

Patterns of Association And Interactions Between Juvenile Corals And Macroalgae
In The Caribbean

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A Thesis Submitted to the
University of North Carolina at Wilmington in Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

Center for Marine Science

University of North Carolina at Wilmington

2003

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ABSTRACT

Caribbean coral reefs have shifted from coral to macroalgal dominated communities within the past two decades. Macroalgae have been shown to affect adult coral colonies by five mechanisms: tissue encroachment, overshadowing, physical abrasion, reduced water flow, and allelochemicals. It has been suspected that macroalgae may interfere with juvenile coral growth and survivorship. The patterns of association between juvenile corals and macroalgae were investigated and a manipulative experiment was conducted to test the effects of particular functional forms of macroalgae on juvenile coral fitness. Results indicated there may be a functional relationship between the density of newly settled corals and macroalgal percent cover and height in the Caribbean. Nutrient concentrations were negatively correlated to macroalgal abundance and juvenile coral density. The experimental results indicated that juvenile coral taxa had species-specific responses to interactions with macroalgae but that different functional forms of macroalgae did not have significantly different effects on juvenile coral growth. It was concluded that the abundance and fitness of juvenile corals are compromised in coral reef communities with prolific macroalgae.

ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge my committee: Dr. Larry Cahoon, Dr. John Bruno, and Dr. Robert Steneck for their guidance and support. I especially thank Dan Strosnider, Kathleen Morrow, Lauren Betheune, Suzanne Holst, Kara Shuster, Luis Edgar Rejon Yam, and Antonio Moo Alfaro, and Omar Gomez for their field support; Evgeny Dafner for his laboratory support; and Dr. James Blum for his statistical support. For photography assistance, I would like to acknowledge John Bruno, Mariano Infante, and Gerardo Beber. My thanks to the Akumal Dive Shop, Scuba Staff Divers in Cozumel, XTC Dive Shop in Xcalak, and the Bonaire National Marine Park for their SCUBA and vessel support. Thanks to Centro Ecológico Akumal for providing field and lab facilities. This research was supported by the University of North Carolina at Wilmington's (UNCW) Center for Marine Science, the UNCW Graduate School, PADI Project Aware, and the International Women's Fishing Association. I would also like to thank Dr. Dan Shapiro and the Shoals Marine Laboratory for inviting me into the Tropical Marine Science Program for without this experience I would not have dedicated my graduate career to coral reefs.

DEDICATION

I would like to dedicate my thesis to the people who stood behind me unconditionally while I pursued my academic goals: my mother, my family, and my friends. I would also like to dedicate this thesis in memory of my late grandmother, Dee Dee Da, who demonstrated that there are no limits to developing one's character.

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INTRODUCTION

Coral reefs are endangered ecosystems (Buddemeier 2001; Fautin and Buddemeier 2002). Degradation appears to be exceeding recovery in the Caribbean as reefs have shifted from coral to macroalgal dominated communities (Hughes 1994; Hughes et al. 1999; Precht and Aronson 2000; Williams and Polunin 2001). It has been hypothesized that this shift from corals to macroalgae has been driven by elevated nutrient concentrations (Tomascik and Sander 1985, 1987) and reductions in herbivory (Lessios 1988; Steneck and Dethier 1994; Williams and Polunin 2001). The result has been increased coral-macroalgal competition. Interactions between adult scleractinian corals and algae have been well documented (Miller 1998; Lirman 2001; McCook and Jompa 2002), however a paucity of information exists on post-settlement events and juvenile coral fitness (Edmunds and Carpenter 2001). Algae have been suspected to interfere with coral recruitment (Birkeland 1977; Bak and Engel 1979; Hughes 1994; Connell 1997b) and juvenile survivorship (Sammarco 1982; Rogers 1984), but few studies have sought to quantify this in nature or conduct experiments to determine the strength of such interactions at the genus-level. This investigation focuses on patterns of association between juvenile corals and macroalgae and the effect that particular functional forms of algae may have on juvenile coral growth and survivorship.

Coral larvae prefer to settle in cryptic spaces or on the undersides of surfaces (Rogers 1984). Preferred settling substrates include crustose coralline algae (Steneck 1988) and bare limestone. Macroalgae grow faster than corals, increasing competition for space, thus recruitment is reduced in communities with prolific macroalgae. Macroalgae have been shown to reduce adult coral growth, fecundity, and live tissue

cover (Potts 1977; Lewis 1986; Coyer et al. 1993; Tanner 1995; Miller and Hay 1996; Tanner 1997). These processes require energy, thus costing corals metabolically. There are five mechanisms by which macroalgae can affect coral colonies: overshadowing, tissue encroachment, physical abrasion, allelochemicals, and reduced flow rates (River and Edmunds 2001). Furthermore, increased macroalgal biomass accumulates sediment, turf algae, and microorganisms, which can further reduce coral fitness (Smith et al. 1981; Roy in publ).

Once a shift to macroalgae occurs, it is frequently associated with limited recovery or death of scleractinian corals (Hughes 1994; Connell 1997a; McClanahan 2001). When faced with competition, colonial organisms, such as corals, may expend energy on survivorship instead of growth (Tanner 1995; Tanner 1997). A decrease in growth leads to a decrease in coral reproduction and survivorship at the population level (Hughes 1984; Tanner 1997). Juvenile coral survivorship is crucial to coral population growth and recovery (Buddemeier and Smith 1992; Tanner 1997) yet newly settled corals often experience high mortality rates (Babcock 1985; Tanner 1997). Macroalgae interfere with coral settlement (McCook et al. 2001) and it is suspected that juvenile coral fitness and survivorship are also reduced (Birkeland 1977).

In order to better understand coral population dynamics and reef community ecology, it is essential to document recruitment and post-settlement events of juvenile corals (Bak and Engel 1979; Hughes and Jackson 1985) in reef communities with varying densities of macroalgae. The major objectives of this study were 1) to quantify the patterns of association between juvenile corals and macroalgae over a large spatial scale, and 2) to manipulate and experimentally test the effect of macroalgal functional forms

(Steneck and Dethier 1994) on three abundant species of juvenile scleractinian corals, *Siderastrea*, *Porites*, and *Agaricia*, in the Caribbean. Limited data on herbivory and ambient nutrient concentrations were also evaluated since they are the two major factors driving macroalgal biomass (Precht and Aronson 2000; Lirman 2001; Williams and Polunin 2001; Steneck and Lang in publication). Three null hypotheses were tested: Ho1: Juvenile coral density is not related to macroalgal abundance (percent cover and height); Ho2: The effect of macroalgae on juvenile coral growth is not related to coral identity (genus); and Ho3: Juvenile coral growth is not related to macroalgal morphology or identity (genus).

METHODS

Study Sites

Research was conducted at 17 reef sites throughout the Western Caribbean between March 2002 and March 2003. All 17 study sites were chosen to represent a range of habitat types and conditions and investigations were conducted at depths between 10-13 meters on the inner lobe or slope of the fore reef to ensure comparable reef zones, hard substratum, at each location. The two major geographical regions studied were the Mesoamerican Barrier Reef System, along the coast of Mexico's Yucatan Peninsula (Figure 1a), and the island of Bonaire in the Netherlands Antilles off the coast of Venezuela, South America (Figure 1b). The Mesoamerican Barrier Reef System along the State of Quintana Roo, Mexico, is a fringing reef approximately 1000 km long, and continues into a barrier reef system further south off Belize. In Mexico, it appeared *a priori* that juvenile coral density was low compared to other Caribbean regions (Edmunds 2000; Edmunds and Carpenter 2001) and macroalgal abundance was

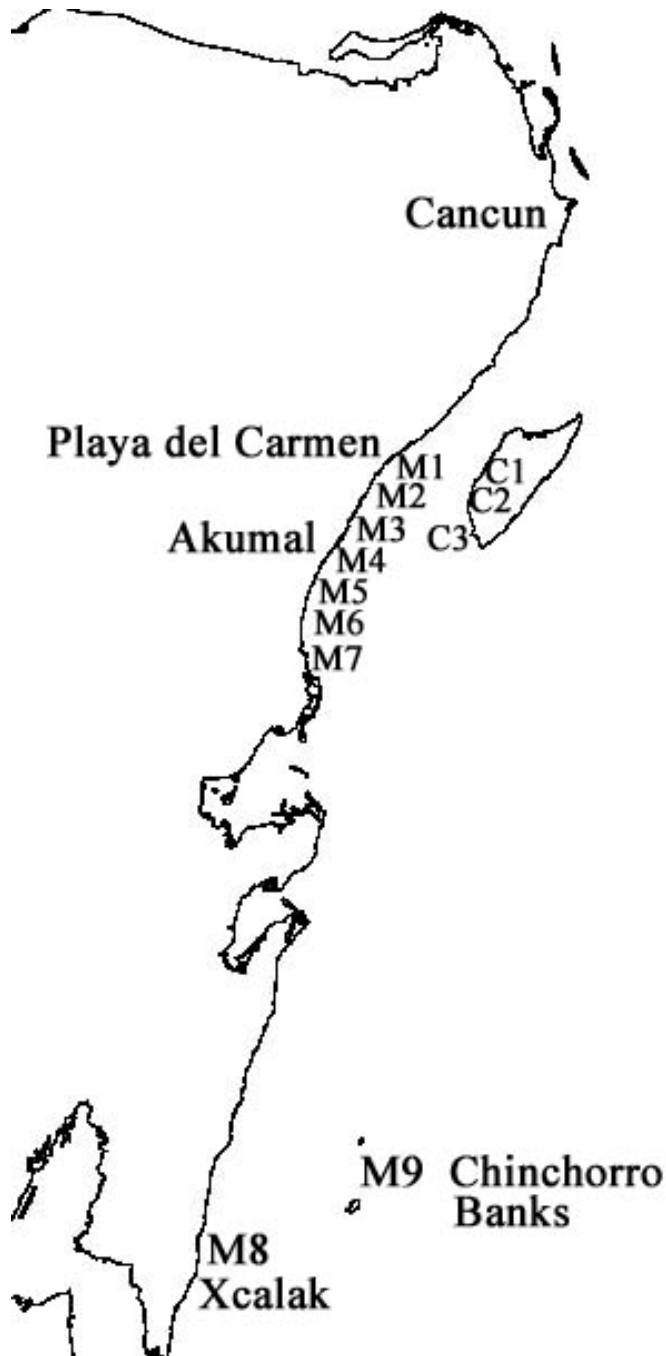


Figure 1: Map of Yucatan Peninsula. Study sites from north to south include: Playa del Carmen (M1), Cozumel (C1-3: Paradise, Chakanaab, and Columbia Shallows), Xaak (M2; north of Akumal), Akumal (M3-M7: Yalku, Media Luna, Las Redes, Escuela, and Xcacel), Chinchorro Banks, and Xcalak.



Figure 2: Map of Bonaire, Netherland Antilles. Study sites from north to south include: Karpata, Barkadera, Klein, Plaza, and Windsock.

high (Steneck and Lang in publication). Bonaire appeared *a priori* to have higher coral recruitment and low macroalgal biomass (Steneck *pers. obs.*). A total of 12 sites were chosen in Quintana Roo, Mexico that lie between 20°25.705' N and 18°17.144' N latitude and 087°17.308' W and 087°49.119' W longitude, including the island of Cozumel and the atoll system of Chinchorro Banks (Table 1). In Bonaire, 5 sites that lie between 12°08.311' N and 12°13.178' N latitude and 68°16.571' W and 68°21.113' W longitude were chosen including the small island of Klein Bonaire (Table 1). Physical and biological parameters of each set of sites are summarized in Table 2 and detailed reef descriptions are provided by the Caribbean Coastal Marine Productivity Program (CARICOMP; www.ccdc.org) and the Atlantic and Gulf Rapid Reef Assessment (AGRRA; www.coral.noaa.gov/agra).

Community Structure and Patterns of Association

To quantify patterns of association between juvenile corals and macroalgae, 10m transects were haphazardly placed parallel to the long axis of the reef. A 0.0625 m² quadrat was positioned on alternating sides of the transect at 1m intervals, thus a total of 10 quadrats were assessed per 10m transect. The small size of this quadrat was purposely chosen to avoid overlooking any juvenile corals and to focus on the small scale interactions between juvenile corals and macroalgae. When compared to belt transects along the same 10m transect line, juvenile density was four orders of magnitude higher when applying the smaller 0.0625 m² quadrats, suggesting that many of the small corals were overlooked with the belt transect method (Bégin *pers. comm.*). A minimum of 40 0.0625 m² quadrats per site were assessed for number of juvenile corals, coral

Site	Latitude	Longitude	PO ₄ ³⁻ (μM)	NO ₃ ⁻ (μM)	NH ₃ ⁺ (μM)
Playa del Carmen	N20°36.30	W87°04.30	0.171	0.367	0.473
Paradise, Cozumel	N20°28.01	W86°58.59	0.093	0.371	0.167
Chakanaab, Cozumel	N20°26.09	W87°00.33	0.317	0.462	0.392
Columbia, Cozumel	N20°19.39	W87°01.53	0.054	0.385	0.068
Xaak	N20°25.70	W87°17.30	0.210	0.407	0.531
Yalku	N20°24.61	W87°17.93	0.139	0.269	0.568
Media Luna	N20°24.16	W87°18.21	0.227	0.727	0.662
Las Redes	N20°23.38	W87°18.65	0.225	0.627	1.070
Escuela	N20°23.01	W87°19.05	0.151	0.255	0.269
Xcaceel	N20°20.31	W87°20.90	0.167	0.179	0.596
Xcalak	N18°17.14	W87°49.12	0.089	0.416	0.157
Chinchorro Banks	N18°32.54	W87°25.46	0.111	0.292	0.038
Karpata, Bonaire	N12°13.17	W68°21.11	0.304	0.296	0.133
Barkadera, Bonaire	N12°11.79	W68°18.16	0.175	0.141	0.092
Klein, Bonaire	N12°08.94	W68°19.60	0.225	-0.001	0.311
Plaza, Bonaire	N12°08.31	W68°16.57	0.217	0.089	0.032
Windsock, Bonaire	N12°13.33	W68°28.16	0.209	0.091	0.087

Table 1: GIS positions and mean nutrient concentrations (μM) for each study site (n=10-100 per site), arranged from north to south.

