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Effects of Multiple Ecological Drivers on Recruitment and Succession of Coral Reef Macroalgal Communities

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

EFFECTS OF MULTIPLE ECOLOGICAL DRIVERS ON RECRUITMENT AND
SUCCESSION OF CORAL REEF MACROALGAL COMMUNITIES

A thesis submitted in partial fulfillment of the

requirements for the degree

of

MASTER OF SCIENCE

in

BIOLOGY

by

Alain Duran

2013

To: Dean Kenneth Furton
College of Arts and Sciences

This thesis, written by Alain Duran, and entitled Effects of Multiple Ecological Drivers on Recruitment and Succession of Coral Reef Macroalgal Communities, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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Date of Defense: June 14, 2013

The thesis of Alain Duran is approved.

Dean Kenneth Furton
College of Arts and Sciences

Dean Lakshmi N. Reddi
University Graduate School

Florida International University, 2013

DEDICATION

Dedicated to my grandpa, a successful family man who never lost his sense of humor, to my son Andy, I hope you see this work as an inspiration for your future professional development, to Mayle, thank you for being always there, and to my mother, who always encourages me to pursue my goals.

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ABSTRACT OF THE THESIS
EFFECTS OF MULTIPLE ECOLOGICAL DRIVERS ON RECRUITMENT AND
SUCCESSION OF CORAL REEF MACROALGAL COMMUNITIES

by

Alain Duran

Florida International University, 2013

Miami, Florida

Professor Ligia Collado-Vides, Co-Major Professor

Professor Deron Burkepile, Co-Major Professor

The study evaluated the effects of herbivory pressure, nutrient availability and potential propagule supply on recruitment and succession of coral reef macroalgal communities. Recruitment and succession tiles were placed in a nutrient-herbivory factorial experiment and macroalgal abundances were evaluated through time. Proportional abundances of macroalgal form-functional groups on recruitment and succession tiles were similar to field established communities within treatments, evidencing possible effects of adult macroalgae as propagule supply. Macroalgal abundance of recruitment tiles increased with nutrient loading and herbivory reduction combined whereas on succession tiles nutrient loading increased abundance of articulated-calcareous only when herbivores were excluded. Macroalgal field established communities were only affected by herbivory reduction.

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CHAPTER 1 – BACKGROUND

1.1 Introduction

Coral reefs provide a wide variety of functional values such as dissipation of wave energy, biogeochemical cycling, and nursery habitats for multiple species (Harborne *et al.*, 2006). Furthermore, human communities living adjacent to coral reefs receive goods and services such as food, recreation, and tourism income that place the value of coral reefs at approximately \$ 29.8 billion per year (Cesar *et al.*, 2003). Despite the economic and ecological importance of coral reef ecosystems, they are threatened by local anthropogenic impacts (e.g., overfishing, eutrophication, habitat destruction among others) that intensify the effects of global stressors such as ocean acidification and thermal stress (Hoegh-Guldberg *et al.*, 2007). Consequently, coral reefs worldwide, particularly in the Caribbean, have suffered long-term degradation caused by the decline of large carnivores and herbivores and the loss of overall coral cover (Pandolfi *et al.*, 2003). In the last three decades coral cover in some places of the Caribbean has been reduced to ten percent or less (Gardner *et al.*, 2003) resulting in a phase shift from a coral-dominated to a coral-depauperate state (Hughes, 1994; Roger and Miller, 2006; Mumby, 2009). Further, there are several causes of coral cover declined such as coral diseases, coral bleaching events, out-break of coral-eating organisms, and storm damage (Goreau *et al.*, 1998; Eakin *et al.*, 2010; Kayal *et al.*, 2012).

As a consequence of reduced coral cover, new available space has been created which can be colonized by macroalgal propagules, leading to increased abundance of macroalgae (Diaz-Pulido and McCook, 2002; Mumby and Steneck, 2008). Once macroalgal propagules have settled, different species or form-functional groups of macroalgae can become dominant throughout time following different successional patterns (Sammarco, 1983; Hixon and Bostroff,

1996; Diaz-Pulido and McCook, 2002). Recruitment of algae species and post-settlement succession of coral reef macroalgae communities are both shaped by different herbivore groups such as farmers (Pomacentridae), fish grazers (Acanthuridae and Scaridae) and sea-urchin grazers (Carpenter, 1986; Hixon and Brostoff, 1996; McClanahan, 1997). Indeed, some authors have suggested loss of herbivory (top-down driver) as a major cause of increasing macroalgal abundance on coral reefs, but nutrient enrichment (bottom-up) can amplify its effects (Burkepile and Hay, 2006; Walsh, 2011). Conversely, it has been proposed that nutrient loading is the primary factor regulating biomass and diversity of reef macroalgal communities (Lapointe *et al.* 1997; Lapointe *et al.*, 2004). However, top-down and bottom-up forces likely interact with one another to shape algal communities (Burkepile and Hay 2006). Little is known about how macroalgal propagule supply interacts with nutrient loading and herbivory to shape the recruitment and succession of coral reef macroalgal communities (De Ruyter and Breeman, 1987; Walters *et al.*, 2002).

1.2 Top-down drivers of coral reef macroalgal community

Several vertebrate and invertebrate herbivores feed on coral reef macroalgae, functioning as important top-down controls (Hay, 1984; Lewis, 1986; Edmunds and Carpenter, 2001; Burkepile and Hay, 2010; Butler and Mojica, 2012). Coral reef herbivores can be classified by body size, foraging range, grazing frequency, and impact on benthic communities (Steneck, 1983). Carpenter (1986) grouped reef herbivores into three categories: micro-herbivores (restricted mobility and small grazing range such as amphipods, tanaids and gastropods), intermediate size herbivores (crabs, sea urchins and blennies), and foragers (larger organisms with higher grazing rates, such as fish including parrotfish (Scaridae), surgeonfish (Acanthuridae) and chubs (Kyphosidae). Damselfish (Pomacentridae) belong to the intermediate sized herbivore

group as they have limited territories and remove small amounts of algal biomass. However, they are unique since their distinctive territorial behavior affects consumption rates of other grazers (Jones *et al.*, 2006). Because of their foraging habits and different effects on algal communities as compared to other herbivores, they are often referred to as farmers (Ceccarelli *et al.* 2005). Despite a high diversity of herbivores, sea urchins and herbivorous fish often remove most of the algal biomass from coral reefs (Solandt and Campbell, 2001; McClanahan *et al.*, 2002; Bellwood, 2003; Steiner and Williams, 2006; Blanco *et al.*, 2011). For instance, the functional importance of the long-spined sea urchin (*Diadema antillarum*) as a top-down driver was well studied before its massive die-off in 1983-84, which resulted in a dramatic increase of macroalgae on many Caribbean coral reefs (Sammarco, 1982; Carpenter, 1986, Lessios *et al.*, 1984). Even though the mass mortality of *D. antillarum* influenced the present-day phase shift from coral to macroalgae domination in some areas of the Caribbean (Hughes, 1994; Mumby *et al.*, 2006), it has been shown that the loss of herbivorous fishes could have major impact (Hay, 1984).

Anatomical, morphological, and physiological traits allow different species of parrotfish (Scaridae) and surgeonfish (Acanthuridae) to remove multiple types of macroalgae, such as small and soft filamentous algae, upright, leathery macroalgae, and crustose macroalgae (Tilghman *et al.*, 2001; Crossman *et al.*, 2005). Nonetheless, herbivore consumption rates are affected by macroalgal morphology, specific chemical defenses and tissue nutrient content, resulting in selective grazing by herbivores (Targett *et al.*, 1986; Duffy and Hay, 1994; Schupp and Paul, 1994; Hay, 1997; Hoey and Bellwood, 2011) which results in herbivore-specific feeding preferences (Hay *et al.*, 1987). For instance, Burkepile and Hay (2010) reported species-specific grazing rates and preferences among three common Caribbean herbivorous fish;

herbivory pressure by *Acanthurus bahianus* (ocean surgeonfish) and *Scarus taeniopterus* (princess parrotfish) kept the macroalgae community at a short turf and crustose coralline algae (CCA) level considered early successional stages. In contrast, foraging activity of *Sparisoma aurofrenatum* (redband parrotfish) resulted in taller macroalgae community, late successional stages, very similar to caged experimental treatments. Thus, coral reef macroalgae communities are controlled by multiple herbivorous fishes capable of limiting abundance of macroalgae and promoting growth of CCA (Burkepile and Hay, 2009; Smith *et al.*, 2010).

1.3 Bottom-up drivers of coral reef macroalgal community

Macroalgal primary production is directly related to nutrient and light availability (Lüning, 1990). In shallow, relatively oligotrophic tropical regions such as the Caribbean, nutrient availability can often limit macroalgal productivity (Lapointe *et al.*, 1997). Although nutrients are recognized to be a major factor determining abundance and diversity of certain macroalgal functional groups, it is still unclear with regards to their role in promoting increases of algal abundance on coral reefs (McClanahan *et al.*, 2004; Burkepile and Hay, 2006; McClanahan *et al.*, 2007). Availability of main macronutrients, nitrogen (N) and phosphorus (P), and their roles in driving macroalgal growth are focus of a strong debate among coral reef ecologists (Hughes, 1994; Lapointe *et al.* 1997; Lapointe *et al.*, 1999; Hughes *et al.*, 1999).

Dissolved inorganic nitrogen (DIN), which includes NH_4^+ , NO_3^- , NO_2^- ; and soluble reactive phosphorus (SRP) are limiting factors of primary production used to evaluate nutrient availability in marine environments (Smith, 1984; Lapointe *et al.*, 2005). Even though some nutrient thresholds have been proposed to predict algal domination on coral reefs, DIN 1.0 μM and SRP 0.1 μM (Lapointe *et al.* 1993; Lapointe *et al.*, 2005) several studies on this topic have not generally supported these concrete thresholds for predicting macroalgal dominance (Lapointe

et al., 1993; Hughes, 1994; Lapointe *et al.*, 1997; Hughes *et al.*, 1999; Lapointe *et al.*, 1999; Lapointe *et al.*, 2005). It is possible that some factors such as species-specific differences in nutrient uptake rate and physiological state of individuals (whether or not individuals are nutrient limited) would limit the potential for establishing nutrient thresholds that could lead to increase abundance of coral reef macroalgae (Fong *et al.*, 2001; Dailer *et al.*, 2012).

Several conceptual models have been put forth to explain the effect and magnitude of major ecological drivers responsible for controlling abundance of coral reef macroalgae (e.g., herbivory and nutrients; Littler and Littler, 1984; Steneck and Dethier, 1994; Littler *et al.*, 2006). The Relative Dominance Model (RDM) was proposed by Littler and Littler (1984) where four groups of benthic reef organisms are predicted to dominate depending upon bottom-up (nutrient levels) and top-down (herbivory activity) ecological controlling forces. According to Littler and Littler (1984) coral reefs with low nutrient levels and low herbivory tend to have higher abundance of filamentous algae whereas high nutrient levels and high herbivores activity favors dominance of coralline algae. Their conceptual model also predicts that a combination of low nutrient levels and high herbivory facilitates coral dominance and contrarily high nutrient levels and low herbivore activity enhances abundance of fleshy algae.

On the basis of Grimes's model (1977) and Littler and Littler's model (1984), Steneck and Dethier (1994) proposed a conceptual model combining productivity potential of different macroalgal form-functional groups and disturbance potential, defined as intensity and frequency of grazing. The model expects higher macroalgal biomass at low disturbance and high productivity potential levels while lower macroalgal biomass at low productivity and high disturbance potential levels (Steneck and Dethier, 1994). Importantly, Steneck and Dethier's model included seven macroalgal form-functional groups having leathery (e.g., *Sargassum* spp.)

and articulated calcareous (e.g., *Amphiroa* spp.) the highest biomass when there is a combination of low disturbance and high productivity potential levels. The Relative Dominance Model was modified in 2006 by Littler *et al.*, by integrating coral reef resiliency and human impact concepts and modifying dominant groups under different levels of both grazing activity and nutrient availability. The new proposed model predicts dominance of coral and crustose coralline algae (CCA) when combining low nutrient and high grazing activity levels suggesting that lower human impact results in more resilient coral reefs.

