 0.8	0.25 \pm 0.01
	T6	4.9 \pm 0.1	8.0 \pm 0.9	13.9 \pm 4.3	2.8 \pm 0.5	0.25 \pm 0.02

Area of coral colonies and height of transplanted cores—We also measured the distance from the sea floor of each core in the experimental colonies and the approximate area of healthy and dead colonies included in the study to test whether these two variables had any effect on the outcome of the changes in cover of coral tissue and MTA. Height of cores was measured by two divers using a metric plastic band (in millimeters) and two plastic tubes: one placed vertically touching the sea bottom and the other horizontally at the height of the core. To estimate the area of a colony, the length of the largest axis was determined and three to eight width measurements were made along that axis. In the laboratory the measurements were scaled onto a millimetric sheet and the area was calculated in the Scion Image program.

Data analyses—Data on the biological parameters of *M. faveolata* were subjected to Cochran's test for homogeneity of group variances. Two-way analysis of variance (ANOVA; factors: treatments and extraction dates) and a student Newman-Keuls post hoc test were performed using the Statistica 4.3 for Windows (Statsoft). Cover data were analyzed as the biological parameters. Pearson's product moment correlation test was used for each treatment to determine the effect of the area of experimental colonies and distance to the bottom of cores on the changes in coral tissue and algal cover.

Results

Reciprocal transplants—MTA caused a deleterious effect on transplanted *M. faveolata* cores. In comparison with the coral controls (T3, T4, and T6), there was a significant ($p < 0.0001$) reduction of zooxanthellae density in *M. faveolata* transplanted to MTA growing on dead corals (T1; Tables 1 and 2). Zooxanthellae density also decreased in T1 in comparison with the remaining control (T2; Table 1), but this difference was not statistically different ($p = 0.17$). In turn, all of the controls (T2, T3, T4, and T6) exhibited significantly ($p < 0.001$) greater concentration of Chl *a* cm^{-2} than *M. faveolata* cores transplanted to MTA (Tables 1 and 2). Tissue thickness was also significantly ($p < 0.001$) reduced in T1 in comparison with the controls (T2, T3, T4, and T6; Tables 1 and 2).

Mean values of zooxanthellae density, mitotic index, and Chl *a* zooxanthellae $^{-1}$ were significantly ($p < 0.0001$) larger in May than in August, whereas Chl *a* cm^{-2} was significantly ($p < 0.0001$) lower in May than in August (Tables 1 and 2). There was no significant interaction between treatment and date for zooxanthellae density, mitotic index, Chl *a* cell^{-1} , and Chl *a* cm^{-2} (Table 2), but there was significant interaction between treatment and date for tissue thickness (Table 2).

Changes in coral and algal cover—*M. faveolata* lost a significant ($p < 0.001$) amount of tissue when in contact with algae (T1, T5) compared with controls (T2, Fig. 3). Overgrowth of *M. faveolata* by MTA was relatively rapid. Four months after initiating the experiment (March 2004), nearly all of the transplanted cores of T1 were at least partially overgrown (see Fig. 4B). In the sixth month (May 2004) we recorded the first coral core completely overgrown by MTA. At the end of the experiment, three of the 14 T1 cores were completely overgrown (Fig. 4C). Overgrowth of algae in T5 was more evident in the fourth month (March), apparently as a result of a sudden appearance of unattached cushions of MTA growing at the edges of the cores. The MTA in the cushions were intermixed with creeping stolons growing laterally from the transplanted cores and were dominated by red filamentous algae, but sometimes by the brown alga *Padina* spp. and *Dictyota* spp. Coral tissue beneath the MTA cushions was alive but much darker in color than the contiguous tissue. Cushions were lost on some occasions, probably because of water movement, but in other cases MTA killed the coral tissue beneath and were eventually attached to the coral skeleton.

Area of coral colonies and height of transplanted cores—There was no significant ($p > 0.05$) correlation between the change in coral cover and the area of the experimental coral colony of T1, T2, and T5 during May ($r^2 = 0.34, 0.06,$ and 0.09 , respectively) and August ($r^2 = 0.02, 0.37,$ and 0.07 , respectively). Similarly, there was no significant ($p > 0.05$) correlation between the change in coral cover and the core's distance from the floor of T1, T2, and T5, either for May ($r^2 = 0.04, 0.04,$ and 0.05 , respectively) or August ($r^2 = 0.32, 0.06,$ and 0.0006 , respectively).