Site	Salinity	Temperature (°C)	#Fish/100m ²	Grazing rates (#bites m ⁻² h ⁻¹)	Coral cover (%)	Macroalgal cover (%)
Bonaire	34.6±0.08	27.5±0.14	69.14±8.43	717	46.1±0.03	11.8 ±3.99
Mexico	35.9±0.02	28.1±0.15	16.6±-6.3	175	14.5±6.9	32.45±3.23

Table 2: Mean values (±SE) for: salinity and bottom seawater temperatures (CARICOMP), herbivorous fish abundance (Bonaire-M. Paddock, Mexico-AGRRA), grazing rates (Bonaire-M. Paddock, Mexico-Steneck and Lang); adult scleractinian coral cover (Bonaire-B. Steneck, Mexico-AGRRA) and macroalgal cover (Slingsby).

genera, coral size, macroalgal cover, macroalgal genera, mean macroalgal height, along with other measurements not reported here. Within each quadrat, juvenile corals, defined as ≤ 4 cm in diameter and visible to the unaided eye (Wittenberg and Hunte 1992; Edmunds and Carpenter 2001), were counted and identified to genus, and species level when possible. Sediment was removed and macroalgae parted in order to carefully examine the substrate for juvenile corals as small as two polyps. Colonies that were clearly the product of fragmentation were omitted. Because coral recruits do not settle on sand or live coral (Bak and Engel 1979), quadrats that fell into these categories were not included in analyses. The maximum diameter of each juvenile coral was measured to the nearest millimeter. Percent cover of all macroalgae was estimated to the nearest 5%, identified to genus, and measured to the nearest millimeter with a pointed ruler in order to estimate an average height per genera. Lastly, the number of direct juvenile coral-macroalgal interactions were counted and the genera of both juvenile corals and macroalgae were recorded.

Experimental Design

From June 2002 to August 2002 a manipulative experiment was established to examine the effects of macroalgal identity (genera and functional group) on juvenile coral growth at Media Luna reef site in Akumal, Mexico. Coral growth was assessed as change in weight and live tissue surface area over time. A strong relationship exists between coral growth and survivorship, thus growth and live tissue surface area are standard measures of coral fitness (River and Edmunds 2001). This experiment was set up as a randomized factorial design, in which coral growth and live tissue cover were the

dependent variables, and macroalgal treatments were the independent variables. Treatments included the three most abundant juvenile coral genera in the Caribbean (*Siderastrea*, *Agaricia*, and *Porites* spp.) (Sammarco 1985; Edmunds and Carpenter 2001; Miller and Barimo 2001) and 6 genera of macroalgae, also common to the Caribbean (Lirman 2001; McCook et al. 2001). The 6 genera of macroalgae represented 3 functional groups: 1) calcareous (*Halimeda* and *Galaxaura* spp.), foliose (*Dictyota* and *Styopodium* spp.), and leathery (*Turbinaria* and *Sargassum* spp.). The control treatment had no macroalgae. Five replicates of each combination (3 coral genera x 7 algal treatments) totaled 105 experimental 'plates'.

Five cages were constructed from UV-resistant polyethylene aquaculture netting with 6 mm size diamond-shaped mesh to protect treatments from macro-herbivores. The cages, approximately 2.5m long, 0.5m high, and 1.5m wide, were oblong-shaped. Eight holes were drilled per cage at 10-meters depth on relatively flat limestone substrate with the aid of SCUBA. Stainless steel eyebolts were epoxied into the holes to ensure stability. Cages were attached to eyebolts with rope on one side of the cage and thick plastic cable ties on the other side so that cages could be opened once per week. The experimental design and sample size were based on a pilot study *a priori* that took place from March to May of 2002.

Thirty-five healthy juvenile corals of the genera: *Siderastrea* sp., *Agaricia* sp., and *Porites* sp. were collected at a standard size of 2 cm in diameter, the most common size identified by the patterns of association data as well as other studies (Edmunds and Carpenter 2001). When possible, juvenile corals (< 4 cm in diameter) were identified to the species level. Once collected, juvenile corals were transported in fresh seawater to

the lab and epoxied (using Koppers Splash Zone Compound A & BTM) to precut 5x5 cm pieces of gutter gard (SimpsonTM). Epoxied corals were left to harden in fresh seawater for about one hour and then weighed (to three significant figures) on a digital balance using the buoyant weighing technique (Davies 1989). Each coral plate, identified by a numbered aluminum tag, was photographed with a digital camera to analyze live tissue surface area (cm²) (to three significant figures) using Image J software. Three photographs of each juvenile coral were taken before and after the experiment so that an average of the three measurements could be calculated. Corals were then attached with cable ties to larger pieces of gutter gard (10x30 cm) and randomly assigned to macroalgal treatments (Figure 3). These plates were immediately transferred in fresh seawater to the study site and nailed to cleared substrate under each of the cages. Each of the 5 cages enclosed one replicate of each treatment combination (n=21) so that if a cage was lost or damaged, only one repetition of each treatment would be lost.

Macroalgae - Previous surveys in the Akumal area (Slingsby *unpubl. data*) established a mean height for each macroalgal genus used in the experiment. Many thalli of each macroalgal group were collected at a standard height for the Akumal area and transported in fresh seawater to Media Luna reef site. Macroalgal thalli were then attached to nails using cable ties. The nails were placed within 1 cm of juvenile corals to ensure interaction and each nail was surrounded by surgical tubing to eliminate breakage of macroalgae. Treatments were arranged by genus and separated by 10 cm (Figure 3).

Maintenance - Every five days, the cages were cut open to be cleaned of any fouling organisms while the gutter gard plates were also cleared of fouling organisms and

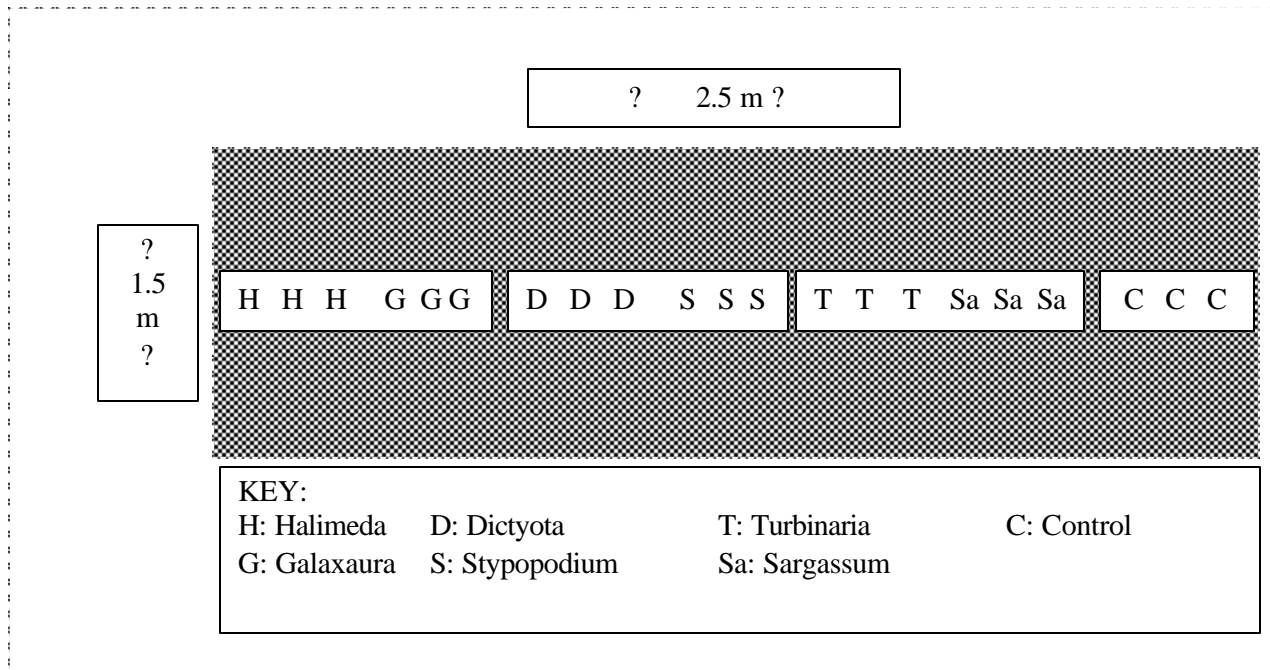


Figure 3: Experimental Design. Each cage had 4 experimental plates, one replicate of each treatment combination (n=21). Each macroalgal treatment (see Key) was assigned to one of each of the 3 coral species.

sediment. A freshly collected macroalga was attached to each nail weekly to replace damaged, lost, or broken thalli and to ensure a live interaction between macroalga and juvenile coral. Cages were re-secured with new cable ties. The experiment ran for eight weeks from June to August of 2002. Plaster of Paris blocks (Doty 1971) were used to detect any variation in flow regimes among cages. Photosynthetically Active Radiation (PAR) was measured inside and outside of the cages using a Li-Cor LI-1000 data logger with 2 pi collectors in order to detect shading effect of the cages. At the end of the experiment, corals were collected, weighed, photographed, and transplanted to a lower coral density area in Akumal Bay.

Ambient Nutrient Concentrations

From March 2002 to 2003, seawater samples were collected on SCUBA at standard depths of 3 m and 10 m, then placed into clean polyethylene Nalgene 50-ml bottles. Only bottom seawater samples (10 m depth) were used in this study for analyses. Water samples were transported in a cooler to the laboratory, filtered using a 1- μm Gelman A/E glass fiber filter, and frozen in the dark until analysis. A minimum of 10 and a maximum of 100 samples were taken at each site. Not all sites represent seasonal variation given logistical constraints. Samples were run in duplicate during analysis. Reactive phosphate (PO_4^{3-}), nitrite-nitrate nitrogen (NO_2^- , NO_3^-), and ammonium (NH_4^+) concentrations were determined using a Bran-Leubbe Auto Analyzer III at the University of North Carolina at Wilmington Center for Marine Science's Nutrient Laboratory. Standard analytical methods (Froelich 1977) were used in order to achieve a standard curve correlation coefficient ≥ 0.9990 for each parameter before running samples.

Statistical Analyses

Large-scale relationships between juvenile coral density, macroalgal percent cover, and macroalgal height were examined by pooling data by site. Juvenile coral density data were square root transformed while percent cover data were arc-sine square root transformed. Normality could not sufficiently be achieved using transformations, thus data were analyzed with the Kruskal-Wallis non-parametric ANOVA and Spearman ranked correlation tests. Juvenile coral density data were reported as # of corals/m² in order to compare results with other studies on juvenile corals. The abundances of juvenile corals and macroalgae were analyzed among sites using the Kruskal-Wallis test and relative abundance of taxa was calculated as frequency (%).

Experimental data did not meet ANOVA assumptions and were also analyzed with the non-parametric Kruskal-Wallis test. Coral weight (g) and live tissue surface area (cm²) were the dependent variables and macroalgal treatment was the independent variable. Water flow and light measurements were normally distributed and differences among cages were analyzed by one-way ANOVA.

Nutrient data were analyzed for significant differences among sites (Kruskal-Wallis) and correlation analyses were used to compare nutrient concentrations to juvenile coral density, macroalgal cover, and macroalgal height. Significance level applied to all tests was $\alpha < 0.05$. All statistical analyses were completed on JMP 5.0 and SAS software.

RESULTS

Patterns of Association

Juvenile coral density varied significantly among sites (Kruskal-Wallis, $\chi^2=51.07$, $df=16$, $p<0.001$) (Figure 4). Mean coral density for all 17 sites was 20.2/m² (SE_±1.43).

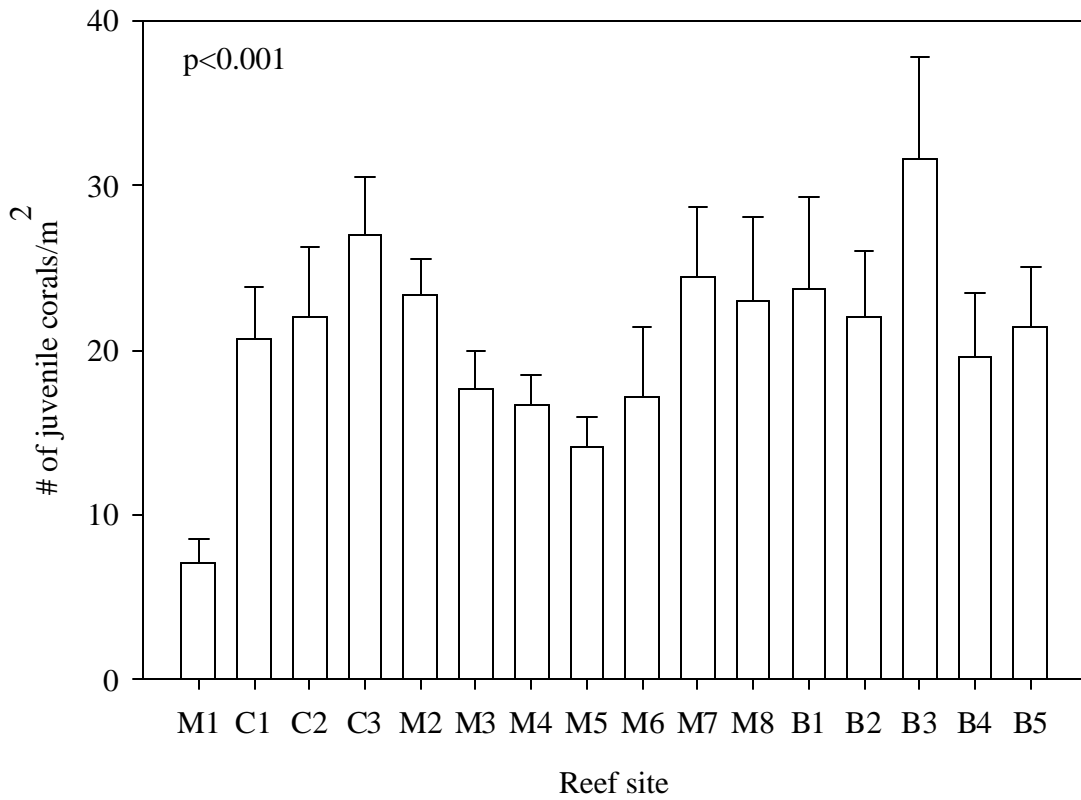


Figure 4: Mean (\pm SE) density of juvenile corals at each reef site (n=17). Sites arranged from north to south: Playa del Carmen, Paradise, Chakanaab, Columbia Shallows, Xaak, Yalku, Media Luna, Las Redes, Escuela, Xcaceel, Xcalak, Chinchorro Banks in Mexico; and Karpata, Barkadera, Klein, Plaza, and Windsock in Bonaire.