Factorial experiments testing the above mentioned conceptual models by manipulating nutrient availability and herbivory level have demonstrated that nutrient loading can affect coral reef macroalgae abundance only when herbivores are absent (Burkepile and Hay, 2006, 2009; Sotka and Hay, 2009). Additionally, it has been revealed that herbivore exclusion could increase reef macroalgae cover faster (less than one month) than nutrient loading (Smith *et al.*, 2010). Moreover, a noticeable response (increased abundance) of coral reef macroalgae to nutrient enrichment could be evident only after approximately three to four months (Smith *et al.*, 2010). Furthermore, it has been shown that grazing intensity could be modified by nutrient availability where enriched algae are preferably consumed by herbivorous fish (Boyer *et al.*, 2004; Burkepile and Hay, 2009). In summary, variations in magnitude effect of nutrient availability depend on the context (e.g., herbivory pressure level, macroalgal species composition) and specific study time scale.

1.4 Propagule supply and recruitment of macroalgae in coral reefs

Recruitment in marine environments, defined as addition of new individuals to populations, is a determinant process structuring open populations (Caley *et al.*, 1996; Roberson and Kaufman, 1998). Furthermore, recruitment rates of marine organisms are determined by the

number of propagules (marine plants) and larvae (marine animal) available as well as natural disturbances and oceanographic processes such winds and currents (Reed *et al.*, 1988; Caley *et al.*, 1996; Wilson and Meekan, 2001; Clark and Johnston, 2005). In that sense, some ecological studies of coral reef fishes have shown that fish recruitment is directly affected by number of larvae (larval supply) and other factors such as microhabitat characteristics and currents (Milicich *et al.*, 1992; Sale, 2004; Grorud-Colvert and Sponaugle, 2009). Likewise, Stoner *et al.* (1996) described substantial differences in larval density (number of veliger) of Queen Conch (*Strombus gigas*) between two separated populations caused by differential abundance of reproductive adults and consequently larval supply. In the case of marine macroalgae, propagule supply and dispersal distance have been also proposed to play an important role on population recruitment but few studies have focused on coral reef macroalgae (Kendrick and Walker, 1991; Stiger and Payri, 1999).

Macroalgae can reproduce either sexually or asexually resulting in a large production of propagules, such as zygotes, parthenogenetic gametes, spores and fragments that are released to the marine environment. However, reproduction events are triggered by several environmental factors such as lunar cycle, photoperiod, water temperature, and natural disturbances (Luning, 1990), which in many species may explain marked seasonality. For instance, Andersson *et al.* (1994) showed a circadian (18:00 to 22:00 h) and fortnightly rhythm for egg release during the reproductive season of *Fucus vesiculosus* in the Baltic Sea. Also, Hay and Norris (1984) found that six sympatric species of the red algae within the genus *Gracilaria* exhibited an increase in the percentage of reproductive plants following the onset of the turbid dry-season in late November. Clifton (2008) suggested that earlier reproductive period of some bryopsidales species (Phylum Chlorophyta) in Panama compared to Florida Keys could be a consequence of warmer water

occurring earlier in Panamanian coastal zone. Additionally, species of *Enteromorpha* recruited abundantly from overwintering propagules in March-April and dominated areas with propagule banks in Baltic rocky shores (Worm *et al.*, 2001). Santos and Duarte (1996) found a spore peak production of *Gelidium sesquipedale* (10.4×10^6 spores/m² and 4.9×10^5 spores/m² of tetrasporophyte and carposporophyte respectively) in March at the coastal area of Portugal. In China, *Sargassum thunbergii* shows a reproductive season from spring to early summer (May-June) where the number of germlings per kg of adult reaches about 1.2×10^5 quantified from natural populations (Zhang *et al.*, 2012). Noticeably, the number of macroalgae propagules in marine systems is high and varied with species-specific reproductive periods. Regardless of the seasonality of reproduction, the role of adult macroalgal assemblage structure as propagule supply is an important factor on determining macroalgal recruitment (Lotze *et al.*, 2000). Indeed, establishment of macroalgal assemblages is affected by the number of mature individuals as well as adult fertility affecting propagule supply (Stiger and Payri, 1999; Bellgrove *et al.*, 2004).

After propagules have been released from the parent plant, they must settle, attach, and become established (Fletcher and Callow, 1992). Environmental factors such as water flow and viscosity can influence propagule sinking speed and subsequent establishment (Chartes *et al.*, 1973; Okuda and Neushul, 1981; Granhag *et al.*, 2004). Further, temperature, salinity and surface roughness affect the ability of propagules to attach and establish on the substrate (Callow *et al.*, 1997; Maggs and Callow, 2002). Diaz-Pulido and McCook (2004) found density of settlement significantly higher on rough surfaces compared to smooth surfaces for reef species of order Fucales (mostly *Sargassum* spp.) and *Lobophora variegata*. Moreover, Ericksson and Johansson (2003) concluded that sediment, particularly organic sedimentation, had a negative effect on macroalgal recruitment.

Along with number of propagules, recruitment success and consequently development of macroalgal community structure are determined by propagule dispersal. Further, it has been proposed that macroalgal dispersal distance is among the shortest for marine organisms with over 60% of propagules being retained within less than one km from the parent plant (Kinlan and Gaines, 2003; Kinlan *et al.*, 2005). However, a high variation of dispersal distance along with type and size of propagule can be found among algal species. For instance, Reed *et al.* (1988) described equal densities of filamentous brown algae recruits from the parent thalli up to 500 m away. Conversely, Kendrick and Walker (1991) found that 96% propagules of *Sargassum spinuligerum* settled within 0.25 meter from the parent thalli. Additionally, propagules of *Macrocystis* sp. could successfully be recruited over 3 km from parent plants (Reed *et al.*, 2004). Hence, species-specific variations in dispersal distances could be a function of parent height, propagule size and abiotic factors with currents being especially important (Okuda and Neushul, 1981; Norton, 1992; Gaylord *et al.*, 2006). Thus, composition of local macroalgal community may strongly determine the abundance and species identity of macroalgal propagules and ultimately recruitment patterns on coral reefs

1.5 Succession of coral reef macroalgal communities

After propagules have established, different species of macroalgae can become dominant at different times following successional dynamics (Hixon and Brostoff, 1996; Diaz-Pulido and McCook, 2002). Several successional patterns have been described for coral reef macroalgal communities depending upon abundance and type of herbivores, as well as substrate type and competition between algae and other benthic organisms for space (McClanahan, 1997; Diaz-Pulido and McCook, 2002). Sammarco (1983) compared the effect of territorial damselfish behavior and large herbivorous fish (parrotfish and surgeonfish) on algal community

composition using four treatments (caged, shaded, territory and open). After three months, plates in all four treatments were covered by turf algae (>67% cover). But in open areas, naturally grazed by fish, turf algae decreased after 11 months resulting in bare substrate and endolithic algae covering 40% and 50% of plots respectively. Interestingly, macroalgal diversity was higher within damselfish territories compared to exclosure treatments (Sammarco, 1983). Additionally, Carpenter (1986) evaluated the impact of different herbivore groups on succession of macroalgal communities. One month after initiation of the experiment, all plates were comprised of approximately 80% turf algae. After nine months, macroalgae (height >1 cm) covered over 50% of the tiles within cages where urchins (primarily *D. antillarum*) and herbivorous fishes were excluded. When only fishes and microherbivores grazed the plates, macroalgae turf (height < 1 cm) had higher biomass and lower diversity (dominated by *Sphacelaria tribuloides*), whereas in treatments only grazed by urchins and microherbivores macroalgae biomass was lower and turf algae encompassed 20-25 species (Carpenter, 1986). Furthermore, Hixon and Brostoff (1996) studied the effect of herbivory on the rate and trajectory of coral reef macroalgae succession. They compared development rate and diversity of reef macroalgal communities under three treatments: damselfish territory (*Stegastes fasciolatus*), grazed areas (open to parrotfish and surgeonfish) and caged areas (herbivore exclusion). Results demonstrated that, compared to open treatments, damselfish decelerated (slowed) succession by maintaining the community at early-successional stages dominated by green and brown filamentous algae for over 230 days. In contrast, in open areas the trajectory of macroalgal succession was different as the early-successional stage was quickly replaced by different groups of macroalgae such as crustose and prostrate algae (Hixon and Bostroff, 1996). Thus, there are evidences of herbivory as a significant driver of coral reef macroalgal succession. Indeed, abundance and diversity of

macroalgae communities at different successional stages are strongly driven by intensity and frequency of grazing (Burkepile and Hay, 2010).

In conclusion, recruitment and post-settlement succession of coral reef macroalgae are driven by a wide variety of ecological factors including the number and species-specific type of arriving propagules, type and availability of substrate and grazing pressure of different herbivores (Hixon and Bostroff, 1996; McClanahan, 1997; Diaz-Pulido, 2002, 2003; Burkepile and Hay, 2010). However, there remains a lack of information regarding the consequences of their combined interactions. Therefore, my research question is: How does seasonality affect recruitment and post-settlement succession of coral reef macroalgal communities under different levels of nutrient availability and herbivory?

There are multiple studies showing nutrient enrichment, eutrophication, as major cause increasing abundance of opportunistic, fast-growing macroalgal species such as *Chaetomorpha* spp. *Ulva* spp., *Codium* spp. *Enteromorpha* spp. *Cladophora* spp. (Lapointe *et al.*, 1993; Lapointe *et al.*, 1997; McClanahan *et al.*, 2004; Smith *et al.*, 2005). However, when considering major drivers of frondose, fleshy macroalgal species, the primacy of nutrient enrichment is still under debate (Hughes, 1994; Hughes *et al.*, 1999; McClanahan *et al.*, 2004). I hypothesized that nutrient enrichment will increase (positive effect in conceptual model, Figure 1) percent cover of opportunistic early successional species whereas the magnitude of its effect on macroalgal abundance will decrease towards late successional stages. The effect of coral reef herbivorous fishes controlling multiple macroalgal successional stages has been well documented (Carpenter, 1986, Hixon and Bostroff, 1996; Burkepile and Hay, 2010). Therefore, I predicted that intense herbivory will decrease abundance (negative effect in conceptual model, Figure 1) of macroalgae at all successional stages. In addition, potential propagule supply, defined as the abundance of

adult macroalgae in close proximity to the studied sites, will increase abundance of macroalgae recruits acting as a propagule source (positive effect in conceptual model, Figure 1).