Table 2. Analysis of variance (ANOVA) of the effects of the factor treatments and date on zooxanthellae density, mitotic index, Chl *a* cm⁻², and Chl *a* zooxanthellae⁻¹ of *Montastraea faveolata*. Data were ln+1 transformed.

Source	df	Mean square	F-ratio	p	SNK conclusion
Zooxanthellae density					
Treatment	4	0.38	3.99	<0.0001	Treatments 3, 4, 6 > 1~2
Date	1	21.13	219.72	<0.0001	Aug→May
Treatment × date	4	0.19	1.96	0.11	ns
Cochran's C=0.29					
Mitotic index					
Treatment	4		0.21	0.93	ns
Date	1		9.04	<0.001	Aug→May
Treatment × date	4	0.036	0.90	0.47	ns
Cochran's C=0.20					
Chl <i>a</i> cm⁻²					
Treatment	4	0.78	5.88	<0.0001	Treatments 2, 3, 4, 6 > 1
Date	1	3.96	29.73	<0.0001	May→Aug
Treatment × date	4	0.25	1.89	0.13	ns
Cochran's C=0.19					
Chl <i>a</i> zooxanthellae⁻¹					
Treatment	4	2.04×10 ⁻¹¹	0.42	0.80	ns
Date	1	3.05×10 ⁻⁹	61.87	<0.0001	Aug→May
Treatment × date	4	7.95×10 ⁻¹¹	1.62	0.18	ns
Cochran's C=0.52					
Tissue thickness					
Treatment	4	0.03	5.35	<0.001	Treatments 2, 3, 4, 6 > 1
Date	1	0.02	2.51	0.12	ns
Treatment × date	4	0.03	4.48	<0.01	Significant
Cochran's C=22.43					

Discussion

The competition for space between MTA and *M. faveolata* had a significant effect on the coral tissue of T1 (coral to alga transplant), reducing zooxanthellae density, Chl *a* cm⁻², and tissue thickness. The reduced mean values of the biological parameters of *M. faveolata* were similar to the low values obtained for those parameters in corals subjected to different kinds of stress or unfavorable biological conditions. Under that stress condition, corals reduce zooxanthellae den-

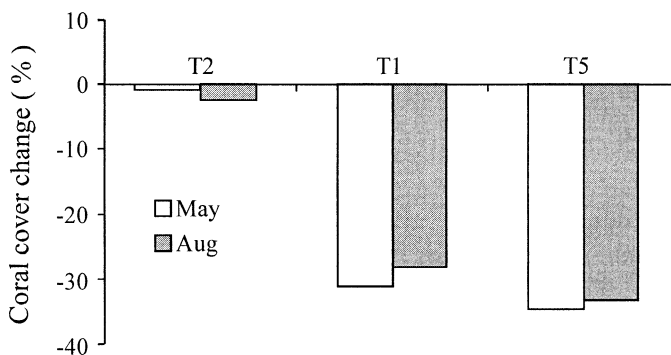
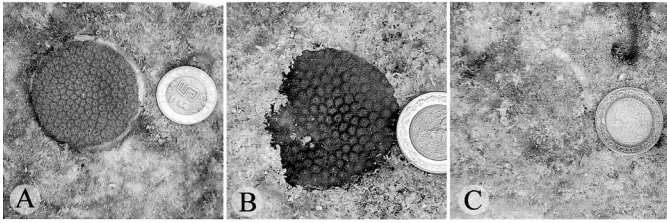


Fig. 3. Percentage of change in coral cover of *M. faveolata* subjected to treatment 2 (control), treatment 1 (coral to alga transplant), and treatment 5 (algae to coral transplant). Data are means of six replicates; negative values indicate that the coral lost area because of MTA. See Fig. 2 and text for details.

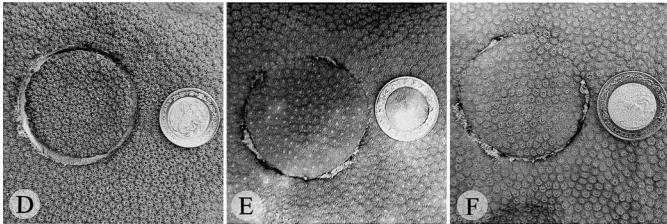
sity, Chl *a* concentration, and tissue thickness (Jones 1997; Ruiz-Zárate et al. 2000; Mendes and Woodley 2002). Thus, Jones (1997) and Barnes and Lough (1999) suggested that zooxanthellae loss and tissue thickness monitoring can be used to assess stress in zooxanthellated corals. The reduction in the biological parameters of *M. faveolata* was apparently caused by the stress imposed on the coral by the competing MTA. It is worth mentioning that coral tissue in T6, next to T5 (with transplanted algae), was not stressed by the algae. This could indicate that a threshold area of colonizing algae surrounding coral tissue needs to be reached in order to have a measurable condition of stress that can be evaluated with coral biological parameters.