Macroalgal percent cover varied significantly among sites (Kruskal-Wallis, $\chi^2=373.71$, $df=16$, $p<0.001$) and ranged from 0-90% (Figure 5). Macroalgal height ranged from 0.1-10.0 cm and differed significantly among sites (Kruskal-Wallis, $\chi^2=414.85$, $df=16$, $p<0.0001$) (Figure 6). There was a significant inverse relationship between juvenile coral density and macroalgal percent cover ($p<0.005$, $r = -0.642$) (Figure 7) as well as with macroalgal height ($p<0.026$, $r = -0.537$) (Figure 8). Macroalgal percent cover and macroalgal height were positively correlated ($p<0.001$, $r = 0.836$) (Figure 9). When zero juvenile coral densities were removed in order to analyze what occurs solely when juveniles are present, the patterns remained the same. Fewer juveniles occurred where more macroalgae were present.

Juvenile coral abundance was significantly different among sites (Kruskal-Wallis, $\chi^2=51.07$, $df=16$, $p<0.0001$) with the three most abundant genera being *Agaricia* sp. (31%), *Siderastrea* sp. (23%) and *Porites* sp. (24%) (Figure 10). A total of 16 juvenile coral taxa were recorded, including *Madracis*, *Stephocoenia*, *Montastraea*, *Dichocenia*, *Diploria*, *Millepora*, *Eusmilia*, *Favia*, *Leptoseris*, *Scolymia*, *Meandrites*, *Rhizosmilia*, and *Mussa* spp. Mean juvenile coral size (all species and all size classes combined; $n=1085$) was 2.20 cm in diameter ($SE=0.032$). Assuming a growth rate of 1-3 mm/month (Bak and Engel 1979), this indicates that most corals were approximately 22 months old.

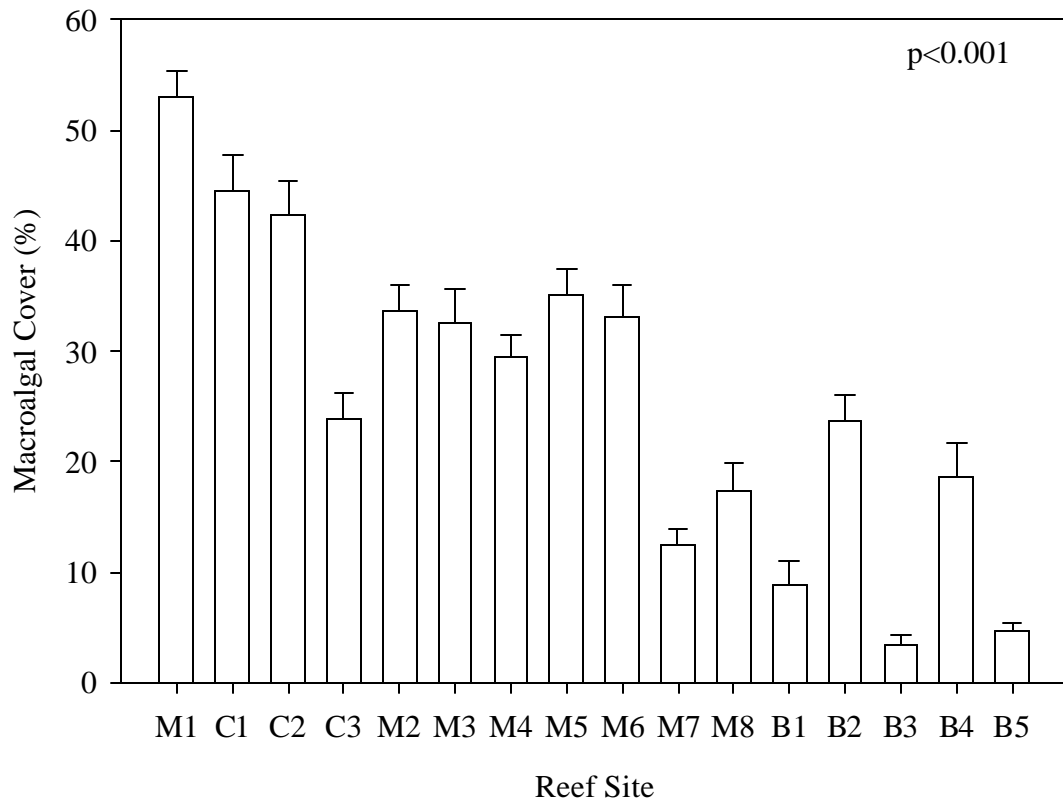


Figure 5: Mean (\pm SE) percent cover of macroalgae at each reef site (n=17). Sites arranged from north to south: Playa del Carmen, Paradise, Chakanaab, Columbia Shallows, Xaak, Yalku, Media Luna, Las Redes, Escuela, Xcaceel, Xcalak, Chinchorro Banks in Mexico; and Karpata, Barkadera, Klein, Plaza, and Windsock in Bonaire.

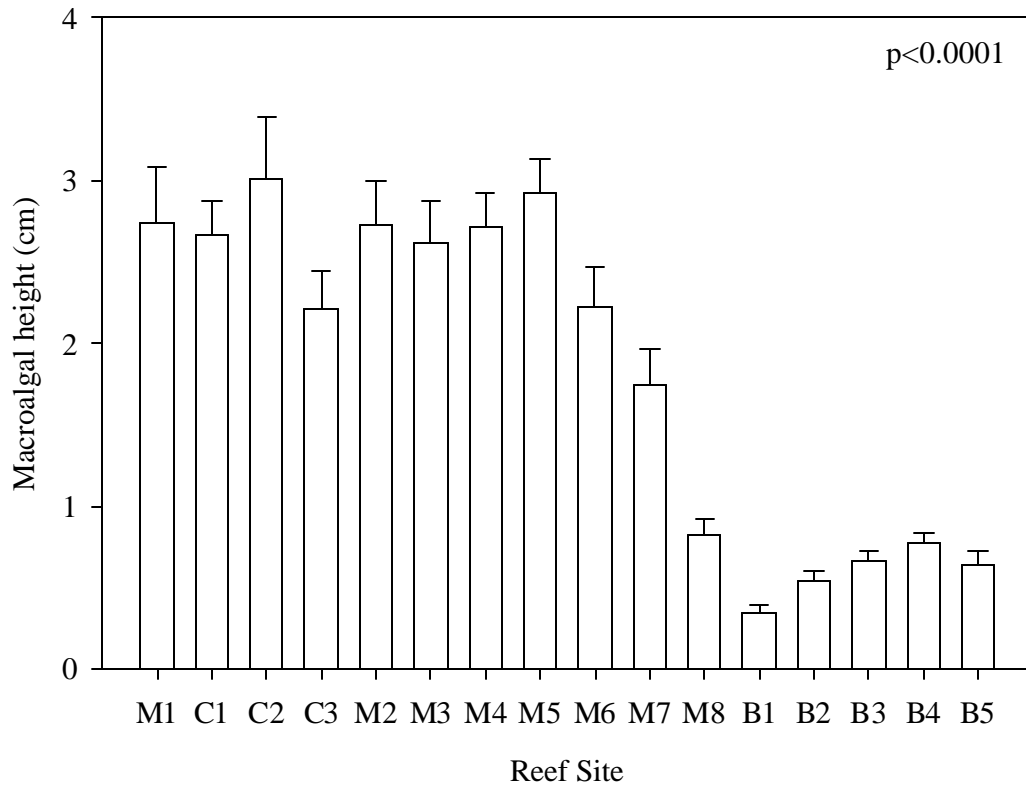


Figure 6: Mean height (\pm SE) of macroalgae at each reef site (n=17). Sites arranged from north to south: Playa del Carmen, Paradise, Chakanaab, Columbia Shallows, Xaak, Yalku, Media Luna, Las Redes, Escuela, Xcaceel, Xcalak, Chinchorro Banks in Mexico; and Karpata, Barkadera, Klein, Plaza, and Windsock in Bonaire.

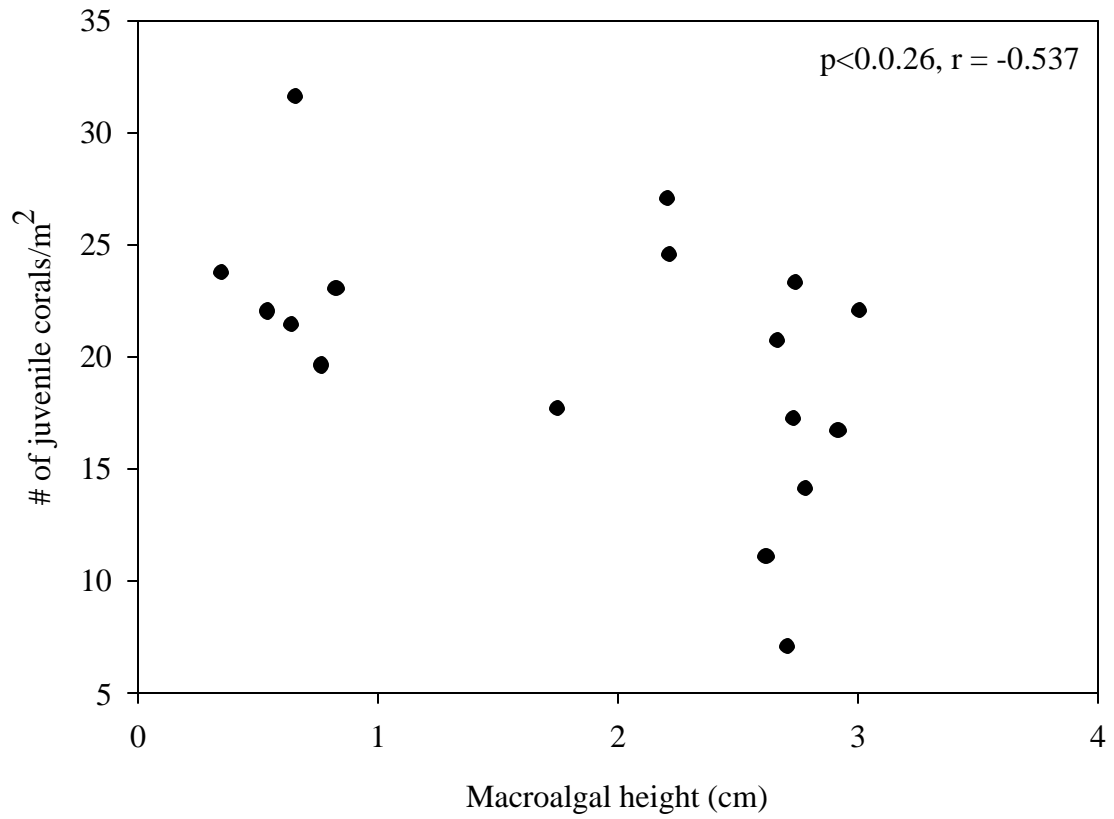


Figure 8: Inverse correlation between juvenile coral density and macroalgal height at 17 reef sites.

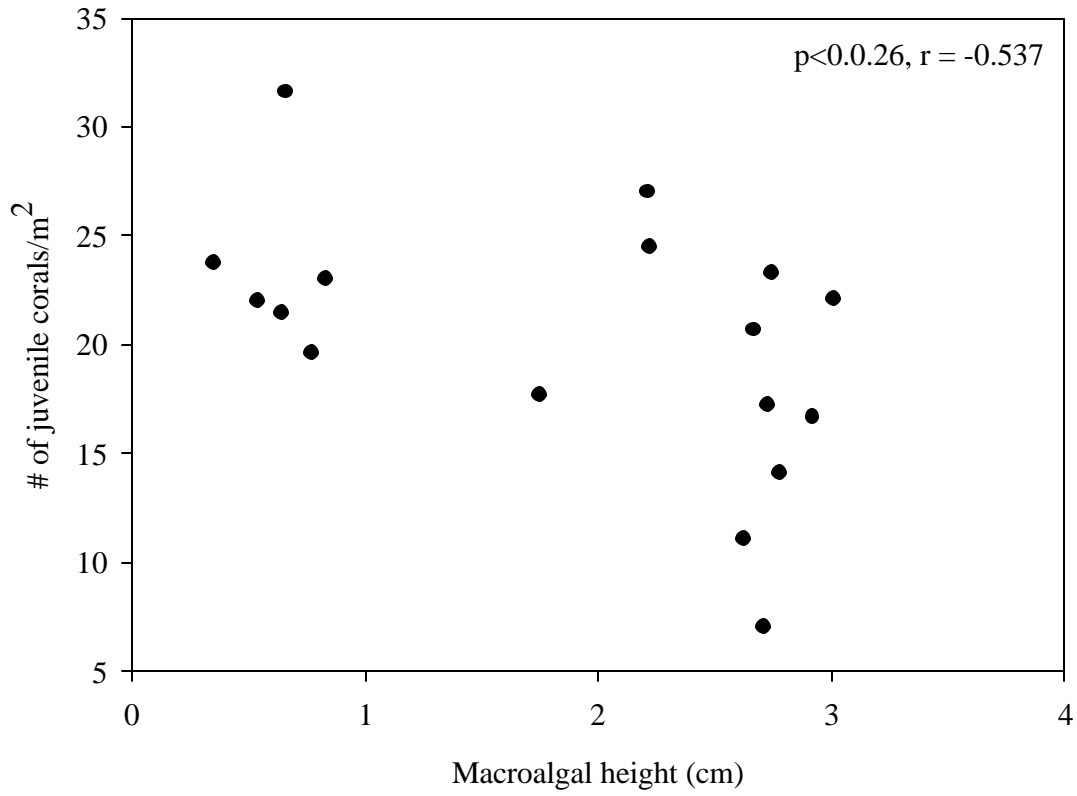


Figure 8: Inverse correlation between juvenile coral density and macroalgal height at 17 reef sites.