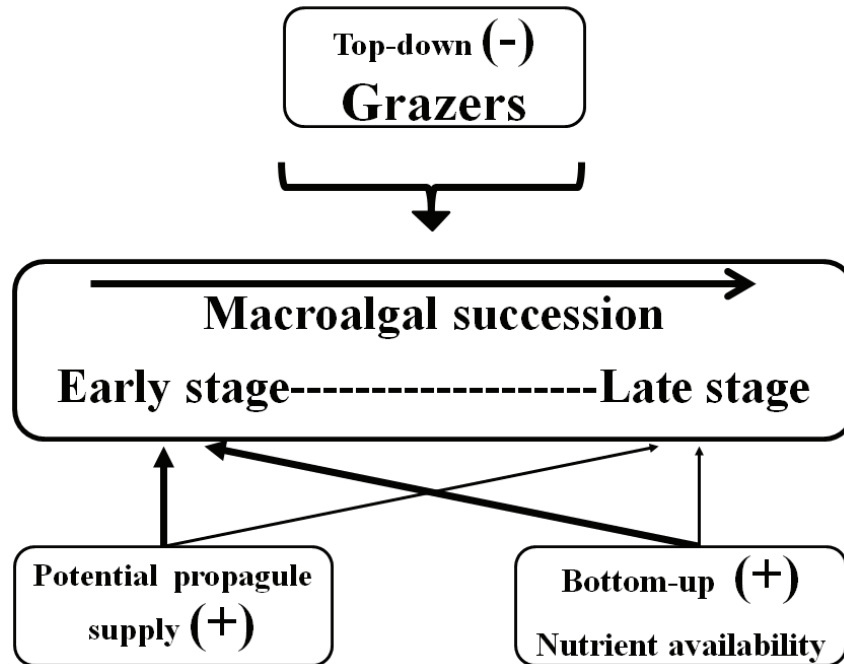


Figure 1. Conceptual model including the ecological factors studied throughout the thesis and their hypothesized effects. (-) symbol indicates overall grazers reducing macroalgal abundance at early and late successional stages; (+) symbols (bottom-up and potential propagule supply) predict increasing of macroalgae cover at early and late successional stages. Effects of nutrient availability and potential propagule supply vary through time with less magnitude effect (thinner arrow) on abundance of macroalgae at late successional stages

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CHAPTER 2 - RECRUITMENT AND SUCCESSION OF CORAL REEF MACROALGAL COMMUNITIES UNDER DIFFERENT ECOLOGICAL DRIVERS

Abstract

Structure of coral reef macroalgal communities is shaped by herbivory pressure and nutrient availability. However, the magnitude of impact of both ecological drivers throughout macroalgal succession remains unclear. Current study evaluated the effects of herbivory pressure, nutrient availability and potential propagule supply, on recruitment and succession of coral reef macroalgae. In September 2011, two limestone tiles were placed in a nutrient-herbivory factorial experiment (25 quadrats). One tile (recruitment tiles) was replaced every three months and abundance of algal species was evaluated in the lab. The remaining tile (succession tiles) was kept in the field throughout the nine-month study period. Percent cover of macroalgal form-functional groups of succession tiles and field established communities within quadrats were assessed in January and June, 2012. Total abundance of macroalgae increased towards June in recruitment and succession tiles and field established communities. Proportional abundance of macroalgal form-functional groups on recruitment and succession tiles were similar to field established communities suggesting possible effects of adult macroalgae as potential propagule supply. Macroalgal abundance of early successional species increased with combined nutrient loading and herbivore removal on recruitment tiles whereas on succession tiles nutrient increased percent cover of articulated calcareous species only when herbivores were excluded. Additionally, nutrients did not affect the abundance of macroalgae in field established communities. In summary, nutrient loading level and herbivory pressure controlled macroalgal communities at early-stages while effects of nutrient loading tended to decrease towards late-successional stages. Moreover, adult assemblages of coral reef macroalgae could affect recruitment and post-settlement succession.

2.1 Introduction

In coral reefs, special attention has been paid to herbivory pressure and nutrient availability as primary ecological drivers of macroalgal communities (Sammarco, 1983; Lewis, 1986; Hixon and Bostroff, 1996; Lapointe *et al.*, 2004; Burkepile and Hay, 2006). However, the relative magnitude of the effect of each ecological driver has on structuring macroalgal assemblages is still under debate, since increases of macroalgal abundance in some coral reefs have been attributed to either eutrophication or reduction of herbivores (Littler *et al.*, 1993; Hughes 1994; Lapointe *et al.*, 1997; Thacker *et al.*, 2001; Littler *et al.*, 2006; Rasher *et al.*, 2012). However, grazing rates of herbivorous fishes vary with season and depends on nutritional value and chemical defenses of macroalgal species (Hay *et al.*, 1987; Bolser and Hay, 1996; Boyer *et al.*, 2004; Burkepile and Hay, 2009, 2010). Furthermore, it is known that coral reef macroalgal species respond differently to nutrient loading since some species (e.g., opportunistic fast-growing) could quickly increase growth rates in nutrient enriched environments (Lapointe *et al.*, 1993; Lapointe *et al.*, 1997; McClanahan *et al.*, 2004; Smith *et al.*, 2005). However, when referring to the abundance of frondose algal species, the controlling effect of nutrient loading remains uncertain (Hugher, 1994; Hughes *et al.*, 1999; McClanahan *et al.*, 2004). Additionally, abundance of coral reef macroalgae species changes seasonally responding to temporal variations of environmental conditions such as salinity, water temperature and light availability (Stiger and Payri, 1999; Ferrarri *et al.*, 2012). Hence, the effect of herbivory pressure and nutrient availability on controlling coral reef macroalgae might vary seasonally, locally and is content dependent.

Plant communities are subjected to progressive temporal changes of both species richness and abundance, defined as community succession (Grime, 1979). Furthermore, terrestrial

ecologists have classified primary succession as colonization of substrate that has never been previously occupied and secondary succession as recolonization after disturbances open free space (Moore *et al.*, 1998). In marine communities some macroalgae have been classified as early-successional species (e.g., filamentous turf algae such as *Ectocarpus* sp., and *Ulva* spp.) whereas others as late-successional species (e.g., *Sargassum* sp., *Corallina* sp., *Amphiroa* sp.) on the basis of their growth and reproduction rates, and morphological characteristics (Littler and Littler, 1980; Dawes, 1998). Biological traits of early-successional species include small size, year-around reproductive cycle, and high growth rates that allow them to rapidly colonize available substrate (Steneck and Dethier, 1994; McClanahan, 1997). Conversely, late successional forms include taller species with higher thallus complexity characterized by slow growth and reproduction rates and usually more resistant to grazing through physical and chemical defenses (Steneck and Dethier, 1994).

Recruitment of macroalgae relies upon several factors such as number of propagules released by parents (propagule supply), propagule dispersal distance, as well as abiotic factors such as space availability, currents, and water temperature (Callow *et al.*, 1997; Lotze *et al.*, 2000; Worm *et al.*, 2001). However, while only few studies have focused on coral reefs, the effects of macroalgal propagule supply on structuring macroalgal marine communities has been mostly studied at temperate ecosystems such as kelp forests and rocky shore, and single, invasive and blooming species (Kendrick and Walker, 1991; Stiger and Paire, 1999; Lotze *et al.*, 2000; Reed *et al.*, 2004; Zhang *et al.*, 2009). Yet, coral reefs have highly diverse macroalgal communities with over 700 species that can reproduce sexually and asexually releasing millions of propagules that could be recruited within approximately one meter from the parent plant (Kendrick and Walker, 1991; Stiger and Payri, 1999; Zhang *et al.*, 2012). Further, macroalgal

reproduction periods are triggered by physical factors such as water temperature, tide cycles, photoperiod and natural disturbances (Hay and Norris, 1984; Luning, 1990; Clifton, 2008). Consequently, multiple species of macroalgae provide propagules that settle on available coral reef space at any given time. Therefore, macroalgal propagule supply may be an important, but underappreciated, driver of macroalgal recruitment and post- settlement succession on coral reefs.

Furthermore, post-settlement success, growth rate, and competition among germlings are controlled primarily by herbivory, nutrient availability, and light availability, among other biotic and abiotic factors (Foster, 1975; Lapointe *et al.*, 1981; Greene *et al.*, 1983; Vance, 1988; Hill *et al.*, 2004; Karez *et al.*, 2004; Collado-Vides *et al.*, 2011; Guimaraens *et al.*, 2011). For instance, some authors have shown herbivory as the primary driver since abundance of coral reef macroalgal assemblages has dramatically increased when herbivores are excluded (Lewis, 1986; Hixon and Brostoff, 1996; Burkepile and Hay, 2009; Sotka and Hay, 2009; Ferrari *et al.*, 2012; Poore *et al.*, 2012). Conversely, Lapointe *et al.* (2010) reported increased macroalgal abundance as solely a consequence of eutrophication on coastal marine ecosystems. Further, Smith *et al.* (2010) indicated that both herbivores and nutrient availability control algal community structure on coral reefs but on different time scales. According to Smith *et al.* (2010), effects of herbivore reduction will be noticed in less than a month while the effects of nutrient enrichment will be visible after three to four months.

Most of the research evaluating the relative magnitude of both nutrient availability and herbivory pressure on controlling abundance of macroalgae have focused on adult macroalgal assemblages (Burkepile and Hay, 2006; Sotka and Hay, 2009; Ferrari *et al.*, 2012; Rasher *et al.*, 2012). However, it is known that species composition and abundance of coral reef macroalgal

communities could change through time following dissimilar successional patterns, as a consequence of type and intensity of grazing (Hixon and Bostroff, 1996; McClanahan, 1997; Burkepille and Hay, 2010). In particular, herbivorous fishes are described as major drivers of macroalgal succession compared with others such as micro-herbivores (small gastropods, polychaetes, etc.) and long-spined sea-urchin *Diadema antillarum* (Hay, 1984; Carpenter, 1986). Indeed, herbivore exclusion experiments report that after 11 months, only uncaged areas (grazed by herbivorous fish) were still covered by early-successional species and bare substrate (Sammarco, 1983). Furthermore, Hixon and Brostroff (1996) showed a successional deceleration, a slower succession rate, with damselfish activity as they selectively removed late-successional species. Conversely, high grazing intensity by parrotfish and surgeonfish in uncaged areas shifted early successional species towards crustose and prostrate species that were rare or absent in ungrazed areas, defined as a deflected successional pattern (Hixon and Bostroff, 1996).

In addition to herbivory, nutrient availability is also considered one of the major drivers of tropical marine primary producers (Duarte, 1992; Fourqurean *et al.*, 2002; Szmant, 2002; Lapointe *et al.*, 2004; Collado-Vides *et al.*, 2011). Indeed, growth rate and abundance of marine macroalgae increase when systems are enriched with nitrogen and phosphorus (Pedersen and Borum, 1997; Larned, 1998; Kuffner and Paul, 2001; Bracken and Nielsen, 2004). However, all macroalgal species do not respond similarly to nutrient enrichment, which could be related to multiple factors such as differences in morphology, initial tissue nutrient status, and species physiology (Larned, 1998; Reef *et al.*, 2012; Fong *et al.*, 2001; Kuffner and Paul, 2001; Fong *et al.*, 2003). In particular, fast-growing species typical of early successional stages (e.g., *Chaetomorpha* sp., *Ceramium* sp., *Ulva* sp., *Cladophora* sp. and cyanobacteria) are well known

for their rapid increase in abundance following increases in nutrient loading (Lapointe *et al.*, 1993; Lapointe *et al.*, 2005; Smith *et al.*, 2005). In contrast, the effect of nutrient enrichment on abundance of mature late successional species is still unclear (Hughes, 1994; McClanahan *et al.*, 2004). Indeed, recent studies suggest that nutrient availability would play a secondary role on controlling adult macroalgal growth only if herbivory pressure level is low or absent (Burkepile and Hay, 2009; Sotka and Hay, 2009; Walsh, 2011).

The general objective of the study was to evaluate seasonal recruitment and post-settlement succession of coral reef macroalgal communities in relation with potential propagule supply under different levels of herbivory pressure and nutrient availability. The specific objectives were: 1) to assess the effect of herbivory pressure and nutrient availability on the abundance of adult macroalgae as potential propagule sources, 2) to evaluate the effect of nutrient availability and herbivory pressure on seasonal recruitment of macroalgal species, and 3) assess the effects of herbivory pressure and nutrient availability on succession of coral reef macroalgal communities. We hypothesized that: 1) reductions in herbivory and increases in nutrient availability will increase abundance of adult macroalgae and indirectly facilitate macroalgal recruitment via increased propagule supply, 2) increases in nutrient availability and reduction of herbivore pressure will increase abundance of macroalgal recruits, enhancing successional rates and 3) reduction of herbivore pressure rather than nutrient availability will accelerate successional rate of macroalgal communities.