Although stress in coral tissue was not measurable in T6, the algae did colonize coral tissue at a similar rate as in the stressed coral cores surrounded by algae (T1). Hence, an initial condition of measurable stress was not needed for MTA to overgrow healthy *M. faveolata*. This is somewhat different to Díaz-Pulido and McCook's (2002) findings. They mentioned that the recovery of bleached *Porites* was a result of the initial degree of an environmental stress (bleaching) of coral colonies: during the first 6 months after a bleaching event, algal overgrowth was greater in severely bleached than in bleached *Porites*. An alternative explanation for MTA overgrowth in T6 is that coral tissue was indeed stressed by the coring treatment or MTA in a way not measured by us, and once tissue coral was stressed MTA overgrew it.

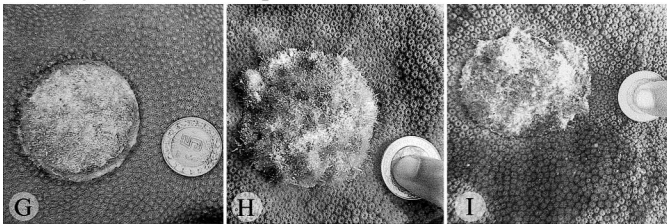
T1- Coral to algae transplant



T2- Coral to coral control



T5- Algae to coral transplant



Nov 2003

March 2004

Aug 2004

Fig. 4. Experimental cores: (A, B, C) Treatment 1 (coral tissue of *M. faveolata* is overgrown by MTA); (D, E, F) Treatment 2 (coral tissue and skeleton fusion occurs between the transplanted core and the receptor colony of *M. faveolata*); and (G, H, I) Treatment 5 (MTA increasingly overgrows healthy coral tissue of *M. faveolata*). Photos of experimental cores were taken in November 2003, May 2004, and August 2004 by H. Bahena-Basave. Coin diameter = 2.5 cm.

A previous condition of stress or death of the coral tissue has been mentioned as a requirement to the replacement of corals by algae (Lirman 2001; Diaz-Pulido and McCook 2004), with more stressed corals being more vulnerable to algal overgrowth and algal overgrowth enhancing the stress (Diaz-Pulido and McCook 2002). The replacement of corals by algae would therefore indicate coral mortality, rather than a competitive capacity of algae (McCook et al. 2001). We found that previous stress in *M. faveolata* tissue was not necessarily needed for algal overgrowth to take place. Although injured corals can be overgrown by algae (Hall 2001), fusion of tissue and skeleton between the transplanted cores and the host colony of *M. faveolata* in T2 always occurred in our experiment (Fig. 4D–F), indicating that tissue in cut edges of cores was regenerated and that algal overgrowth was not necessarily related to the initial injuries caused to the coral cores. In relation to other studies (see above and below), our results emphasize that coral-algal competition is highly variable in both process and outcome and is not simple or uniform (Jompa and McCook 2003a; Diaz-Pulido and McCook 2004).

According to McCook et al. (2001), the interaction between corals and algae could have several outcomes, but in the absence of disturbances corals are the superior competitors. In that sense, McCook (2001) also demonstrated, contrary to general belief, the competitive superiority of corals even in relatively eutrophic waters, which is supposed to be a promoting growth condition for algae. Nevertheless, our results indicate for the first time that MTA by themselves overgrows and cause stress to healthy *M. faveolata* and are superior competitors with corals under our experimental conditions.