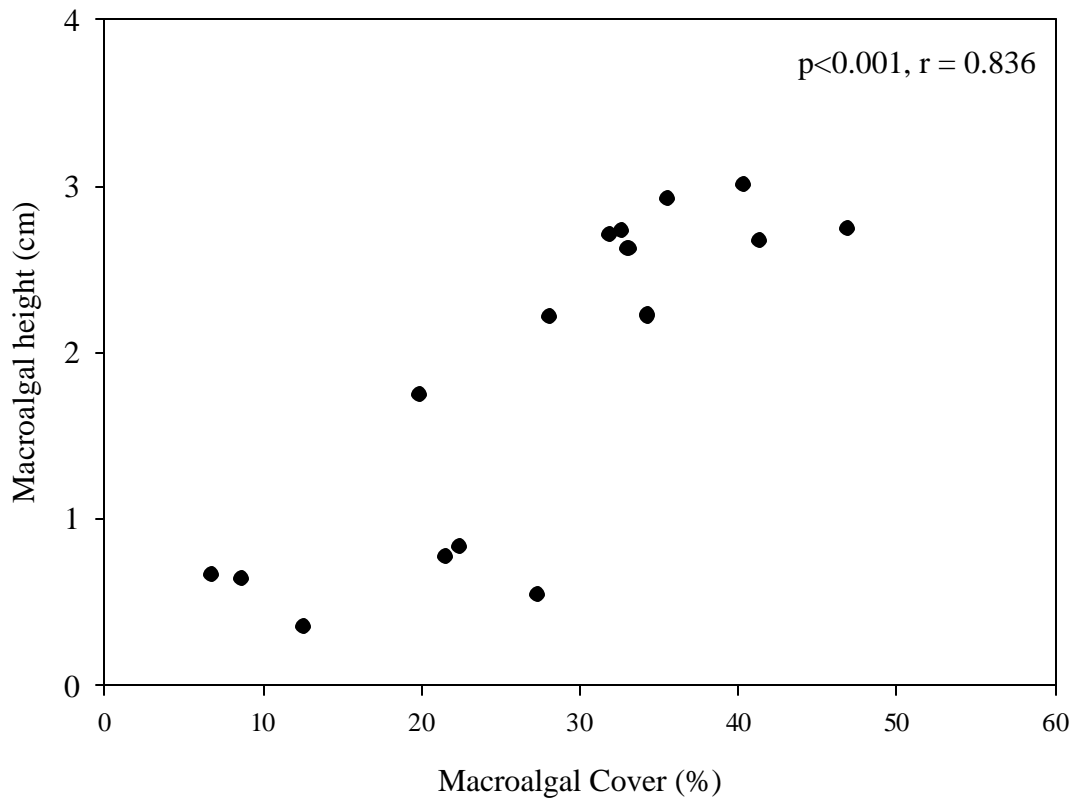


Figure 9: Positive correlation between macroalgal percent cover and macroalgal height among 17 sites.

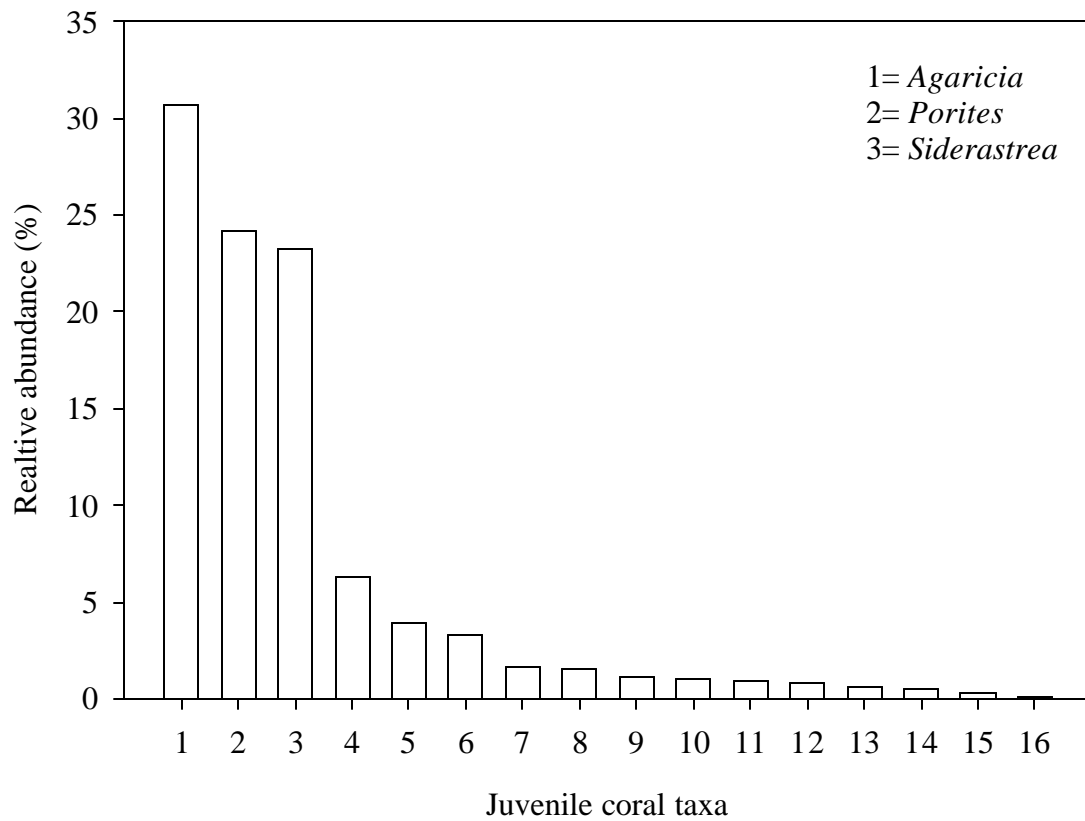


Figure 10: Relative abundance of juvenile corals among 17 reef sties (Kruskal-Wallis, $\chi^2=51.07$, $df=16$, $p<0.0001$). A total of 16 genera were observed. *Agaricia*, *Porites*, and *Siderastrea* spp. accounted for 78% of all juvenile corals observed.

A total of 22 macroalgal taxa were observed, including *Dictyota*, *Halimeda*, *Laurencia*, *Caulerpa*, *Amphiroa*, *Jania*, *Galaxaura*, *Rhipocephalus*, *Lobophora*, *Udotea*, *Padina*, *Sargassum*, *Avrainvillea*, *Ventricaria*, *Penicillus*, *Peyssonelia*, *Wrangelia*, *Turbinaria*, *Styopodium*, *Halymenia*, *Valonia*, and *Coelthrix* spp. Relative abundances of macroalgal genera differed among sites (Kruskal-Wallis, $\chi^2=226.77$, $df=16$, $p<0.0001$). Approximately 50% of all macroalgal cover recorded at the 17 reef sites was either *Halimeda* (22%) or *Dictyota* (27%) (Figure 11). Regionally, 99% of *Halimeda* observed in this study was recorded in Mexico while less than 1% was observed in Bonaire. *Dictyota*, the most common macroalga in Bonaire, only accounted for 20% of all *Dictyota* observed while 80% was measured in Mexico. Mean heights of these two major macroalgal taxa varied regionally. *Halimeda* averaged 3.0 cm high in Bonaire and 4.4 cm high in Mexico. *Dictyota* heights averaged 1.8 cm in Mexico and 0.64 cm in Bonaire. According to functional group, approximately 57% of all macroalgae was fleshy, 39% calcified, and 4% leathery.

Direct juvenile coral-macroalgal contacts primarily involved *Dictyota*, approximately 60% of the time (Figure 12). *Dictyota* interacted with *Agaricia* and *Siderastrea* juveniles most frequently (34% and 33% respectively) and *Porites* juveniles less frequently (17%). *Halimeda* interacted with juvenile corals 16% of the time (Figure 12), specifically with *Agaricia* (~40%), *Porites* (~30%), and *Siderastrea* (<10%).

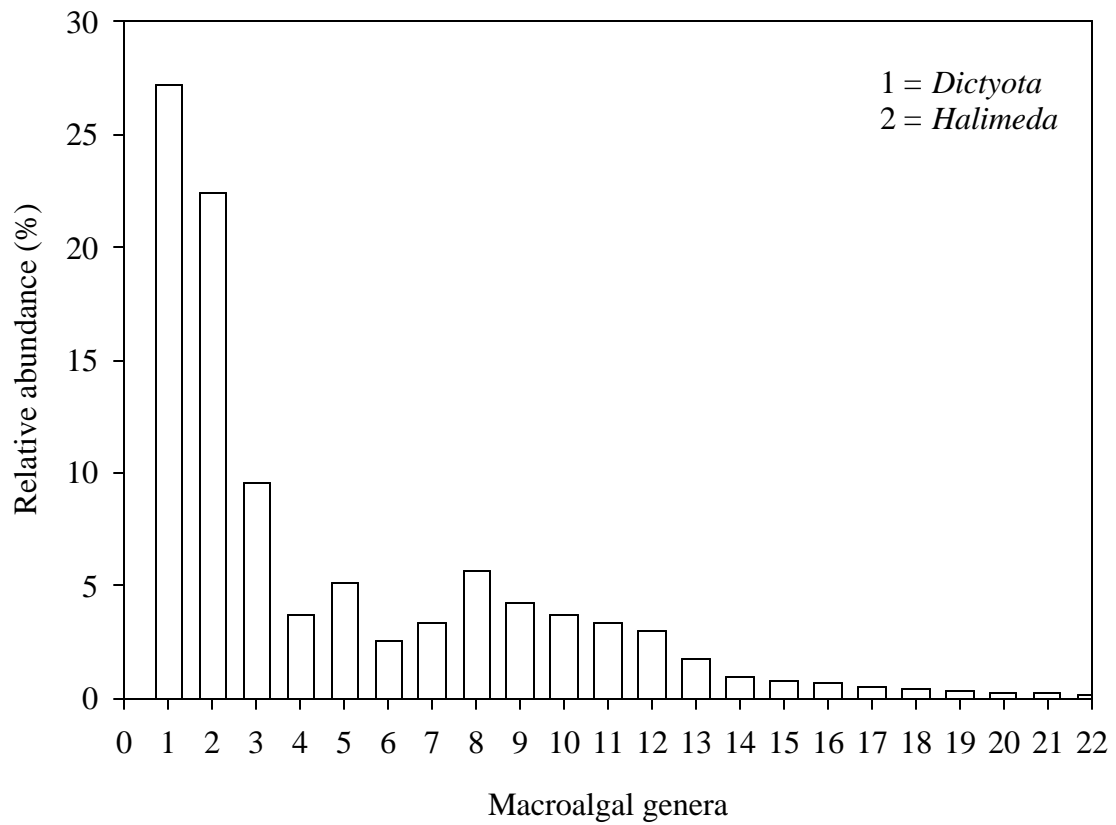


Figure 11: Relative abundance of macroalgae among 17 sites (Kruskal-Wallis, $x^2=226.77$, $df=16$, $p<0.0001$). *Dictyota* and *Halimeda* comprise 50% of abundance.

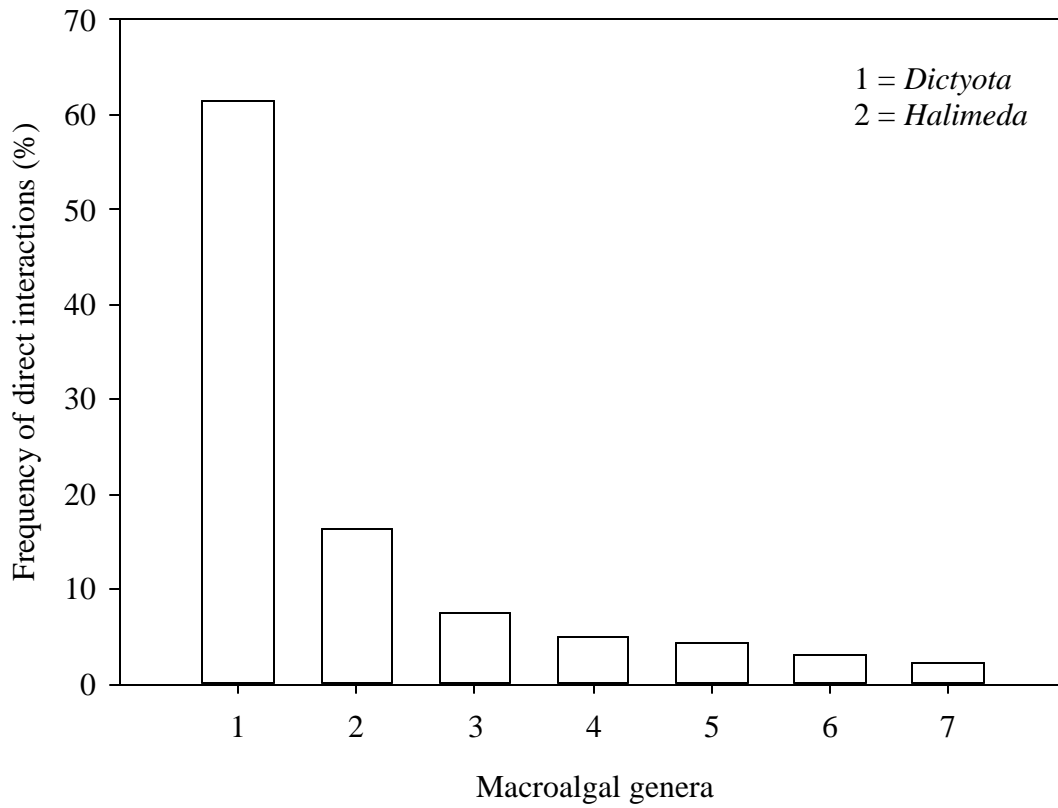


Figure 12: Frequency of macroalgae (by genera) coming into direct contact with juvenile corals. 75% of direct contacts involved *Dictyota* and *Halimeda*.

Nutrient Concentrations

All bottom seawater nutrient parameters varied significantly among sites (Figure 13). Macroalgal percent cover ($p < 0.0006$, $r = 0.748$) and height ($p < 0.0001$, $r = 0.828$) were significantly correlated to Total Inorganic Nitrogen (TIN), which is the sum of nitrate-nitrite and ammonium concentrations (Figures 14 a and b). There were no significant relationships between PO_4^{3-} and macroalgal percent cover or height. There were no significant relationships between bottom PO_4^{3-} and NO_3^- levels and juvenile coral density, however a significant inverse relationship existed between NH_4^+ and juvenile coral density at 10m depth ($p < 0.047$, $r = -0.488$) (Figure 15).

Interactions Between Juvenile Corals and Macroalgae

Changes in juvenile coral weight and surface area over time were calculated as post-initial. The intention was to combine both measures of juvenile coral fitness, buoyant weight and surface area, in order to calculate growth rate/day, however due to the net loss in surface area among corals, these two measures were analyzed separately. Over the 8-week experiment, juvenile coral calcification rate (excluding the controls) differed significantly among genera (Kruskal-Wallis, $\chi^2 = 13.975$, $df = 2$, $p < 0.0009$) (Figure 16). All 3 coral taxa, *Siderastrea*, *Porites*, and *Agaricia*, gained an average of 0.431 grams over the 8 weeks, or $7.18 (\pm 0.05 \text{ SE})$ mg/day. *Siderastrea* juvenile corals had the slowest calcification rate. Controls differed significantly (Kruskal-Wallis, $\chi^2 = 14.821$, $df = 3$, $p < 0.002$) and calcified faster than the treatments (0.526 grams/8 weeks).