2.2 Materials and methods

Study site and experimental design

The study was conducted at a spur and groove reef system, located in the upper Florida Keys (25°00'05"N, 80°24'55"W) nearby Pickles Reef. The reef is a mid-depth area (5-6 m) off

of Key Largo, where parrotfish and surgeonfish are the dominant herbivorous fish and the long-spined urchin *Diadema antillarum* is present at low densities (<1 individual per 50 m², personal observations). Eight experimental plots (3x3m) separated from each other by at least 5m (Figure 1) were established in June 2009 to examine the interactive effects of herbivory and nutrient availability on reef benthic dynamics. Each plot was delineated with metal nails driven into the reef at the corners and centers of each 1m² subplot (quadrat). Each plot contains two quadrats (1x1m²) for herbivore exclusion covered with plastic-coated wire mesh (2.5 cm diameter holes). Two other three-sided plots (1x1 m²) were used as herbivore exclusion controls (Figure 2). Four of the eight 9m² experimental plots were enriched with total 4375 g of Osmocote (19-6-12, N-P-K) slow-release garden fertilizer since June 2009. The Osmocote was placed in a 15 cm diameter PVC tube with 10 (1.5 cm) holes drilled into it. These tubes were open on each end but wrapped in fine plastic mesh to keep the fertilizer inside and attached to a metal nail within the plot for a total of 25 enrichment tubes (175 g of Osmocote) per enrichment plot. Enrichment tubes were replaced every 4-6 weeks to ensure consistent nutrient addition. The field sampling period was meant for a full year but as a consequence of Hurricane Isaac in August 2012, the study took place from September 2011 to June 2012 and laboratory work from January 2012 to September 2012. As a consequence of tropical storm damages, the sample size was different among treatments: NE=5 (Nutrient enrichment-Exclusion), CE=4 (Control-Exclusion), CO=8 (Control-Open) and NO=8 (Nutrient enrichment-Open).

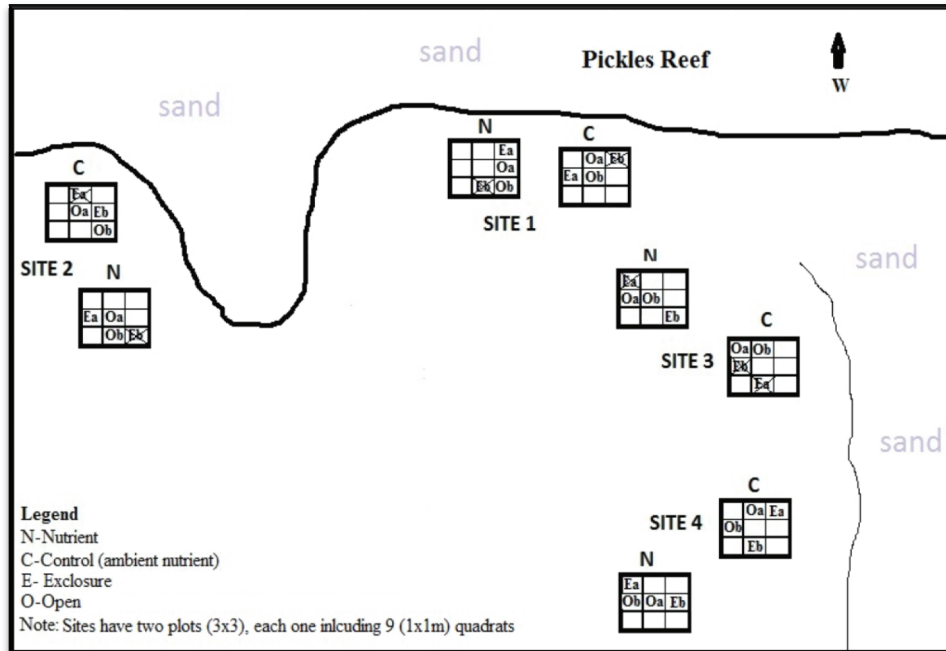


Figure 2. Study site and experimental design

Fish community structure and nutrient levels of the study site

Fish community structure was evaluated four times during the study period (September, 2011; January, 2012; April, 2012 and July 2012) via 30 x 2m belt transects (n=12) placed haphazardly across the study site following AGRRA methodology (Protocols Version 5.4; Lang *et al.*, 2010). All fishes were identified and their size estimated to the nearest cm. Size estimates were converted to biomass for each fish using published length:weight relationships (Bohnsack and Harper, 1988). Density and biomass of total and herbivorous fish were estimated at each time.

To evaluate the effectiveness of nutrient enrichment treatments versus ambient nutrient controls of the experiment, twenty samples of water (nutrient enrichment treatment=10 and control treatment=10) were collected by divers from approximately 3 cm above the benthos in July 2009 to be analyzed for dissolve inorganic nitrogen (DIN) and soluble reactive phosphorous (SRP). A few minutes after collection, samples were filtered into acid-washed bottles and placed

on ice for posterior laboratory analyzes. Dissolved inorganic nitrogen (DIN = ammonium and nitrite + nitrate) and soluble reactive phosphorus (SRP) concentrations were determined via autoanalyzer. Additionally, twenty samples of *Dictyota* sp. were collected in July and August 2009, (n=10 control, n=10 enriched treatments) to analyze tissue carbon:nitrogen (C:N) levels. Collected algal material was kept in separate bags and transported on ice to the Florida International University Seagrass Lab. Once in the lab, the samples were clean, dried for 48 hours at 60 °C and ground to a fine powder. Carbon and nitrogen content were determined using a CHN analyzer (Fisons NA1500; Fisons Instruments, Milan, Italy; Fourqurean *et al.*, 1992).

Field established communities

Abundance (% cover) of field established macroalgal communities within each square meter quadrat (n=25), hereafter field established communities, was visually assessed at the form-functional groups (FFG, Steneck and Dethier, 1994) in January and June 2012. Macroalgal species were identified following criteria of Littler and Littler (2000) and Dawes and Mathieson (2008) identification keys. A list of species was created from field and laboratory (recruitment tiles) observations to determine the pool of potential existing species available for propagule settlement (Appendix 1 shows the list of algal species identified throughout the study and corresponding form-functional group).

Recruitment of coral reef macroalgal communities

To study macroalgal recruitment and succession, two tiles (10x10 cm) made of Pleistocene coral skeleton were placed inside each quadrat in September 2011. One of the tiles (*recruitment tile*) was replaced every three month (set I: September-December 2011, set II: December 2011-March 2012 and set III: March- June, 2012). After three months in the field, recruitment tiles were taken to the FIU Marine Macroalgae Research Laboratory and placed in

individual aquariums previously prepared to replicate the field conditions as closely as possible (salinity: 35-36ppt, temperature: 25-28°C, constant water circulation and air pump). Light values were elevated to $369 \pm 58 \mu\text{mol/s/m}^2$ at the surface and $163 \pm 19 \mu\text{mol/s/m}^2$ at the bottom. The light cycle at the laboratory was set up with four fluorescent low output bulbs (Lithonia Lighting All Season Shoplight) from 6:00am to 8:00pm ($\sim 50 \mu\text{mol/s/m}^2$ underwater) and two Very High Output bulbs (VHO) from 8:00am to 6:00pm ($\sim 162 \mu\text{mol/s/m}^2$ underwater). For recruitment tiles, two evaluation rounds of percent cover at the lowest taxonomic possible level occurred at the laboratory, one evaluation immediately after retrieving the tiles from the field and the second evaluation after three months in laboratory conditions. Tiles were kept in aquariums to promote growth of algae recruits that could not be identified in the first evaluation round as a consequence of too small size or lacking of identifiable species features.

Succession of coral reef macroalgal communities

For macroalgae successional patterns, the second tile (*succession tile*) was kept in the field during the entire study period (September 2011 to June 2012). Percent cover of succession tiles at FFG level, following a Steneck and Dethier (1994) classification, was recorded “*in situ*” in January and June, 2012.

Statistical analyses

Data were assessed for normality and homogeneity of variances using Levene’s test before running statistical analysis. When data did not conform to assumptions of normality and homogeneity, the data were transformed as appropriate. Biomass and density of total and herbivorous fish were compared between seasons using one-factor ANOVAs. Dissolve inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) in water and *Dictyota* sp. tissue nutrient content, carbon(C), nitrogen (N), and C:N ratio were compared between treatments using one-

factor ANOVA. Macroalgae abundances among treatments and seasons were statistically evaluated through three-factor ANOVA (nutrient, herbivores and season). In the case of leathery and articulated calcareous macroalgae FFG, statistical analyses were carried out using Kruskal-Wallis since data could not be normalized using transformation.

To evaluate possible effects of both nutrient and herbivory levels on macroalgal species diversity, differences in diversity indexes (richness, Margalef diversity and Shannon heterogeneity index) calculated from recruitment tiles among sets were statistically tested with one-factor ANOVAs and among treatments with Kruskal Wallis. A Similarity Percentages (SIMPER) analysis was used to estimate the most abundant species among treatments. Analyses of most common species abundances were carried out with parametric or non-parametric tests as shown in table 3. Multi-dimensional Scaling (MDS) and Analysis of similarity (ANOSIM) were performed to calculate the effects of treatments and seasonality on macroalgae composition of recruitment tiles. To estimate the possible role of field established communities as potential propagule supply, Pearson correlation analyses using overall and FFG abundances of macroalgae were run: 1) set II of recruitment tiles (Dec-Mar) and January surveys of field established communities, 2) Set III of recruitment tiles (Mar-Jun) and June surveys of field established communities, 3) January surveys of succession tiles and field established communities, 4) June surveys of succession tiles and field established communities. To evaluate macroalgal abundance of succession tiles among treatments and seasons three-factor ANOVA (herbivores, nutrients and seasons) were used. In the case of filamentous, corticated foliose, leathery, articulated calcareous and crustose, Kruskal Wallis was used to evaluate treatment and season effects. Multi-dimensional Scaling and ANOSIM analyses were performed with abundance of all FFG to calculate the effects of treatments on community succession. Descriptive, parametric and non-

parametric analyses such as ANOVAs, correlations and Kruskal Wallis were performance using SPSS version 19.0 software package, whereas MDS and SIMPER analyses were completed with PRIMER 6.1.5 software package.

2.3 Results

Fish community structure and nutrient levels of the study site

Means of overall fish biomass and density at the study site were 6495.6 ± 508.1 g/100m², and 39.9 ± 3.2 Ind./100m² respectively. Grazers (Family Scaridae and Acanthuridae) comprised 78% of overall fish biomass with an average of 5086.1 ± 569.5 g/100m², and 74% of overall fish density 29.9 ± 2.1 Ind./100m². Total biomass of parrotfish and surgeonfish were 2771.7 ± 526.6 g/100m² and 2315.5 ± 370.6 g/100m² respectively. There were no differences among seasons of total fish (Figure 3, one-factor ANOVA, $F=0.23$, $p=0.885$) or herbivore biomass (one-factor ANOVA, $F=0.30$, $p=0.82$). Similarly, there was no evidence of seasonality on total fish density ($F=0.45$, $p=0.72$) or herbivorous fish density (Figure 3, one-factor ANOVA, $F=0.75$, $p=0.53$).

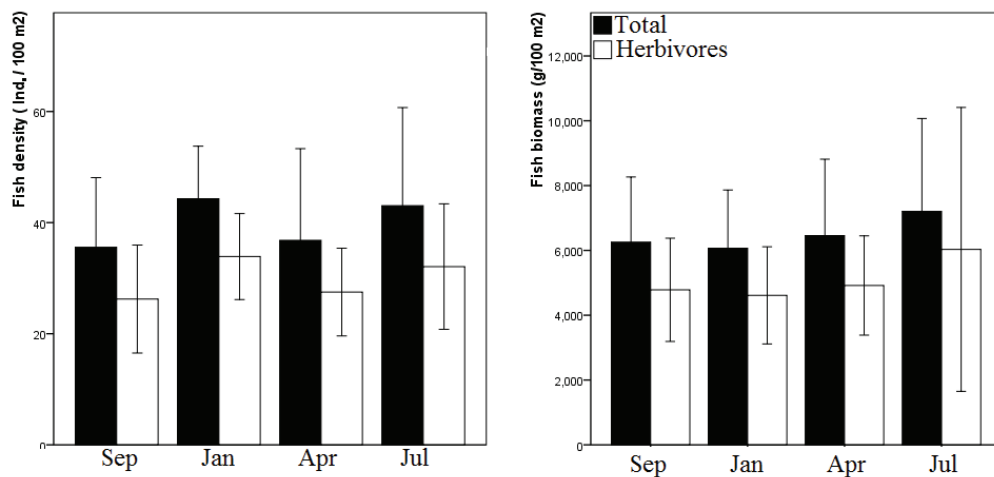


Figure 3. Total and herbivorous fish biomass and density at experimental site during the four sampling seasons. Bars represent standard errors

Dissolve inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) of water surrounding experimental plots, were threefold and sixfold higher in enriched plots than ambient plots respectively (Table 1). No statistical differences were found on Carbon (C) and nitrogen (N) tissue content of *Dictyota* sp., but C:N ratio in control treatments resulted 1.14 higher ($p=0.01$) than enriched nutrient treatments (Table 1).