It was experimentally demonstrated by Jompa and McCook (2003a) that mortality of coral *Porites* spp. is much greater as a result of the active colonization of a single filamentous species (*Anotrichium tenue*) than of mixed filamentous species forming turfs (dominated by species of *Polysiphonia*, *Cladophora*, *Centroceras*, *Sphacelaria*, *Hincksia*, *Ostreobium*, and *Herposiphonia*, with very little, if any, *A. tenue*). Mixed filamentous algae did not cause any mortality of coral tissue (Jompa and McCook 2003a). In the same line of evidence, there are several reports about the overgrowth of coral tissue by single algal species, including filamentous (the blue-green alga *Oscillatoria submembranacea* and *Schizothrix mexicana*; Antonius and Ballesteros 1998), noncoralline encrusting (*Metapeyssonnelia corallepida*; Antonius and Ballesteros 1998), coralline encrusting (*Pneophyllum conicum*; Antonius 2001), corticated terete (*Dasyopsis spinuligera*; Littler and Littler 1997), and creeping foliose (*Lobophora variegata*; Antonius and Ballesteros 1998; Jompa and McCook 2002a,b). However, we are experimentally demonstrating that death of healthy coral tissue can be a result of the overgrowth of MTA apparently mediating direct and indirect (McCook et al. 2001) mechanisms.

Few mechanisms or processes are involved in the competition by which algae can affect corals (Jompa and McCook 2003a): from five to six (McCook et al. 2001; River and Edmunds 2001), but summarized in three by Diaz-Pulido and McCook (2004). The second mechanism listed by Diaz-Pulido and McCook (2004), the competitive vegetative overgrowth from adjacent algal thalli, is one (direct) mechanism by which MTA overgrew *M. faveolata*. A variant of this mechanism, not reported before and involving two indirect processes, was the lateral growth of unattached MTA cushions. First, the cushions affected the coral tissue beneath MTA by shading, probably stressing coral tissue (changed to a much pigmented one) similarly to a coral species (*Manicina areolata*) receiving lower light levels (Ruiz-Zárte et al. 2000; see also McCook et al. 2001; River and Edmunds 2001). Second, cushions of MTA could be affecting *M. faveolata* by trapping sediments as other turf algae do (Airoldi 2001). Then, sedimentation could cause the death of *M. faveolata* tissue by smothering or burial, decreasing coral growth by abrasion, depressing zooxanthellae density activity, and increasing respiration, among other deleterious effects (Nugues and Roberts 2003).

Considering the size of the transplanted cores, an arbitrary interpretation of our results on algal overgrowth of *M. faveolata* is that once the tissue of a stressed colony is surrounded by MTA and reduced to a live area of approximately 17 cm², it will eventually be overgrown and killed

by the algae. Experimental studies are needed to determine the minimal remaining area of living coral tissue surrounded by MTA that will start to show reduced biological parameter values related to stress and the probable fatal destiny of the coral. Another interpretation of our results is that if a patch of MTA is colonizing a healthy *M. faveolata* colony and reaches an area of 17 cm², it will probably continue to grow and overgrow the whole coral colony. Any factor promoting the growth of algae, such as nutrient enrichment and removal of herbivores (Jompa and McCook 2002b), could unbalance the competition between MTA and *M. faveolata* in favor of the first organisms and could accelerate the algal overgrowth of that coral species in the Caribbean. We are aware of the potential pitfalls of extrapolating our results from cores to colonies and from a limited experiment to regional patterns. However, algae are indeed involved in the persisting decline of coral loss in the Caribbean (Gardner et al. 2003), and this degradation is more severe than reported from reefs in Australia or the Red Sea (Pandolfi et al. 2003).

M. faveolata seems to be an algal- and bacterial-sensitive coral species. Thus, (1) MTA overgrew healthy coral tissue in the Mexican Caribbean (this study), (2) relatively rapid tissue losses by colonizing algae at the living margins was recorded in apparently nonstressed colonies of the same species from Florida (Lirman 2001), and (3) the bacterium *Aurantimonas corallicida* is fatal to *M. faveolata* and uses the green alga *Halimeda opuntia* as vector (Nugues et al. 2004). A negative future scenario can be envisioned if these mechanisms are killing *M. faveolata* in other parts of the Caribbean Sea, especially if they are acting together at the same reef site.

In summary, our results showed that during the competition with MTA, *M. faveolata* was stressed by MTA, resulting in a reduction of the zooxanthellae density, Chl *a* cm⁻², and tissue thickness of the coral. Healthy *M. faveolata* cores were always overgrown by the algae, and in some cases were completely overgrown and killed by MTA. These results and others from the literature imply a negative scenario for *M. faveolata* and probably for the three *Montastraea* sibling species of our study site, the most important reef builders in the Mexican Caribbean.

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