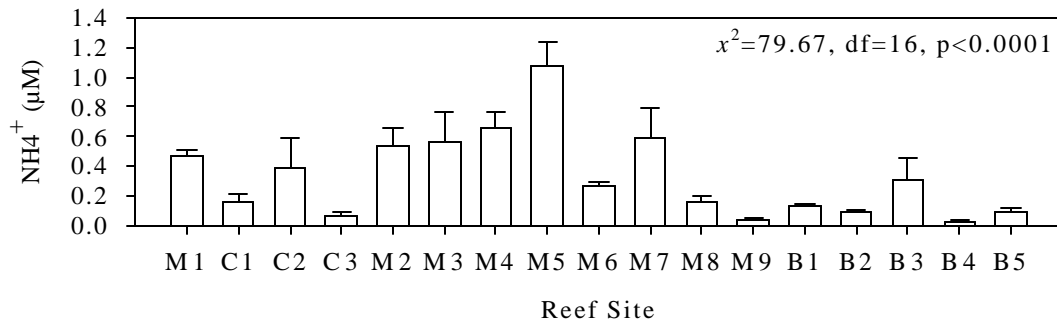
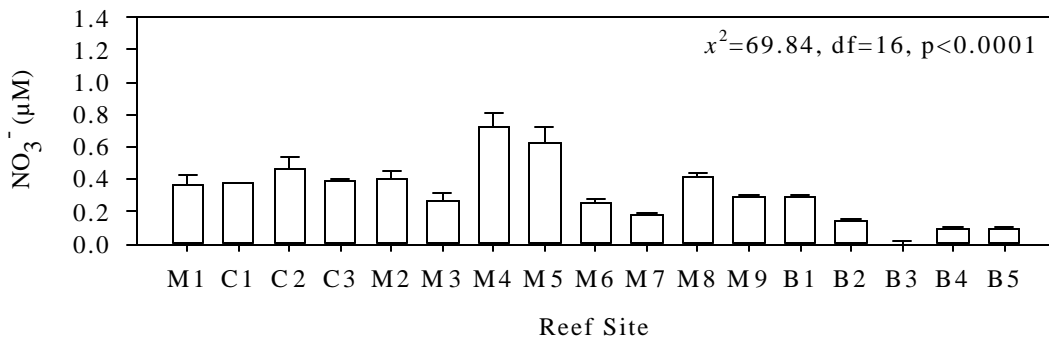
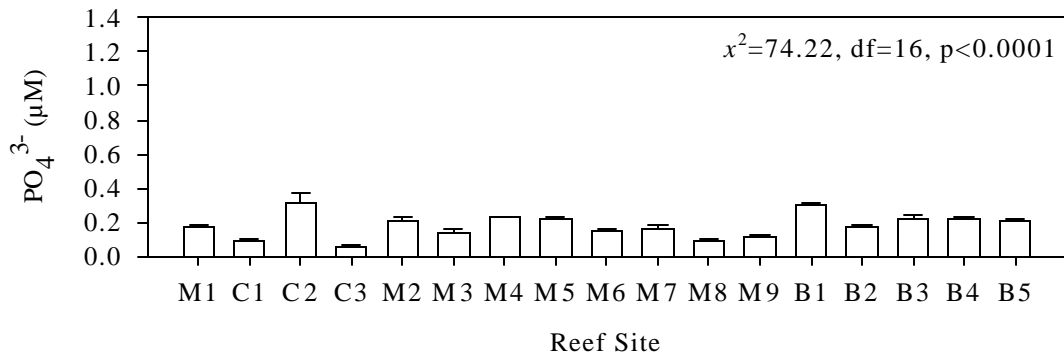


Figure 13: Bottom (10m) nutrient concentrations (mean \pm SE) at 17 sites. From north to south: Playa del Carmen, Paradise, Chakanaab, Columbia Shallows, Xaak, Yalku, Media Luna, Las Redes, Escuela, Xcaacel, Xcalak, Chinchorro Banks in Mexico; and Karpata, Barkadera, Klein, Plaza, and Windsock in Bonaire.

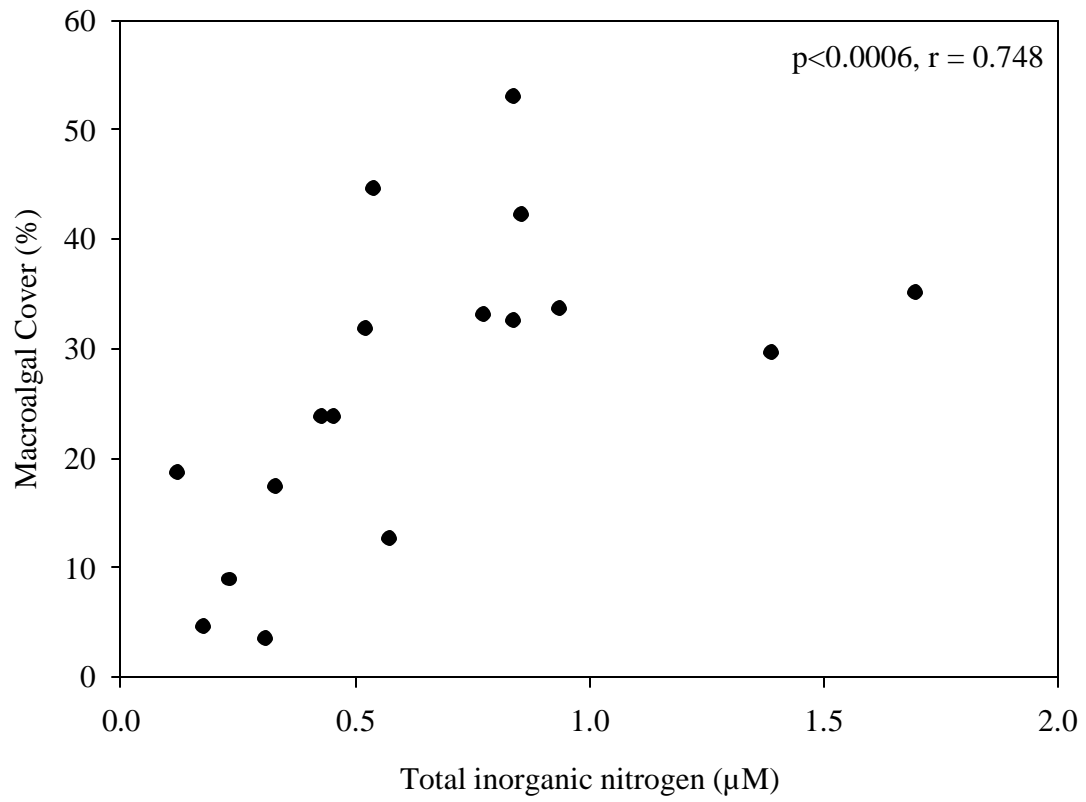


Figure 14a: Correlation between macroalgal percent cover and TIN across 17 reef sites.

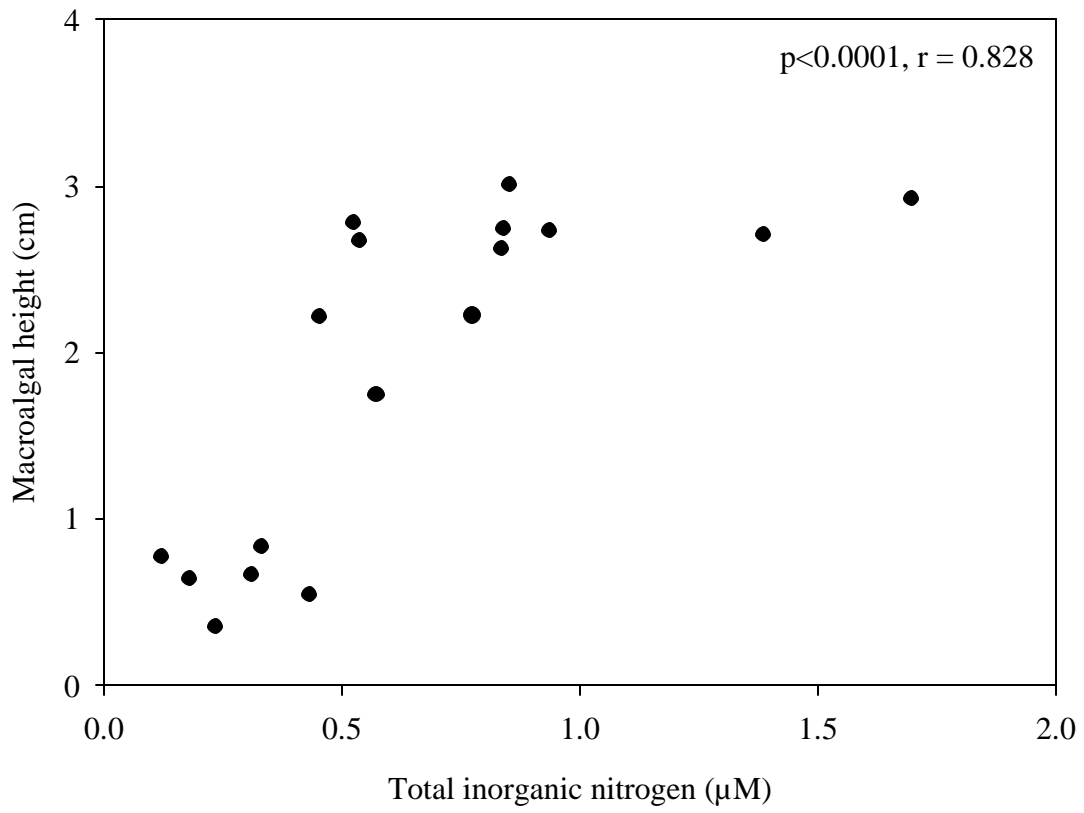


Figure 14b: Correlation between macroalgal height and TIN across 17 reef sites.

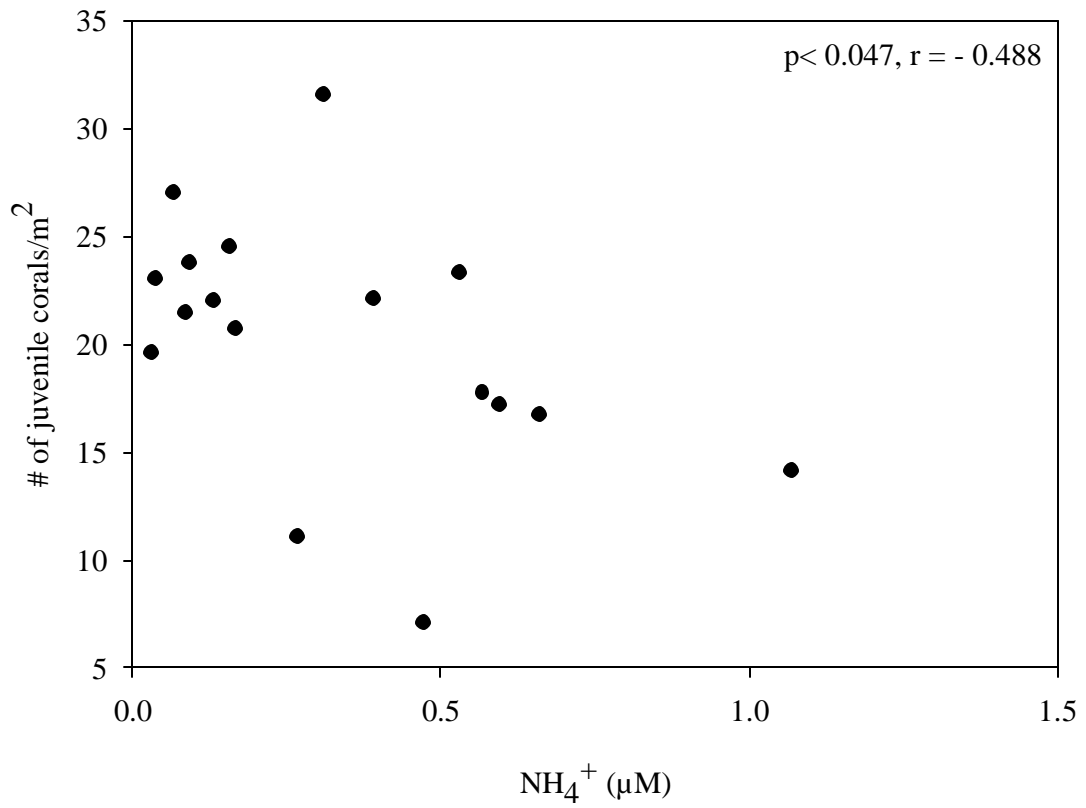


Figure 15: Inverse correlation between NH_4^+ concentrations (mean \pm SE) and juvenile coral density at 17 reef sites.

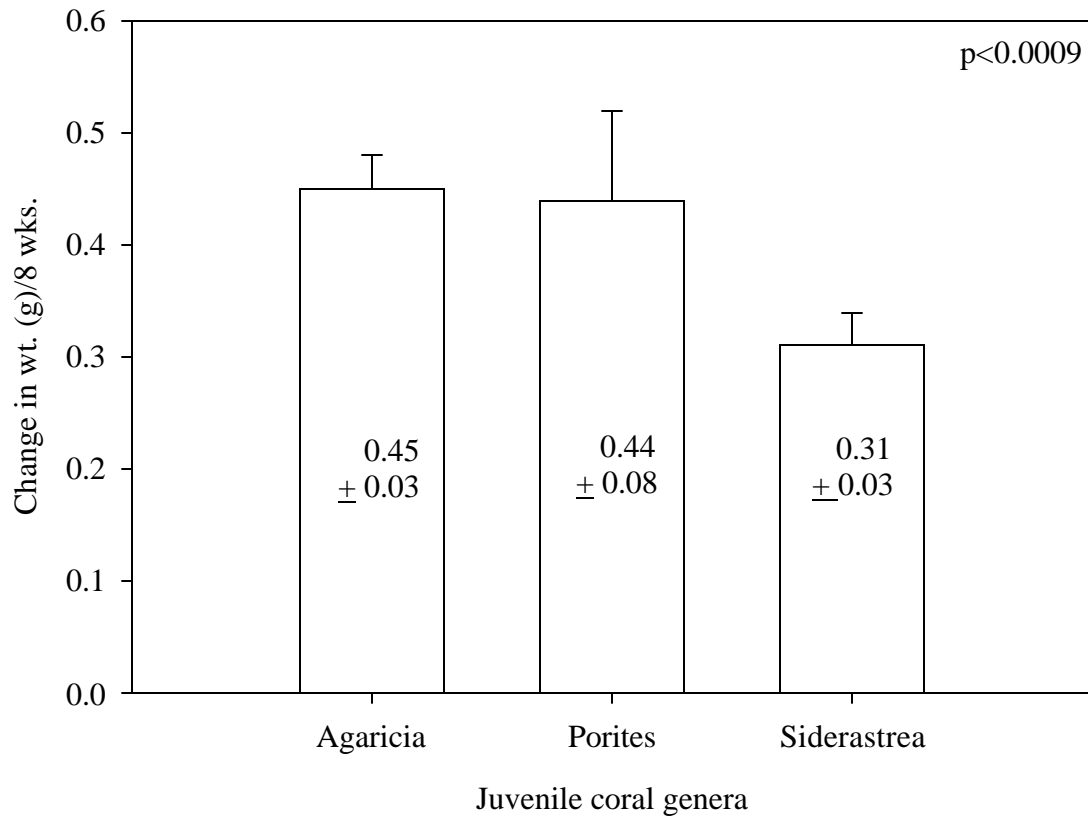


Figure 16: Calcification rate of juvenile corals adjacent to macroalgae over 8-week study period. Controls averaged 0.526g/8 weeks.