Table 1. Water nutrient contents (DIN and SRP) and percentage of nutrient tissues of *Dictyota* sp (carbon (C), nitrogen (N) and carbon:nitrogen (C:N) in ambient and enriched nutrient treatments

Nutrient	Ambient nutrient		Nutrient enrichment		Statistical	
	Mean	St. error	Mean	St. error	F	<i>p</i>
Dissolved inorganic nitrogen (DIN)	1.15	0.05	3.91	1.34	N/A	0.002**
Soluble reactive phosphorus (SRP)	0.04	0.01	0.27	0.07	10.7	0.02**
Carbon (C)	22.44	0.79	22.47	1.27	0.179	0.676
Nitrogen (N)	1.11	0.05	1.27	0.09	1.688	0.206
C:N	20.53	0.57	17.98	0.55	9.821	0.004**

Field established communities

Including field and laboratory observations, 101 algal species were identified, with 60 species belonging to the Rhodophyta, 11 to Ochrophyta, 26 Chlorophyta, Phyla, and 4 Cyanobacteria (Appendix 1). Overall algal cover of field established communities was lower in January, 33.4 ± 5.5 % and over twofold higher in June with 83.3 ± 6.2 % (three-factor ANOVA, $F=151.30$, $p=0.001$). Furthermore, abundance of overall macroalgae of field established communities was twofold higher within cages compared to open areas, with 89.6 % and 40.1 % respectively (Figure 4, three-factor ANOVA $F=149.20$, $p=0.001$) and a significant interaction between season and herbivores factors was found (three-factor ANOVA, $F=41.2$, $p=0.001$). No effects of nutrient treatment or its interactions with season and herbivores factors over macroalgal cover in field established communities were found (Figure 4. three-factor ANOVA, nutrient $F=3.8$, $p=0.059$; nutrient-season $F=0.10$, $p=0.730$; nutrient-herbivore $F=1.30$, $p=0.262$).

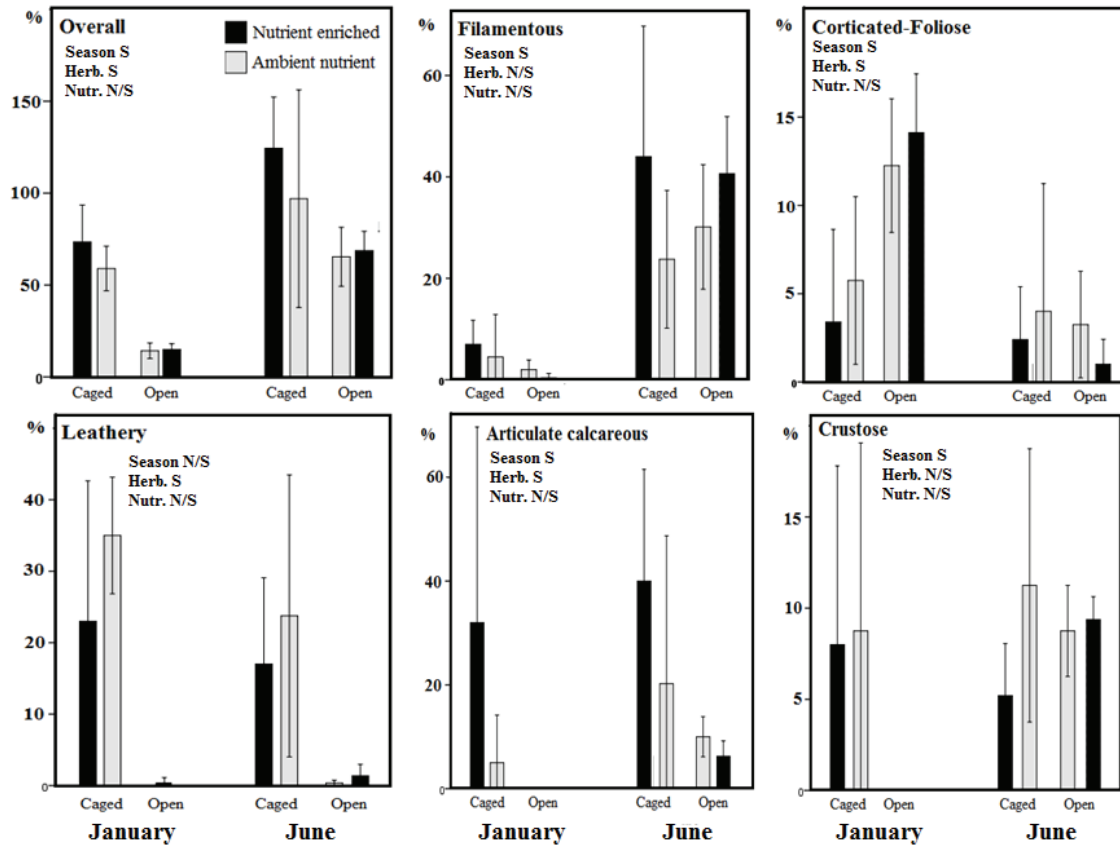


Figure 4. Percent cover of overall macroalgae and form-functional groups of field established communities in January and June. Bars represent standard errors. Statistical significant of analyzed variables, season, herbivores and nutrient, are indicated by S (significant) and N/S (no significant).

In field established communities percent cover of filamentous algae in June was 35.2 ± 3.2 %, tenfold higher than January with 2.9 ± 0.8 (Kruskal Wallis $p=0.001$). No effects of either nutrient enrichment or herbivorous exclusion were found (Figure 4, Kruskal Wallis, nutrient $p=0.43$; herbivores $p=0.34$). Corticated-foliose macroalgae (e.g., *Dictyota* spp.) showed a significant cover decrease in June compare with January (Figure 4, three-factor ANOVA, $F=33.81$, $p=0.001$). In January, field established communities had higher percent cover of corticated foliose algae in uncaged (Open) compared to caged treatments (three-factor ANOVA, $F=12.42$, $p=0.001$) whereas nutrient did not indicate statistical significance at any season (Figure 4, three-factor ANOVA $F=1.02$, $p=0.318$). Abundances of leathery macroalgae (e.g., *Sargassum* spp.) was dramatically higher (over 40 times) within cages compared to open treatments (Figure

4, $p=0.001$). Conversely, no seasonal changes or nutrient enrichment effect were observed (Kruskal Wallis $p=0.49$ and $p=0.75$ respectively). Calcareous articulated algae (e.g., *Amphiroa* spp. and *Jania* spp.) were over fivefold higher when herbivorous fish were excluded in both seasons ($p=0.01$ respectively). Percent cover of articulated calcareous algae showed a two-fold increase from January towards June (Kruskal Wallis, $p=0.001$). No nutrient enrichment effects on abundance of articulated calcareous algae were detected (Kruskal Wallis, $p = 0.557$ respectively). Abundance of crustose algae (e.g., *Peyssonelia* sp. and crustose coralline algae, CCA) was twofold higher in June, 8.6 ± 0.8 compared 3.0 ± 1.4 in January (Kruskal Wallis, $p=0.001$). No statistical effects of either nutrients or herbivores were found in crustose percentage cover (Kruskal Wallis, $p=0.760$, $p=0.114$ respectively).

There was a significant correlation of overall macroalgal abundances of field established communities with corresponding recruitment tiles in January (January-Set II $r=0.59$, $p=0.002$); and June (June-Set III $r=0.53$, $p=0.006$). Moreover, there was a significant relationship in total abundance between permanent tiles in January and June with field established communities ($r=0.86$, $p=0.001$; $r=0.43$, $p=0.031$, respectively). Furthermore, abundance of field established communities at form-functional group, articulated calcareous and leathery macroalgae, was correlated with the abundances found on recruitment and succession tiles in January and June (Table 2).

Season	Form-Functional group	Recruitment tiles		Succession tiles	
		Coef. Corr (r)	p	Coef. Corr (r)	p
January	Filamentous	0.89	0.11	0.35	0.65
	Corticated-Foliose	0.49	0.51	0.44	0.56
	Leathery	0.97	0.03	0.28	0.72
	Articulated-Calcareous	1.00	0.00	0.99	0.01
	Crustose	-0.94	0.04	-0.77	0.23
June	Filamentous	-0.33	0.67	-0.51	0.49
	Corticated-Foliose	-0.09	0.91	N/S	N/S
	Leathery	0.88	0.12	0.95	0.05
	Articulated-Calcareous	0.95	0.05	1.00	0.01
	Crustose	0.47	0.53	0.12	0.88

Table 2.

Pearson correlation between abundance of macroalgal form-functional groups of field established communities with recruitment and succession tiles.

Recruitment of coral reef macroalgal communities

Of the 96 macroalgal species identified throughout the study, only five, *Penicillus capitatus*, *Halimeda opuntia*, *H. tuna*, *Neomeris* sp. and *Spyridia clavata* were found in field established communities and not recruited onto tiles (Appendix 1). The total numbers of species recruited were 38, 62 and 61 for sets I (Sep-Dec), Set II (Jan-Mar) and Set III (Mar-Jun) respectively. However, species richness averaged 8.48 per tile with no significant difference among seasons, the Rhodophyta phylum exhibited the highest species richness (Figure 5; Table 3, one-factor ANOVA, $F=0.96$, $p=0.38$). Among treatments, there was no significant differences in species richness, Margalef's or Shannon Heterogeneity indexes (one-factor ANOVA, $F = 0.31$, $p = 0.82$; $F = 1.18$, $p=0.32$ and $F=0.70$, $p=0.55$ respectively).

Overall macroalgal abundance of recruitment tiles was similar before and after laboratory conditions, (two-factor ANOVA, $F=0.01$, $p=0.95$). However, analysis of macroalgal abundances was completed using data from before laboratory conditions surveys. Percent cover of total macroalgae doubled from Set I (Sep-Dec) and Set II (Jan-Mar) with 56.1 ± 28.7 and 49.4 ± 30.1 to Set III with 111.6 ± 35.9 (Figure 6, two-factor ANOVA, $F=39.35$, $p=0.0001$). Overall percent

cover of nutrient enrichment-exclusion treatment (NE = 103.9±52.9) was higher compared with the other three treatments ranging between 62.9±31.2 and 72.4±41.9 (Figure 6, two-factor ANOVA, $F=8.78$, $p=0.001$). No interaction between set and treatment was found in the two-factor ANOVA analysis ($F=2.00$, $p=0.08$).

Table 3. Diversity indexes by set of macroalgal species recruited on tiles. Letters indicate post-hoc (SNK) analysis when significant differences were found.