Change in live tissue surface area (excluding the controls) differed significantly among juvenile coral taxa (Kruskal-Wallis, $\chi^2=7.373$, $df=2$, $p<0.0251$) (Figure 17). Most juvenile corals lost live tissue throughout the study period, however some of the *Agaricia* juvenile corals appeared to have gained live tissue. Average tissue loss across all genera was -0.174 cm^2 over the 8-week period, or -2.95 mm/month . Controls differed significantly (Kruskal-Wallis, $\chi^2=9.3771$, $df=3$, $p<0.0247$), and lost an average of 0.160 cm^2 of live tissue in 8 weeks.

No significant differences were observed among macroalgal treatments (genera) for juvenile coral weight (Kruskal-Wallis $\chi^2=4.85$, $df=6$, $p<0.563$) (Figure 18) or surface area throughout the 8-week study period (Kruskal-Wallis, $\chi^2=5.58$, $df=6$, $p<0.472$) (Figure 19). Consequently, there were no significant differences between macroalgal morphology (functional group) and juvenile coral weight (Kruskal-Wallis, $\chi^2=1.27$, $df=3$, $p<0.736$) or surface area (Kruskal-Wallis, $\chi^2=3.65$, $df=3$, $p<0.302$). Although not statistically significant, interesting trends were observed. Juvenile corals under all treatments calcified over the 8-week period, and most treatments grew at a slower rate than the control (Figure 18). Most treatments experienced tissue mortality although some juvenile corals adjacent to *Dictyota* treatments appeared to have gained live tissue throughout the experiment (Figure 19). *Halimeda* and *Sargassum* treatments had the most negative effect on tissue encroachment (-0.335 cm^2 and -0.325 cm^2 respectively) (Figure 19).

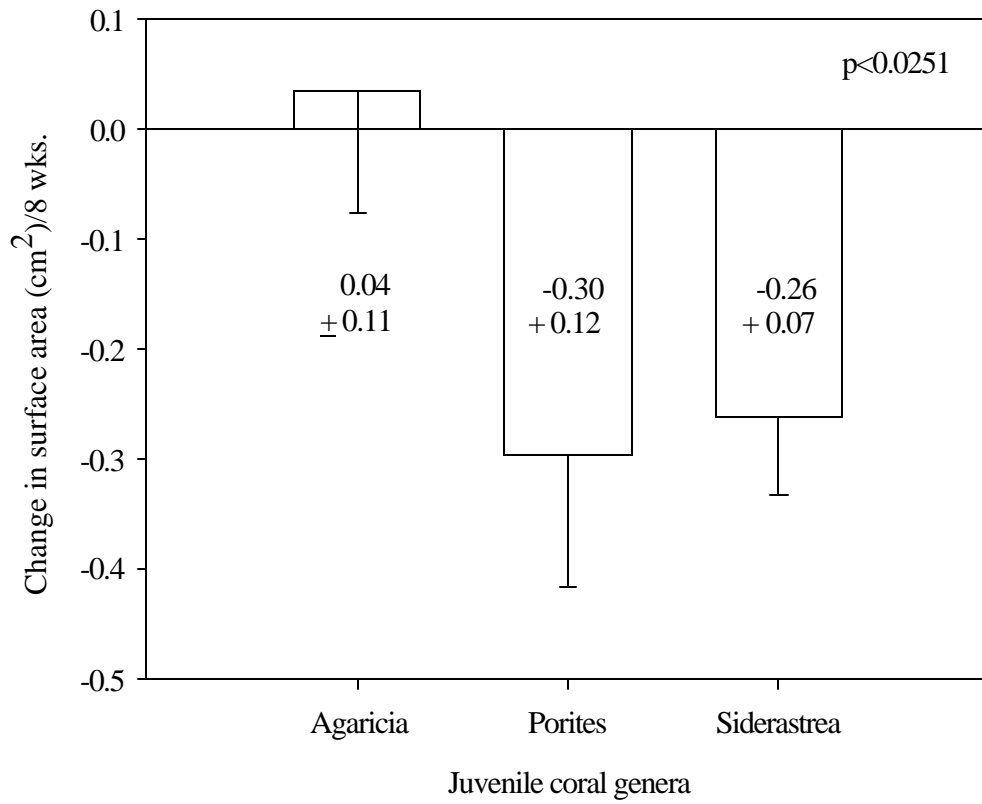


Figure 17: Change in live tissue surface area among 3 juvenile coral genera (treatments only) over the 8-week study period. Controls lost an average of 0.160 cm²/8 weeks.

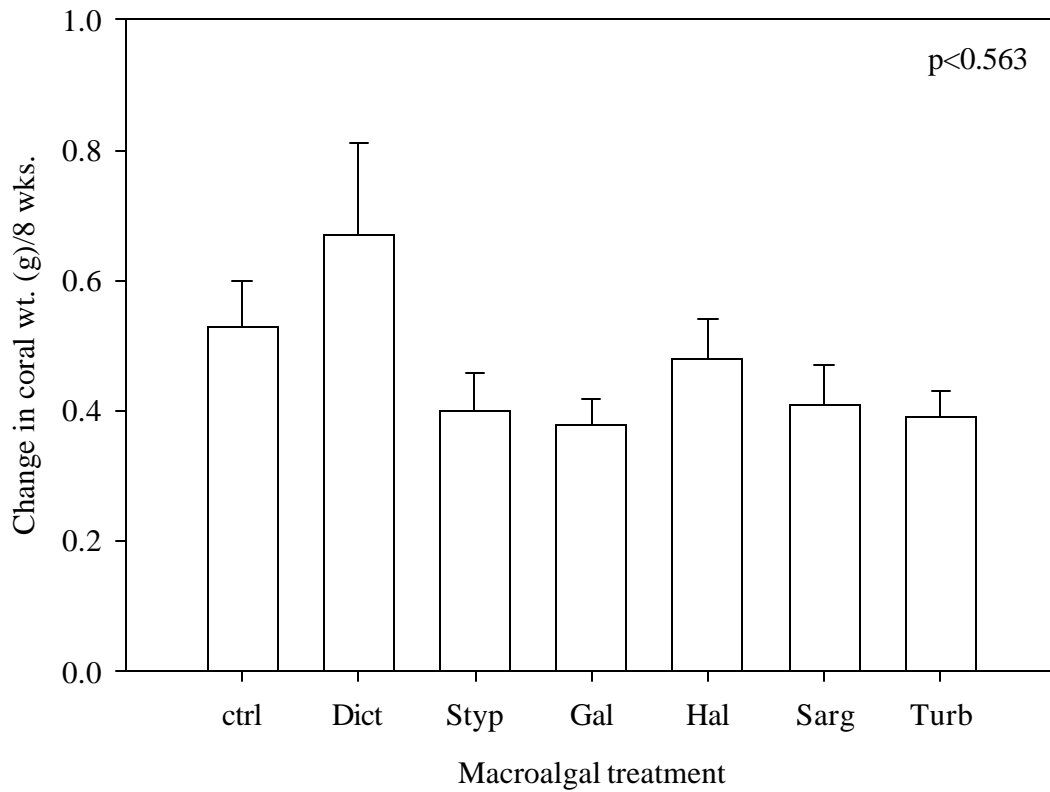


Figure 18: Change in juvenile coral weight over the 8-week study period. Macroalgal treatments from left to right: control, *Dictyota* and *Styopodium* (fleshy group), *Galaxaura* and *Halimenda* (calcareous group), and *Sargassum* *Turbinaria* (leathery group).

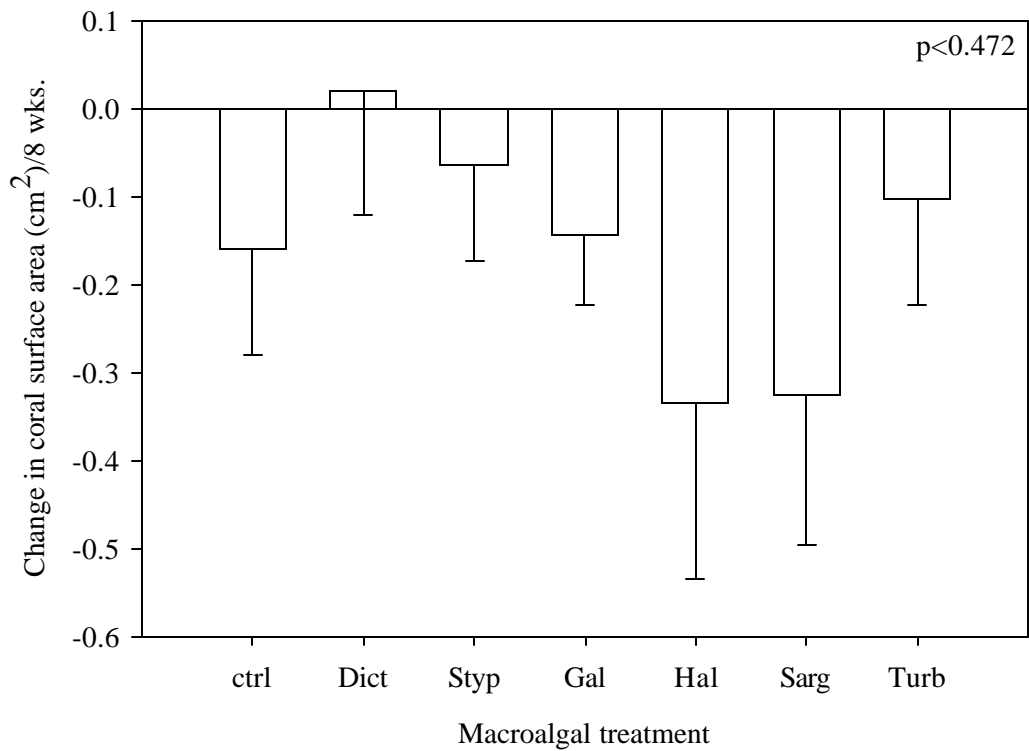


Figure 19: Change in juvenile coral surface area over the 8-week experimental period. Macroalgal treatments from left to right: control, *Dictyota* and *Styopodium* (fleshy group), *Galaxaura* and *Halimenda* (calcareous group), and *Sargassum Turbinaria* (leathery group).

Water Flow and Light

Relative water flow measurements were normally distributed (Wilk's $\chi^2=0.941$) and did not vary significantly among cages (ANOVA, $p<0.347$, $df=4$, $r^2=0.54$). Light measurements (PAR) were normally distributed (Wilk's $\chi^2=0.941$) and varied significantly among the inside of cages (ANOVA, $p<0.001$, $df=4$, $r^2=0.820$) but not among the outside (ANOVA, $p<0.805$, $df=4$, $r^2=0.138$). Cages decreased PAR by approximately 50% (Figure 20).

DISCUSSION

Patterns of Association

Coral reef communities are dynamic systems and many variables contribute to spatial variability of juvenile corals and macroalgae, such as substrate availability, variations in light, availability to nutrients, larval supply, physical disturbances, grazing rates, topographical complexity, and life history strategies (Sammarco 1980; Wittenberg and Hunte 1992; Chiappone and Sullivan 1996; Edmunds and Bruno 1996; Hughes et al. 1999; Edmunds 2000; Hughes and Tanner 2000; McCook et al. 2001). In this study, the density of juvenile corals and the abundance of macroalgae varied significantly among sites (Figures 4-6). Reef sites along the Mesoamerican Reef in Mexico had lower densities of juvenile corals ($18.7/\text{m}^2 \pm \text{SE } 1.7$), on average, compared to Bonaire ($23.7/\text{m}^2 \pm \text{SE } 2.6$). The lowest juvenile coral density among 17 sites was recorded at Playa del Carmen ($7.1/\text{m}^2 \pm \text{SE } 1.5$), the fastest growing city in Mexico, and the highest mean density of newly settled corals occurred at Klein, Bonaire ($31.6/\text{m}^2 \pm \text{SE } 6.2$). Although

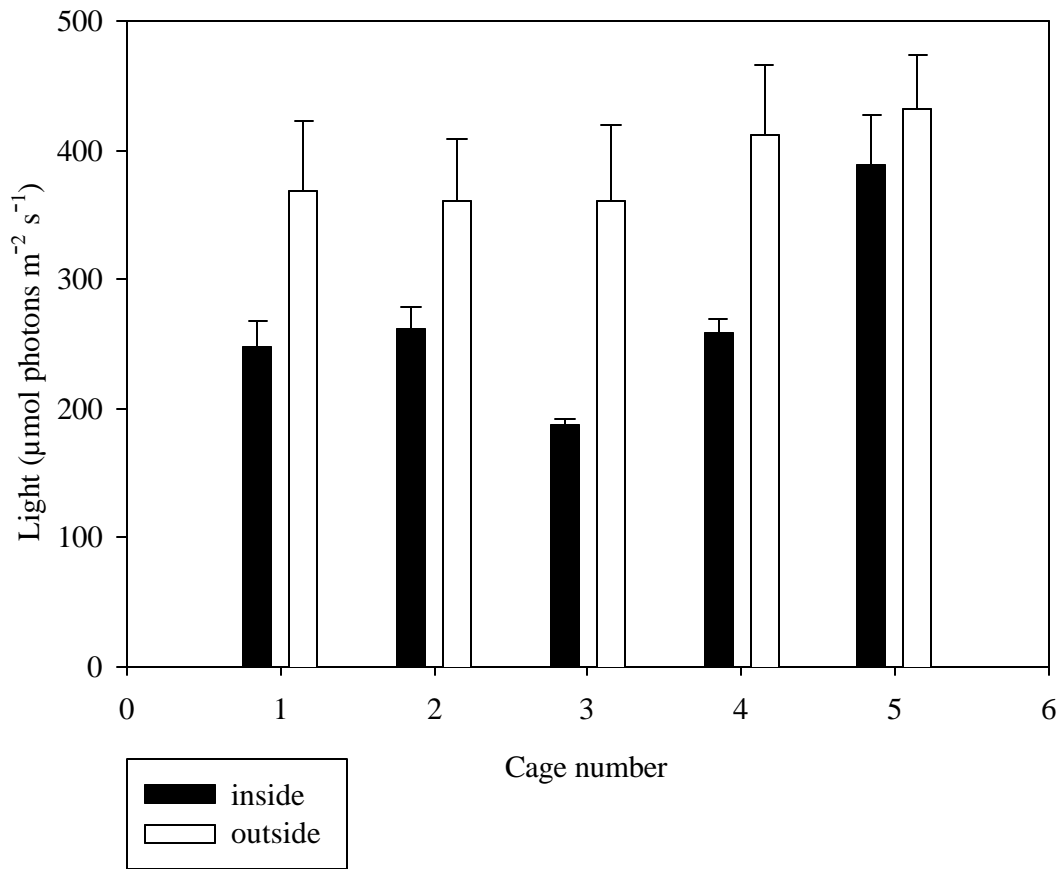


Figure 20: Mean (\pm SE) light readings of Photosynthetically Available Radiation inside and outside of the 5 cages.

some studies have assessed juvenile coral distribution in the Caribbean (Bak and Engel 1979; Rogers 1984; Chiappone and Sullivan 1996; Edmunds 2000), different methodologies were used, making it difficult to draw comparisons.

Juvenile coral density may be higher in Bonaire due to more substrate availability, less macroalgal cover ($11.8\% \pm \text{SE } 4.0$), higher topography (*pers. obs.*), and more intense grazing (Rogers 1984). Not only were grazing rates 4 times higher in Bonaire ($717 \text{ bites m}^{-2}\text{h}^{-1}$; Paddock *in prep.*) than in Mexico ($175 \text{ bites m}^{-2}\text{h}^{-1}$) (Steneck and Lang in publication), but ambient nutrient concentrations, especially nitrate and ammonium, were relatively low (Figure 13). Low nutrients contribute to clearer water and higher coral growth rates (Miller and Barimo 2001). Bonaire's hydro-geology differs from Mexico's Yucatan coast because it is a semi-tropical dry island with little river and sediment runoff. It is also possible that Bonaire has experienced fewer physical disturbances, such as hurricanes, than Mexico, since it is located south of the major Caribbean hurricane path (National Oceanic and Atmospheric Administration, www.noaa.gov). Bonaire may exemplify a 'stable' reef community, where nutrients are low and herbivory is high, contributing to more available substrate for coral recruitment and juvenile coral survivorship (Done 1992). Localized physical, chemical, and biological parameters in Bonaire are most likely responsible for higher juvenile coral densities.

Mexico, on the other hand, has high macroalgal cover ($32.5\% \pm \text{SE } 3.2$) and canopy height ($2.4 \text{ cm} \pm \text{SE } 0.18$) compared to Bonaire's macroalgal cover ($11.8\% \pm \text{SE } 4.0$) and canopy height ($0.6 \text{ cm} \pm \text{SE } 0.07$). This is most likely due to low herbivory (Carpenter 1986; Steneck and Lang in publication) and high nutrient concentrations (Done 1992) (Figure 13). Mexico's Yucatan coast is comprised of a karst limestone floor

with an extensive underground river system that exchanges daily with coastal waters due to tidal flux, increasing nutrient runoff (Doehring and Butler 1974; Ward 1985; Brown and Shaw 2002). Additionally, reefs are close to shore, making this reef region more vulnerable to nutrient enrichment (Steneck and Lang in publication). Nutrients drive macroalgal growth (Littler and Littler 1985) and increase turbidity (Tomascik and Sander 1987), both of which negatively affect coral growth. Hurricanes have also been responsible for killing corals and contributing to macroalgal blooms along the Yucatan coast (*pers. obs.*). Littler and Littler's Relative Dominance Model suggests that major disturbances can drive stable coral reefs to communities of high algal cover (Done 1992). The lack of substrate availability due to high macroalgal abundance, low grazing, and physical disturbances most likely contribute to lower juvenile coral densities along the Mesoamerican Barrier Reef System.

Both macroalgal percent cover and height contribute to macroalgal biomass, supported here by a significant positive correlation between the two (Figure 9). It has already been established that macroalgal biomass is correlated with low adult coral cover (Hughes 1994; Hughes and Jackson 1985; Smith 1981), however, this study has identified that it may also hinder juvenile coral survivorship (Figure 7). Over a relatively large spatial scale, juvenile coral density was negatively correlated to macroalgal abundance, both percent cover and canopy height (Figure 7 & 8). Macroalgae occupy available substrate, dominate crevices where coral larvae prefer to settle (Lessios 1988; Maida 1994; Chiappone and Sullivan 1996), and accumulate at the edges of coral colonies, causing live tissue to recede (Lirman 2001; McCook and Jompa 2002). Furthermore, high canopy height intensifies the effects of shading, overgrowth, physical

abrasion, reduced water flow, sediment trapping, and toxins on juvenile corals (River and Edmunds 2001; Smith et al. 2001; Roy in publ). These conditions cost corals metabolically because energy is allocated toward competition instead of growth or tissue repair (Tanner 1995). Juvenile corals are also more susceptible to stresses than adult coral colonies due to their small size and proximity to substrate (Wittenberg and Hunte 1992). It is likely that a functional relationship exists between the number of newly settled corals and the abundance of macroalgae due to competition for space. The first hypothesis was, therefore, rejected because juvenile coral density does appear to be negatively affected by both macroalgal percent cover and height.

One of the major driving factors of macroalgal abundance is elevated nutrients (Hatcher and Larkum 1983; Wittenberg and Hunte 1992), as was seen along the Yucatan coast of Mexico (Figure 13). Significant correlations between Total Inorganic Nitrogen (TIN) and macroalgal percent cover and height (Figures 14 a & b) suggest that the abundance of macroalgae may be driven, in part, by elevated nutrients (Figure 13). It has already been established that subsurface waters along the northern coast of the Yucatan are contaminated by seepage from sewage, landfills, and golf course fertilizers (Brown and Shaw 2002), however these data are the first to suggest that elevated nutrients may be reaching local reef waters. This is significant because if ambient herbivory is low, as it is at many sites throughout the Caribbean, then herbivory may not be able to keep up with macroalgal growth. This affects coral population growth and recovery because macroalgae indirectly hinder juvenile coral survivorship (Tomascik and Sander 1987; Wittenberg and Hunte 1992).

Elevated nutrients can also directly affect juvenile coral growth, evidenced by the significant inverse correlation between juvenile coral density and NH_4^+ concentrations (Figure 15). Nutrient loading can hinder coral processes, such as calcification, growth, and respiration rates (Maragos 1972; Smith et al. 1981; Tomascik and Sander 1985; Marubini and Davies 1996; Ferrier-Pages et al. 2000). Coral growth rates have been reduced by as much as 60% when exposed to $2 \mu\text{m PO}_4^{3-}$ (Ferrier-Pages et al. 2000), and coral calcification rates have declined under NO_3^- concentrations as low as $1 \mu\text{m}$ (Marubini and Davies 1996). Little is known about the effects of NH_4^+ on juvenile coral growth, however previous studies have found that elevated concentrations of NH_4^+ ($20 \mu\text{m}$) significantly reduce coral growth rates (Ferrier-Pages et al. 2000). Tomasick and Sander (1987) found that adult colonies of *Porites* in polluted reef areas reproduced earlier and had lower larval densities than colonies on non-polluted reefs. Elevated nutrient concentrations have the potential to affect juvenile corals at both the cellular and community levels, however additional controlled experiments are necessary.

The other major mediator of reef algae is herbivory (Carpenter 1986; Steneck 1988). It is thought that overfishing (Birkeland 1977; Sammarco and Carleton 1981; Hughes 1994) and the die-off of *Diadema antillarum* have contributed to the dominance of macroalgae in the Caribbean (Carpenter 1986; de Ruyter van Stevenick and Bak 1986; Hughes et al. 1987; Lessios 1988). In Jamaica, Edmunds and Carpenter (2001) recently discovered that macroalgal cover was reduced in areas where *Diadema* populations have begun to recover. Consequently, juvenile corals in these grazed areas have reached densities of $43/\text{m}^2$, implying that phase shifts may be locally reversible if *Diadema* populations recover to pre-1980's densities (Edmunds and Carpenter 2001). High

grazing rates in Bonaire were related to low macroalgal biomass and higher juvenile coral densities (Figure 4), but inorganic nitrogen levels were also low. The most favorable conditions for successful coral recruitment and survival appear to be high grazing rates, relatively low nutrient concentrations, and sufficient substrate.

Relative Abundance of Juvenile Corals

The abundance of *Porites*, *Siderastrea*, and *Agaricia* juvenile corals among sites (Figure 10) concurs with other studies that have assessed juvenile coral distribution in the Caribbean (Dustan 1977; Bak and Engel 1979; Rogers 1984; Smith 1992; Wittenberg and Hunte 1992; Edmunds and Carpenter 2001). These 3 genera comprised 78% of juvenile corals observed in this study (Figure 10), although in Bonaire, *Siderastrea* was less common. *Agaricia*, *Siderastrea*, and *Porites*, except for the species, *Siderastrea siderea*, are brooders, which is a mode of reproduction. Brooders release larvae, recruit locally, reproduce more than once a year, and are considered short-lived species (Sammarco 1985; Buddemeier and Smith 1992; Hughes and Tanner 2000). Reef-building corals, or spawners, only reproduce once a year and release gametes that fertilize in the water column (Richmond and Hunter 1990). Juvenile densities of spawning corals in this study were low (<5%), which has been noted by other authors (Bak and Engel 1979; Sammarco 1985; Richmond and Hunter 1990; Edmunds and Carpenter 2001). The abundance of brooding juvenile corals could be due to their mode of reproduction as well as the lack of available substrate. It has also been suggested in other studies that brooders are more fit competitors in disturbed environments (Tomascik and Sander 1987). Since some authors have demonstrated a positive correlation between the distribution of adult and juvenile

corals (Wittenberg and Hunte 1992; Chiappone and Sullivan 1996), the lack of scleractinian juvenile spawners observed here presents major implications for coral reef populations because these corals are responsible for producing the reef framework (Sheppard 1982; Hughes et al. 1999).

Relative Abundance of Macroalgae

The relative abundance of macroalgae differed significantly among sites, however 50% of all macroalgae observed was either *Dictyota* or *Halimeda* (Figure 11). Additionally, 75% of macroalgae in direct contact with juvenile corals was either *Dictyota* (60%) or *Halimeda* (16%) (Figure 12). Other studies have found that *Dictyota* and *Halimeda* also come into frequent contact with adult corals in the Caribbean (Lirman 2001). *Dictyota* was the major macroalgae in Bonaire, hence most of the diversity was observed in Mexico. This is most likely due to levels of herbivory because both cover and height of *Dictyota* were low in Bonaire. Macroalgal diversity, percent cover, and height differed among Mexico's reefs sites due to the varying levels of nutrients and herbivory along the Mesoamerican Barrier Reef. The Caribbean is currently dominated by macroalgae that were not common before, such as *Dictyota*, *Halimeda*, *Jania*, *Laurencia*, *Lobophora*, *Sargassum*, and *Turbinaria* (Lessios 1988; Hughes 1994; Andres and Witman 1995). These algae are considered invasive because they recruit and grow quickly (Steneck and Dethier 1994) and are chemically and morphologically defended against grazers (Hay et al. 1987; Williams and Polunin 2001). They also occupy cryptic spaces and grow on the edges of coral colonies (Maida 1994), increasing competition for space. One of the reasons for their abundance may be due to the die-off of *Diadema*

antillarum, a more intense and less preferential grazer (Carpenter 1986; de Ruyter van Stevenick and Bak 1986; Hughes et al. 1987; Lessios 1988; Stimson et al. 2001) than herbivorous fish. One aspect of macroalgal abundance that has not been thoroughly explored is how the homogeneity of reef macroalgae, such as *Dictyota* and *Halimeda*, may affect juvenile coral survivorship. Do macroalgae of various chemical and morphological characteristics (functional groups) affect juvenile coral growth and survivorship differently?

Interactions Between Juvenile Corals and Macroalgae

This was the first study to test the effects of macroalgae, both genera and functional form, on juvenile scleractinian coral growth. Previous studies have observed interactions between corals and algae in the field (McCook et al. 2001), yet no attempt has been made to isolate the effects of particular forms of macroalgae on juvenile coral growth. Results indicated that juvenile corals respond differently to stress, such as interactions with macroalgae, most likely due to different life history characteristics, such as growth, feeding, and tissue repair (Connell 1978; Bak and Engel 1979; Wittenberg and Hunte 1992). Previous studies have identified that corals can compete with macroalgae by the use of mesenterial filaments or sweeper tentacles as well as by chemical, or allelopathic, defenses (McCook et al. 2001). The ability of corals to apply these defense mechanisms is species-specific, and little is known about energy allocation in juvenile corals. Thus, it is not surprising that *Siderastrea*, *Agaricia*, and *Porites* juvenile corals responded differently to the effects of macroalgae.

Both calcification and tissue growth rates varied significantly among the 3 juvenile coral genera (Figures 16 & 17). There are currently no published calcification rates for juvenile corals using the buoyant weighing technique, however in this study the controls calcified at a significantly faster rate (0.263 g/month) than the juvenile corals adjacent to treatments (0.215 g/month). This indicates that macroalgae may have hindered the rate of juvenile coral calcification. Bak and Engel (1979) reported that juvenile scleractinian corals *in situ* grow, on average, 1-3 mm/month in diameter (live tissue). In the present investigation, juvenile corals adjacent to treatments lost an average of 2.95 mm/month, while the controls lost an average of 2.83 mm/month. This suggests that macroalgae may have contributed to tissue encroachment, but other variables (undetected here) were also a factor.