Diversity Indexes	Set I (Sep-Dec)		Set II (Jan-Mar)		Set III (Mar-Jun)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Richness (S)	7.46	0.31	8.48	0.37	9.5	0.44
Margalef Diversity Index (d)	1.67	0.07	1.99	0.18	1.99	0.11
Shannon Heterogeneity index (H')	1.52 (B)	0.05	1.23 (A)	0.06	1.38 (B)	0.07

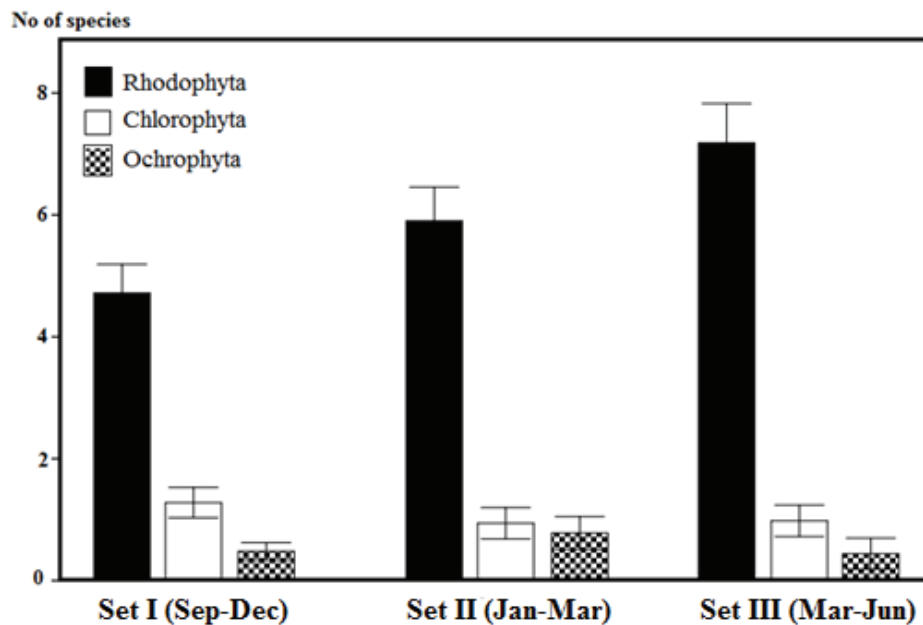


Figure 5. Average number of algal species found on recruitment tiles by phylum in each set. Bars represent standard error.

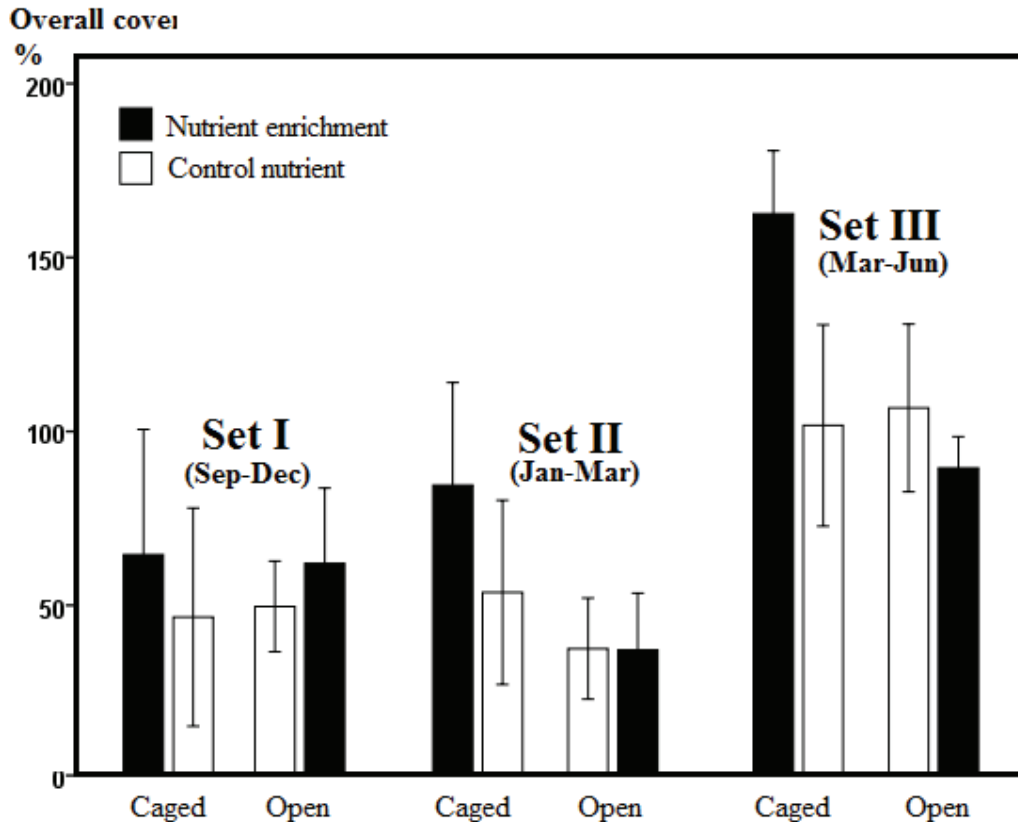


Figure 6. Total percent cover of macroalgal by treatments within each set of recruitment tiles. Bars represent standard error.

The non-metric Multidimensional Scaling analysis ran with abundance of all present species on recruitment tiles showed significant differences among seasons (Figure 7, ANOSIM, $R=0.436$, $p=0.001$). Additionally, a similarity percentages-species contribution analysis (SIMPER) was performed to evaluate the effect of treatments on macroalgal communities of recruitment tiles (Table 4). Accordingly, only four taxa of algae, crustose coralline algae (CCA), *Peyssonnelia* sp., *Jania capillacea* and cyanobacteria were present throughout all treatments with some variation in their abundances (Table 4).

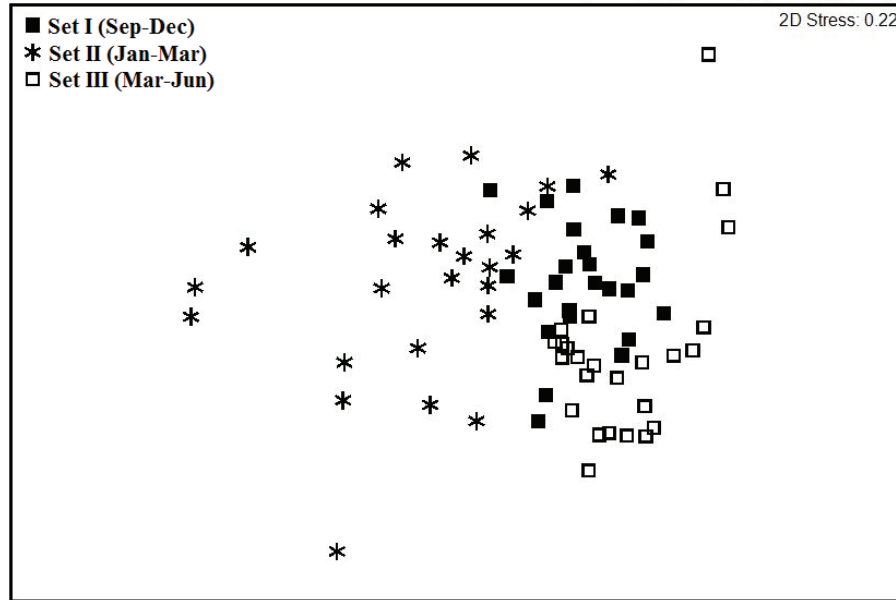


Figure 7. Non-metric Multidimensional Scaling analysis using abundance of all species of algae on recruitment tiles by set.

Table 4. Abundance and similarity percentage-species contribution to overall percent cover of recruitment tiles of most common species (species that cover at least 90 %) by treatments. Data calculated using SIMPER analysis from PRIMER 6. Asterisks indicate most common species by sets.

Species	Nutrient enrichment-Exclusion (NE)		Control-Exclusion (CE)		Control-Open (CO)		Nutrient enrichment-Open (NO)		Statistical sign.	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	F	p
<i>Jania capillacea</i>	19.80	6.64	4.67*	2.63	1.17	0.85	2.17*	0.63	N/A	0.002
Crustose coralline algae	5.78*	1.46	8.25*	4.86	7.09*	1.71	11.28*	2.55	0.887	0.453
<i>Peyssonmelia</i> spp.	4.70*	1.32	8.42*	2.43	10.30*	1.83	11.8*	2.21	2.357	0.080
Cyanobacteria	9.73*	3.89	9.25*	3.56	21.08*	5.81	18.21*	4.86	N/A	0.322
<i>Ectocarpus</i> sp.	7.33*	3.58	4.33	3.31	3.41	2.90	2.54	2.08	0.719	0.544
<i>Hypnea spinella</i>	4.33*	1.82	1.33	1.25	1.77	0.64	1.81	1.06	N/A	0.642
<i>Jania adhaerens</i>	6.00*	3.53	0.50	0.42	0.09	0.06	0.67	0.46	N/A	0.475
<i>Amphiroa fragilissima</i>	9.00*	5.03	0.33	0.33	0.28	0.21	0.00	0.00	N/A	0.150
<i>Hypnea valentiae</i>	5.00*	2.88	1.66	1.12	0.90	0.65	0.54	0.42	N/A	0.502
<i>Sargassum</i> sp.	1.94	0.91	6.38*	3.36	0.05	0.03	0.01	0.00	N/A	0.001
<i>Laurencia cervicornis</i>	2.47	1.99	5.25*	2.57	5.08*	2.03	0.23	0.08	N/A	0.001
<i>Laurencia intricata</i>	0.67	0.67	3.83*	2.22	0.73	0.34	0.50	0.29	N/A	0.289
<i>Polysiphonia</i> sp. 1	1.00	1.00	1.33*	0.64	0.35	0.21	0.42	0.42	N/A	0.173
<i>Heterosiphonia gibbesi</i>	1.33	1.03	0.08	0.08	1.50*	0.56	0.00	0.00	N/A	0.029
Average Similarity	18.04		19.14		25.13		27.00			

The non-metric Multidimensional Scaling used to analyze treatment effects on macroalgal cover of recruitment tiles revealed a clear treatment pattern for all sets together, Set I and II (Figure 8, ANOSIM $R=0.11$, $p=0.003$; $R=0.33$, $p=0.002$; $R=0.48$, $p=0.001$ respectively). Contrarily, neither statistical differences nor clear pattern among treatments were found for Set II (Figure 8, ANOSIM $R=0.03$, $p=0.700$).

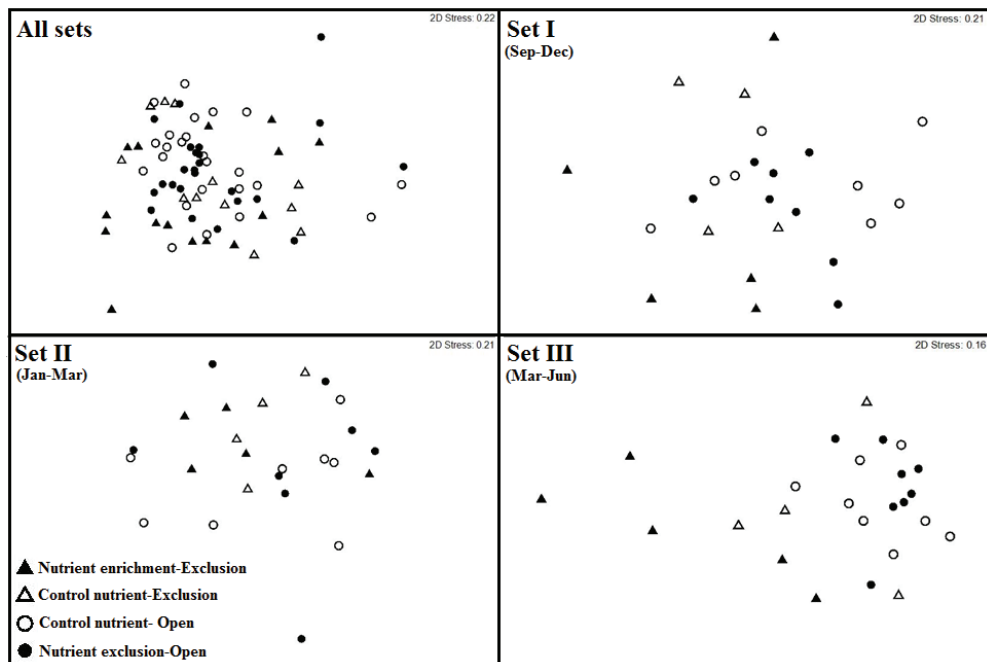


Figure 8. Non-metric Multidimensional Scaling analysis among treatments including abundance of all algal species found on recruitment tiles, for all sets together and set I, II, and III separately.