Tissue encroachment also differed among juvenile coral genera. *Porites* lost the most live tissue throughout the experiment, which concurs with other studies that have suggested that *Porites* corals have high mortality rates (Smith 1992) and a susceptibility to disturbance (Hughes and Jackson 1985; Hughes and Tanner 2000). This may be due to autotrophy and the fact that this genus dedicates little energy to tissue growth (Edmunds and Davies 1986). *Agaricia* corals lost the least live tissue overall but calcified the most over 2 months. This, again, can be explained by the ability of corals to allocate energy differently (Sammarco 1985; Wittenberg and Hunte 1992; Tanner 1995). The second hypothesis was rejected because the effect of macroalgae on juvenile coral growth (surface area and weight) may be due to coral identity (genus).

After pooling juvenile coral genera to analyze the effect of macroalgal morphology and identity (genus) on juvenile coral growth, there were no significant

differences among treatments. Thus, the third hypothesis was accepted. Although not statistically significant, there were some interesting trends that emerged. All juvenile corals calcified over the length of the experiment, however most treatments calcified at a slower rate than the control (Figure 18). This implies that macroalgae had an effect on calcification, but unfortunately this experiment was unable to detect differences among macroalgal genera. *Dictyota* appeared to have had a beneficial effect on juvenile coral growth compared to the control (Figure 18). This could have been due to an artifact in the experimental design because *Dictyota* detached easily, or perhaps a nutritional benefit could have been occurring (de Nys 1991; McCook and Jompa 2002). Based on observations in the field, it is unlikely that *Dictyota* promotes coral growth because it often accumulates around the edges of coral colonies and has been observed to cause tissue mortality.

The trends were similar when analyzing the effects of macroalgal treatments on surface area. The majority of juvenile corals lost live tissue over the 8-week period, with the exception of some juvenile corals adjacent to *Dictyota* (Figure 19). This is the first record of negative growth rates in juvenile corals. The *Halimeda* (calcareous group) and *Sargassum* (leathery group) treatments caused the most tissue encroachment (Figure 19). This may be due to morphology and/or allelochemicals (Hay et al. 1987; Duffy and Hay 1990; Steneck and Dethier 1994; McCook et al. 2001). River and Edmunds (2001) found that physical abrasion of *Sargassum* reduced coral growth up to 80% compared to plastic algal mimics, which only reduced growth by 25% despite shading effects. This was due to polyp retraction, which limited energy allocated towards coral growth and calcification (Coyer et al. 1993; Tanner 1995; River and Edmunds 2001). *Halimeda* and *Sargassum*

are morphologically and chemically defended algae (Duffy and Hay 1990), thus it is possible that allelochemicals, undetected in this study, may play a significant role in mediating juvenile coral tissue (Done 1992; Hughes 1994). Hay et al. (Hay et al. 1987) found that herbivorous fish and *Diadema antillarum* grazed less on *Thalassia* leaves that were inoculated with chemical compounds from *Dictyota*, *Laurencia*, and *Styopodium*. If coral reef herbivores detect differences in morphologically identical but chemically different plants, corals may also respond to macroalgae based on their allelochemical makeup. This experiment suggests that macroalgae reduce juvenile coral growth rates (calcification and tissue), yet it is undetermined which macroalgal genera impose the greatest threat. Implications for coral populations are severe since decreased growth rates lead to smaller, less fecund coral colonies (Tanner 1997) as well as lower coral recruitment (Done 1992; Hughes 1994). This investigation illustrated the importance of concentrating on macroalgal genera, rather than functional group, when assessing juvenile coral-macroalgal interactions in the future.

CONCLUSION

Little is known about juvenile coral survivorship (Lee 1992) yet the post-settlement period is crucial to population growth and recovery (Sammarco 1980; Hughes and Jackson 1985; Smith 1992). This investigation concurs that there is spatial variability in the distribution of juvenile corals and macroalgae, and new evidence here suggests that a strong negative correlation exists between these two primary coral reef competitors. Yucatan reefs appear to be in decline, evidenced by low juvenile coral densities, corresponding with high macroalgal cover and height. Bonaire reefs exhibited

the opposite trend, a higher number of newly settled corals and a lower abundance of macroalgae. Thus, community structure among Caribbean reef sites exhibits similar associations between juvenile corals and macroalgae. Since disturbance appears to be exceeding resilience in the Caribbean region, juvenile coral survivorship is a major concern. Detailed and longer-term studies on juvenile corals at the species-level may better explain their distribution and the factors that contribute to their survivorship.

In this study, *Dictyota* and *Halimeda* were the most abundant macroalgae among 17 sites in the Caribbean and therefore require more attention on the part of researchers. Why does the diversity of macroalgae differ among reef sites? What factors control the distribution of particular functional forms of algae? It seems that the physical and chemical attributes of macroalgae contribute to juvenile coral mortality rates although little work has been done on allelochemicals of reef algae. Reef communities prolific with macroalgae, mainly *Dictyota* and *Halimeda*, occupy space necessary for coral recruitment and reduce juvenile coral growth and survivorship.

This study also identified a nutrient signal between macroalgal abundance and elevated concentrations of inorganic nitrogen. The role of localized nutrient concentrations should be incorporated into long-term monitoring programs to better understand their cascading effects on juvenile coral survivorship. Understanding species-specific mechanisms between juvenile corals and macroalgae and the factors that contribute to decreased juvenile coral growth rates may affect how coral reefs are managed in the future. By increasing grazing rates and reducing nutrient loading, homogenous macroalgal communities could be altered so that recovery of coral populations may be sustained in the future (Adey et al. 2000). The presence of juvenile

corals may be the result of the microhabitat in which they can survive, as opposed to the microhabitat where they can recruit.

Literature Cited

- Adey W, McConnaughey T, Small A, Spoon D (2000) Coral Reefs: endangered, biodiverse, genetic resources. *Seas at the Millennium: An Environmental Evaluation III*, chapt 109: 33-41
- Andres N, Witman J (1995) Trends in community structure on a Jamaican reef. *Mar Ecol Prog Ser* 118: 305-310
- Babcock R (1985) Growth and mortality in juvenile corals (*Goniastrea*, *Platygyra*, and *Acropora*): the first year. *Proc. 5th Int. Coral Reef Symp.* 4: 355-360
- Bak R, Engel M (1979) Distribution, abundance and survival of juvenile hermatypic corals (*Scleractinia*) and the importance of life history strategies in the parent coral community. *Marine Biology* 54: 341-352
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc. 3rd Int. Coral Reef Symposium* 1: 15-21
- Brown H, Shaw C (2002) Constructed wetlands result in reduced contamination of groundwater at Akumal: summer 2002. *Centro Ecologico Akumal's Environmental Report* 2: 1-11
- Buddemeier R (2001) Is it time to give up? *Bull Mar Sci* 69: 317-326
- Buddemeier R, Smith S (1992) Global change and coral reef ecosystems. *Annu Rev Ecol system* 23: 89-118
- Carpenter R (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monog* 56: 345-363
- Chiappone M, Sullivan K (1996) Distribution, abundance, and species composition of juvenile scleractinian corals in the Florida reef tract. *Bulletin of Marine Science* 58: 555-569
- Connell J (1997a) Disturbance and recovery of coral assemblages. *Coral Reefs*: S101-S113
- Connell J (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310
- Connell J, Hughes, TP, and Wallace, CC (1997b) A 30-year study of coral abundance, recruitment and disturbance at several scales in space and time. *Ecol Monog* 67: 461-488
- Coyer J, Ambrose R, Engle J, Carroll J (1993) Interactions between corals and algae on a temperate zone rocky reef: mediation by sea urchins. *Jour Exp Mar Biol Ecol* 167: 21-37
- Davies P (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. *Mar Biol* 101: 389-395

- de Nys R, Coll, JC, Price, IR (1991) Chemically mediated interactions between the red alga *Plocamium hamatum* (Rhodophyta) and the octocoral *Sinularia cruciata* (Alcyonacea). *Mar Biol* 108: 315-320
- de Ruyter van Stevenick E, Bak R (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar Ecol Prog Ser* 34: 87-94
- Doehring D, Butler J (1974) Hydrogeologic constraints on Yucatan's development. *Science* 186: 591-595
- Done T (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247: 121-132
- Doty M (1971) Measurements of water movement in reference to benthic algal growth. *Bot Mar* 24: 32-35
- Duffy J, Hay M (1990) Seaweed Adaptations to herbivory. *Bioscience* 40: 368-375
- Dustan P (1977) Vitality of reef coral populations off Key Largo, Florida: recruitment and mortality. *Env Geol* 2: 51-58
- Edmunds P (2000) Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Marine Ecology Progress Series* 202: 113-124
- Edmunds P, Bruno J (1996) The importance of sampling scale in ecology: kilometer-wide variation in coral reef communities. *Marine Ecology Progress Series* 143: 165-171
- Edmunds P, Davies P (1986) An energy budget for *Porites porites*. *Marine Biology* 92: 339-347
- Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5067-5071
- Fautin D, Buddemeier R (2002) Large-scale dynamics: the state of science, the state of the reef, and the research issues. *Coral Reefs* 21: 1-8
- Ferrier-Pages C, Gattuso J, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19: 103-113
- Froelich P, Pilson, MEQ, and Froelich, A (1977) General Operations Manual for the Technicon Autoanalyzer II
- Hatcher B, Larkum A (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *Jour Exp Mar Biol Ecol* 69: 61-84

- Hay M, Gustafson K, Fenical W (1987) Chemical defense against diverse coral-reef herbivores. *Ecology* 68: 1581-1591
- Hughes T (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551
- Hughes T (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. *American Naturalist* 123: 778-795
- Hughes T, Baird A, Dinsdale E, Moltschaniwskyj N, Pratchett M, Tanner J, Willis B (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397: 59-63
- Hughes T, Jackson J (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monog* 55: 141-166
- Hughes T, Reed D, Boyle M (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *Jour Exp Mar Biol Ecol* 113: 39-59
- Hughes T, Tanner J (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81: 2250-2263
- Lee T, Rooth, C, Williams, E, McGowan, M, Szmant, AF, and Clarke, ME (1992) Influence of Florida current, gyres, and wind-driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. *Cont Shelf Res* 12: 971-1002
- Lessios H (1988) Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Ann Rev Ecol Sys* 19
- Lewis S (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monog* 56: 183-200
- Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19: 392-399
- Littler D, Littler M (1985) Factors controlling relative dominance of primary producers on biotic reefs. *Proc. 5th Int. Coral Reef Symp.* 4: 35-39
- Maida M, Coll, JC, Sammarco, PW (1994) Shedding new light on scleractinian coral recruitment. *Jour Exp Mar Biol Ecol* 180: 189-202
- Maragos J (1972) A study of the ecology of Hawaiian corals. PhD Dissertation, University of Hawaii: 290 pp
- Marubini F, Davies P (1996) Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Mar Biol* 127: 319-328

- McClanahan (2001) Responses of algae, corals, and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* 19: 367-379
- McCook L, Jompa J (2002) Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Exp Mar Bio and Ecol* 271: 25-39
- McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19: 400-417
- Miller M (1998) Coral/Seaweed competition and the control of reef community structure within and between latitudes. *Ocean and Mar Bio* 36: 65-96
- Miller M, Barimo J (2001) Assessment of juvenile coral populations at two reef restoration sites in the Florida keys national marine sanctuary: Indicators of success? *Bulletin of Marine Science* 69: 395-405
- Miller M, Hay M (1996) Coral-Seaweed-Grazer-Nutrient Interactions on temperate reefs. *Ecol Monog* 66: 323-344
- Potts D (1977) Suppression of coral populations by filamentous algae within damselfish territories. *Jour Exp Mar Biol Ecol* 28: 207-216
- Precht W, Aronson R (2000) Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnology and Oceanography* 45: 251-255
- Richmond R, Hunter C (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60: 185-203
- River G, Edmunds P (2001) Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *Jour Exp Mar Biol Ecol* 261: 159-172
- Rogers C, Fitz, HCIII, Gilnack, M, Beets, J, Hardin, J (1984) Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Croix, US Virgin Islands. *Coral Reefs* 3: 69-76
- Roy R (in publ) Akumal's Reefs: stony coral communities along the developing Mexican Caribbean coastline
- Sammarco P (1980) *Diadema* and its relationship to coral spat mortality: grazing competition and biological disturbance. *Jour Exp Mar Biol Ecol* 45: 245-272
- Sammarco P (1982) Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *Jour Exp Mar Biol Ecol* 61: 31-55
- Sammarco P (1985) The Great Barrier Reef vs. the Caribbean: comparisons of grazers, coral recruitment patterns and reef recovery. *Proc. 5th Intl. Coral Reef Congress* 4: 391-395

- Sammarco P, Carleton J (1981) Damselfish territory and coral community structure: reduced grazing and effects on coral spat. *Proc 4th Intl Coral Reef Symp* 2: 339-344
- Sheppard C (1982) Coral populations on reef slopes and their major controls. *Mar Ecol Prog Ser* 7: 83-115
- Smith J, Smith C, Hunter C (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19: 332-342
- Smith S (1992) Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: comparisons to Caribbean and Pacific reefs. *American Zoology* 32: 663-673
- Smith S, Kimmerer W, Laws E, Brock R, Walsh T (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35: 279-402
- Steneck R (1988) Herbivory on coral reefs: a synthesis. *Proc of 6th Intl coral Reef Symp* 1: 37-49
- Steneck R, Dethier M (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476-498
- Steneck R, Lang J (in publication) Rapid assessment of Mexico's Yucatan reef in 1997 and 1999: Pre and post-1988 mass bleaching and hurricane Mitch. *Atoll Research Bulletin*
- Stimson J, Larned S, Conklin E (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19: 343-357
- Tanner J (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival, and reproduction. *Journal of Exp Mar Bio and Ecol* 190: 150-168
- Tanner JE (1997) Interspecific competition reduces fitness in scleractinian corals. *Journal of Exp Mar Bio and Ecol* 214: 19-34
- Tomascik T, Sander F (1987) Effects of eutrophication on reef-building corals. *Marine Biology* 94: 77-94
- Tomascik T, Sander F (1985) Effects of eutrophication on reef-building corals I. Growth rate of the reef building coral *Montastraea annularis*. *Mar Biol* 87: 143-155
- Ward W (1985) Quaternary geology of northeastern Yucatan Peninsula. *Geology and Hydrogeology of northeastern Yucatan and Quaternary geology of northeastern Yucatan*: 23-95

Williams I, Polunin N (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19: 358-366

Wittenberg M, Hunte W (1992) Effects of eutrophication and sedimentation on juvenile corals. *Marine Biology* 112: 131-138