Succession of coral reef macroalgal communities

Overall macroalgal percent cover of succession tiles doubled by June, 62.4 ± 5.8 , compared to January with 31.5 ± 5.3 for all treatments (Figure 9, three-factor ANOVA, $F=24.02$, $p=0.001$). In both January and June, abundance was significantly higher when herbivores were excluded in both control and nutrient enriched treatments (Figure 9, three-factor ANOVA, $F=32.72$, $p=0.001$) but no effects of nutrient enriched treatments were found (Figure 9, three-factor ANOVA, $F=0.482$, $p=0.491$). The abundance of filamentous algae in June (average 35.8 ± 3.8) was twice as high as January, 16.4 ± 3.4 (Figure 9, three-factor ANOVA, $F=11.33$, $p=0.002$). Percent cover of filamentous algae was negatively affected by nutrient availability having enriched nutrient treatments lower abundance compared to ambient treatments (three-factor ANOVA, $F=9.81$, $p=0.003$). No effects related with herbivory level were found on filamentous algae cover of succession tiles (three-factor ANOVA, $F=0.040$, $p=0.843$).

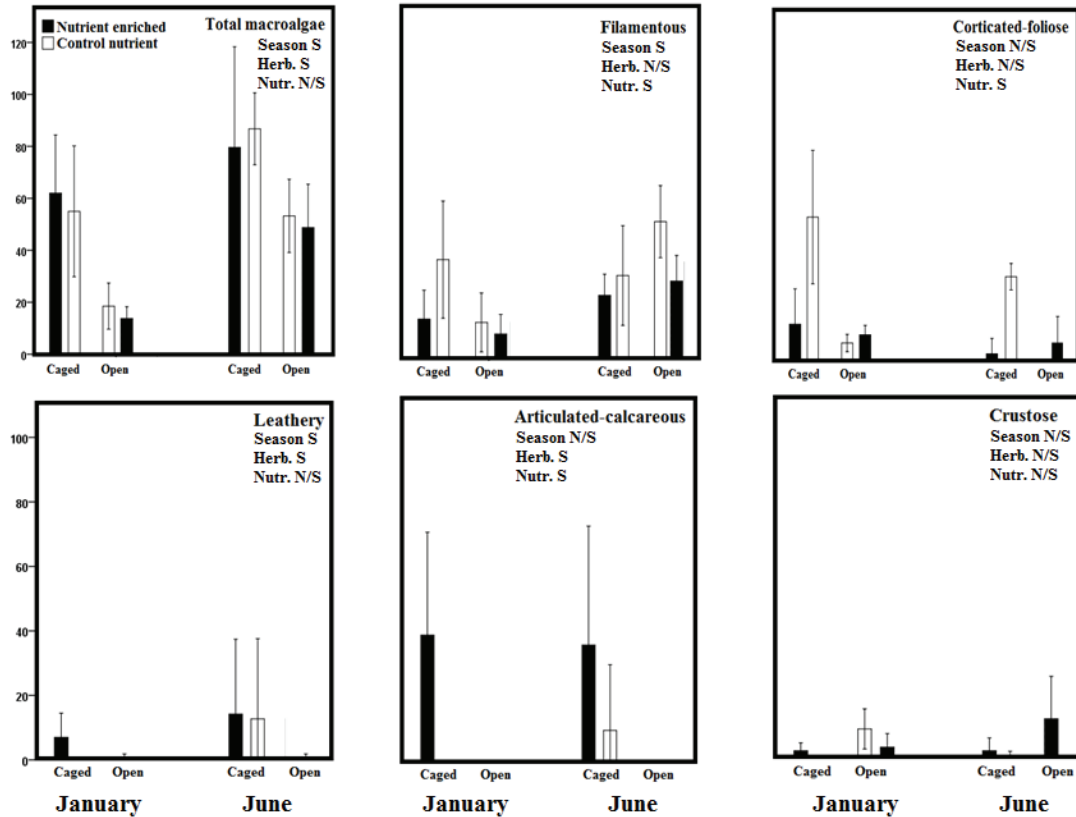


Figure 9. Abundance of macroalgal form-functional group on succession tiles by treatment in January and June. Whiskers represent standard errors. Statistical significant of analyzed variables, season, herbivores and nutrient, are indicated by S (significant) and N/S (no significant).

Conversely to filamentous algae, corticated-foliose macroalgae (e.g., *Dictyota* spp.), was $17.7 \pm 4.0\%$ in January compared to June (average 7.2 ± 2.4) with no significant differences (three-factor ANOVA $F=3.77$, $p=0.06$). No effects of herbivore exclusion were observed (three-factor ANOVA $F=2.1$, $p=0.15$) while nutrient enrichment treatments depleted percent cover of corticated-foliose within cages (Figure 9, three-factor ANOVA $F=5.5$, $p=0.03$). Leathery macroalgae were mainly represented by *Turbinaria turbinata* and *Sargassum* sp., while articulated calcareous were mostly specimens of *Amphiroa* spp. and *Jania* spp. Leathery and articulated calcareous were present only when herbivorous fish were excluded (Figure 9, Kruskal Wallis, $p=0.001$, $p=0.001$ respectively). Percent cover of articulated calcareous was higher in nutrient enriched treatments (Figure 9, Kruskal Wallis, $p=0.02$). Conversely, nutrient or

herbivores exclusion had no effect on crustose algae (e.g., *Peyssonnelia* spp. and crustose coralline algae) average of 4.3 ± 1.3 , at any season (Figure 9, Kruskal Wallis, $p=0.11$, $p=0.6$ respectively).

In the fourth month, (January) percent cover of overall macroalgae on succession tiles was higher within caged treatments compared to open treatments (Figure 10, one-factor ANOVA $F=10.80$, $p=0.001$). Filamentous and corticated-foliose covered part of all four treatments, where leathery and articulated calcareous were only present within nutrient enriched treatment (Figure 9). Crustose coralline algae covered less than 10% only in open treatments. By the ninth month (June), percent cover of filamentous algae increased in all treatments while leathery and calcareous-articulated increased in abundance within both caged treatments (Figure, 10). The abundance of corticated-foliose (e.g., *Dictyota* sp) decreased through time within cage enriched with nutrient. Approximately 50 % of empty spaces in open areas (uncaged treatments) persisted nine months after tiles were placed on the reef (Figure 10). When open areas were nutrient enriched, the total abundance did not increase, and differently to control treatment, crustose and corticated-foliose algae covered part of the tiles (Figure 10).

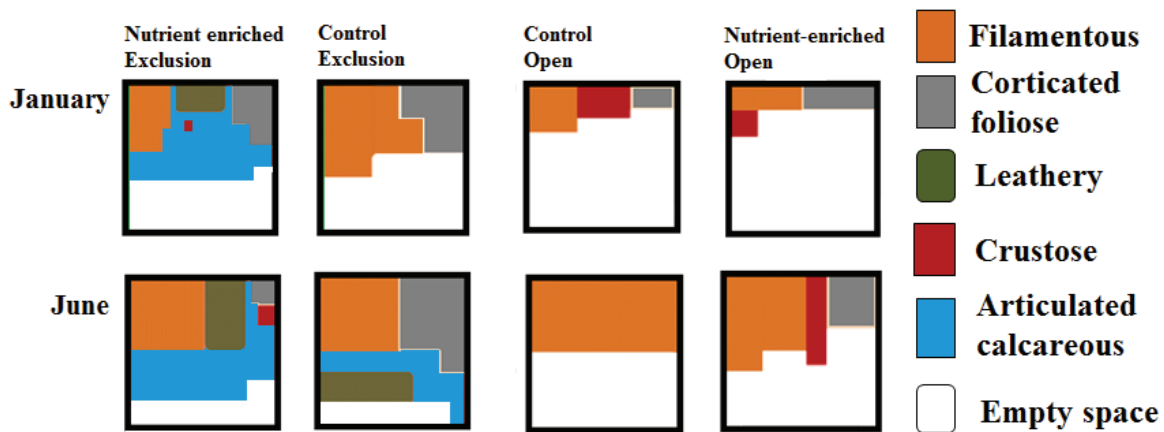


Figure 10. Graphical representation of macroalgal succession on permanent tiles by treatment. Size of colors represent mean of percent cover of macroalgal form-functional groups.

To estimate the impact of different treatments on macroalgal, a MDS was run including abundance of all macroalgal form-functional groups on permanent tiles from each survey time, January and June. In January the MDS separated nutrient enrichment-exclusion from the other three treatments (Figure 11, ANOSIM, $R=0.19$, $p=0.02$). Whereas, by June, nutrient enrichment-exclusion treatment and control nutrient-exclusion treatments seem to differ from open treatments (Figure 11, ANOSIM, $R=0.46$, $p=0.01$).

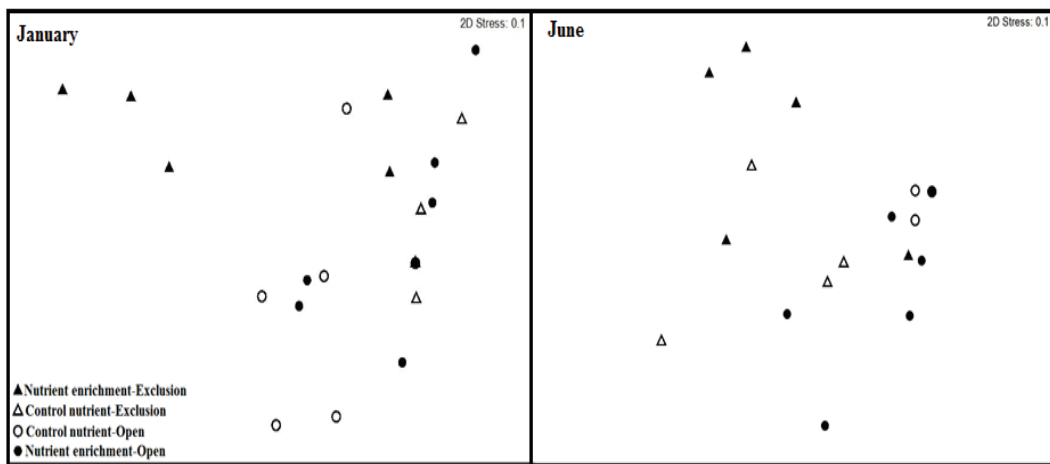


Figure 11. Non-metric Multidimensional Scaling analysis by treatment including abundance of all macroalgal form-functional group on succession tiles in January and June

2. 4 Discussion

The magnitude of the effects of nutrient availability and herbivore pressure on controlling macroalgal abundance varied with community successional stage. While both bottom-up (nutrient availability) and top-down (herbivory pressure) drivers were important at early-successional stages, only top-down (fish grazing) remained determinant at late-successional stages. In addition, total abundance and FFG composition of field established communities within quadrats, was similar to macroalgal communities of recruitment and succession tiles,

suggesting that adult coral reef macroalgal communities could play an important role regulating recruitment via propagule supply.

Fish community structure and nutrient levels of the study site

The experimental site presented a high density and biomass of herbivorous fish compared to other Caribbean reefs such as Guanacahabibes National Park, Cuba and Virgin Islands Coral Reef Monument (Claro and Cantelar, 2003; Nemeth *et al.*, 2003; Lang and Ginsburg, 2006). In addition, higher DIN and SRP in water content and lower C:N ratio in *Dictyota* sp. tissue evidenced higher availability and uptake of nitrogen in nutrient enriched treatments. In fact, similar results have been found by other authors where nutrient enrichment of marine systems has led to rapid uptake of nitrogen and consequently decrease of C:N ratio (Ferdie and Fourqurean, 2004; Littler *et al.*, 2010). Thus, the experimental setting could be considered operative and reliable.

Analyses of total macroalgae abundance of established communities across the study period showed a clear increase towards spring season (June). Comparable seasonal patterns have been reported for other Caribbean reefs such as Glover Reef Atoll, Belize and Puerto Rico (Ruiz and Ballantine, 2009; Ferrari *et al.*, 2012). Three macroalgal form-functional groups, filamentous, calcareous articulated and crustose coralline algae were the major components of summer seasonal increase which could be related with higher water temperature and light availability (Tsai *et al.*, 2005; Ferrari *et al.*, 2012). In the case of corticated-foliose algae (e.g., *Dictyota* sp.) abundance decreased towards June (spring/summer). Since corticated-foliose algae presented higher abundance in open treatments in January, the decrease of percent cover could be caused by increased grazing rate in spring-summer season. It has been demonstrated that parrotfish and surgeonfish, increase their grazing frequency during wet (spring-summer) season

(Smith, 2008; Duran and Claro, 2009). However, herbivory studies completed in Floridian coral reefs have shown reduction of abundance of *Dictyota* sp. in areas grazed by herbivorous fish (Burkepile and Hay, 2006; Burkepile and Hay, 2008; Sotka and Hay, 2009). On the other hand, Lirman and Biber (2000) reported abundance peak of *Dictyota* sp. in July-August covering 57 % of coral reef at northern Florida Reef Tract. According to Lirman and Biber (2000), growth rate and monopolization of *Dictyota* sp. at their site are consequence of insufficiently control of herbivores. In addition, seasonal variation in abundance of *Dictyota* sp. could be related with water temperature and light availability rather than herbivory consumption (Ferrari *et al.*, 2012).

Significant higher abundance of total macroalgae of field established communities within caged treatments supports the hypothesis that herbivory is a major driver of reef macroalgal assemblages (Lewis, 1986). Substantial evidences of herbivores exclusion treatment showing strong effects on controlling reef macroalgal assemblages could be found in multiple recent scientific studies (Burkepile and Hay, 2009; Sotka and Hay, 2009; Rasher *et al.*, 2012). Furthermore, herbivore pressure could also regulate macroalgal interspecific competition. In fact, when herbivorous were excluded, abundance of leathery and calcareous articulated macroalgae (late successional species) increased while corticated-foliose decreased. Contrarily to herbivory, no effects of nutrient enrichment treatments on total macroalgal abundance field established communities were observed indicating that nutrient loading did not exert major control of adult macroalgal assemblages at the study site. According to Smith *et al.*, (2010) effects of nutrient loading on coral reef macroalgae become tangible after three to four months of releasing nutrients but the current study was started after for two years of steadily nutrient release at the experimental site. Therefore, the study time period should be long enough to notice any effect of nutrient enrichment on macroalgae within experimental setting. On the other hand, similarities

(correlations) of community composition at FFG across different successional stages, recruitment tiles, succession tiles and field established communities could be taken as the first evidence of adult macroalgal community acting as propagule supply on coral reefs.

Recruitment of coral reef macroalgal communities

It was found a seasonal recruitment marked by differential species composition and abundances on recruitment tiles across sets. Indeed, cover of algae was higher in Set III (Mar-Jun, spring season). Total number of species was higher in Sets II and III. However, only Rhodophyta species number increase towards Set III. It is well documented that some red macroalgal species (*Laurencia* sp. and *Gracilaria* sp.) have a reproductive peak towards summer season triggered by warmer water temperature (Tsai *et al.*, 2005). Nevertheless, less reproduction between March-June of unidentified species of *Gracilaria* has been also reported (Hay and Norris, 1984). However, a different experimental design and metrics could be useful to address the topic such as examination of reproductive tissue in multiple macroalgal species and potential responses to ambient factors (light, nutrient availability and temperature). In addition, reduction of herbivory and nutrient loading combined (Nutrient enrichment-Exclusion) was the only treatment showing effects on abundance of macroalgae on recruitment tiles. Particularly, nutrient loading could enhance germination and increase growth rate of new arrival and overwinter propagules (Cecere *et al.*, 2011). Therefore, the combination of denser propagule areas and nutrient loading could override grazing rate and consequently increase abundance of macroalgae (Worm *et al.*, 1999). However, such situations have been mostly reported for fast-growing species of macroalgal such as *Ulva* spp., *Cladophora* sp., *Polysiphonia* sp. and *Ceramium* sp. (Worm and Lotze, 2006; Karez *et al.*, 2004; Imchen, 2012). Importantly, in coral reefs,

abundance of macroalgal recruits could also be related with type of substrate, herbivory and nutrient availability (Diaz-Pulido and McCook, 2002, 2003, 2004).

Succession of coral reef macroalgal communities

Succession patterns are expected to follow a replacement of early stages species such as filamentous turf (e.g., *Enteromorpha* sp., *Ceramium* sp., *Felmania* sp.) by late successional species such as leathery and calcareous articulated. Results of this study show that succession was affected by nutrient enrichment treatment that significantly increased percent cover of articulated-calcareous macroalgae but only in succession tiles when herbivorous were excluded, and not on field established communities. Thus, it is thought that the magnitude of nutrient availability effects reduces towards late successional stages and it is noticed only when herbivory pressure is reduced or absent. For instance, after nine months, late succession species of macroalgae (e.g., *Sargassum* sp. and *Amphiroa* sp.) were present only on succession tiles placed within cages with and without nutrient enrichment. Contrarily, both open nutrient enriched and open control treatments, still mostly covered by early successional species after nine experimental months (e.g., filamentous turf). Thus, both nutrient availability and herbivory were significant drivers at early successional stages whereas only herbivory showed significant effects of macroalgal abundance towards later successional stages.

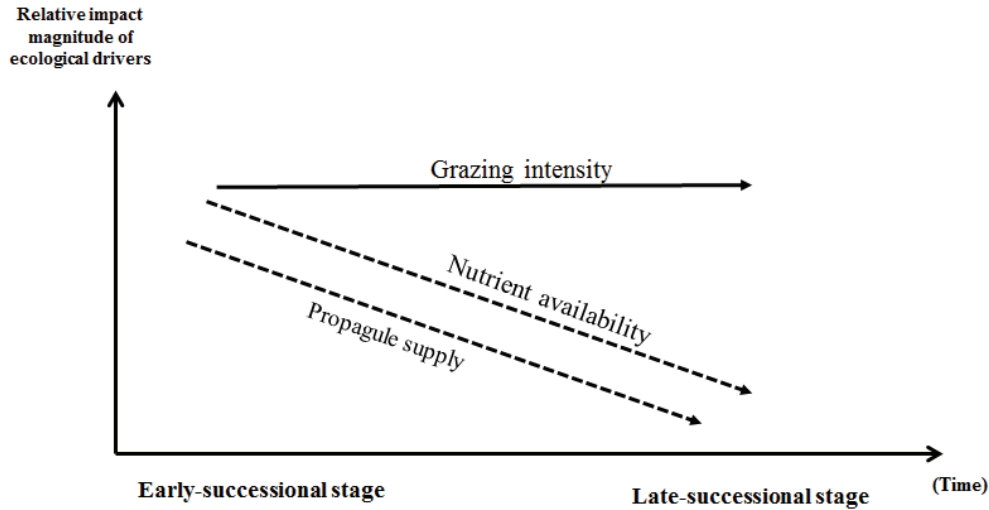


Figure 12. Schematic representation of magnitude effects of grazing intensity, nutrient availability and propagule effects on recruitment and succession of coral reef macroalgal communities. Propagule supply, grazing intensity and nutrient availability are determinant at early succession stages. Towards late successional stages, grazing intensity (solid line) remains constant while impact magnitude of nutrient availability and propagule supply (dashed lines) decrease.

Furthermore, macroalgal cover of different form-functional groups onto succession tiles varied with treatments which suggest treatments effects on interspecific macroalgal competition. For instance, abundance of calcareous articulated and leathery species increased in June while corticated-foliose (e.g., *Dictyota* sp.) decreased. Similar results were found by Hixon and Bostroff (1996) where removal of grazers led to a rapid shift from green and brown filaments to finely branched filaments and succeeded by blades and coarsely thick filaments. Macroalgal species of late successional stages such as leathery (e.g., *Sargassum* spp. and *Turbinaria* spp.) and calcareous articulated (e.g., *Amphiroa* spp., *Halimeda* spp. and *Jania* spp.) are well known to be consumed by coral reef grazers (Lobel and Ogden, 1981; Hoey and Bellwood, 2010). However, their resistance to herbivory has been also suggested (Littler *et al.* 1983; Steneck and Dethier, 1994). Current results support the hypothesis that high abundance and diversity of herbivorous fish can control growth rate of late-successional macroalgal species and

consequently increase coral reef resilience (Burkepile and Hay, 2011). Additionally, some successional trajectories (pathways) of coral reef macroalgal assemblages have been proposed where abundances and species composition of different successional stage species vary depending upon predominant herbivore groups (Sammarco, 1983; Hixon and Bostroff, 1996). For instance, Ceccarelli *et al.* (2011) described damselfish species (Pomacentridae) capable of decelerating successional rate by keeping macroalgal assemblages dominated by palatable filamentous algae species. At the present experimental study site no differences of damselfish density among treatments were found (pers. observations) so it is likely that damselfish would not affect results of studied macroalgal succession in our site. Also, McClanahan (1997) reported dominance of early-succession filamentous species over 450 day period for highly sea-urchin populated coral reefs. Nevertheless, at the current studied site only a single individual long-spiny sea-urchin (*Diadema antillarum*) was observed during the entire study period (September 2011 - July 2012). Therefore, macroalgal successional patterns of present study are mostly influenced by fish grazers (Scaridae and Acanthuridae) and nutrient loading effects. Ultimately, results of present study have some important implications in terms of coral reef ecosystem functioning. Mumby and Steneck (2008) described two ecosystem process feedbacks, positive and negative, depending upon grazing intensity. In that sense, present study supports the hypothesis of high grazing rate as primary ecological driver or positive process feedback at late-successional stage. By controlling abundance of late-successional species, larger and more structural complex species, and increasing abundance of crustose algae, herbivores fish could indirectly enhance coral recruitment. It has been shown that coral larvae preferentially settle on crustose coralline algae while fleshy algae inhibit coral recruitment (Harrington *et al.*, 2004; Ritson-Williams *et al.*, 2009). Additionally, coral reef macroalgal overgrowths usually proceed after natural

disturbances such as hurricanes or coral bleaching events (Gardner *et al.*, 2005; Diaz-Pulido and McCook, 2002), where new substrate is available to be colonized. Thus, higher abundance of mature macroalgal prevailing right after disturbances would provide propagules and consequently facilitate algal overgrowths. In addition, coral depauperate reefs as a consequence of storm and physical damages that constantly provide new substrate for algal recruitment might be the most vulnerable sites to detrimental effects of high nutrient levels. Therefore, I recommend to managers to support policies that will result in reduction of nutrient and increase grazers in order to reinforce resilience of coral reef ecosystems.

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CHAPTER 3 – CONCLUSIONS, IMPLICATIONS AND FUTURE DIRECTIONS

Results of present study showed that nutrient loading and herbivory pressure significantly affect abundance of early-successional species while late-successional species are primarily controlled by herbivory and secondarily by nutrient availability. Thus, it is reinforced the importance of preventing overfishing of coral reef herbivorous fish since they are capable of controlling macroalgal assemblages in all successional stages, early and late stages. Indeed, several authors have reported that reduction of herbivores as a consequence of harvesting could seriously reduce coral reef resilience (Hughes *et al.*, 2010; Mumby and Steneck, 2008). Additionally, assuming the role of adult macroalgal assemblages as potential propagule supply, coral reef herbivorous fishes could exert an indirect effect on controlling macroalgal by limiting abundance of adults and consequently production of new propagules. In contrast, the impact of nutrient loading was found significant only on early-successional species of coral reef macroalgal (e.g., filamentous algae such as *Chaetomorpha* sp., and *Ceramium* sp.) while decreasing in magnitude towards late-successional species (*Sargassum* sp., and *Turbinaria* sp.). In the case of calcareous articulated algae, nutrient significantly raised abundance but only in absent or reduction of herbivorous fish.

Grazing pressure as primary ecological driver and nutrient availability as secondary ecological driver have been also found in several recent coral reef studies (Burkepile and Hay, 2009; Sotka and Hay, 2009; Ferrari *et al.*, 2012; Poore *et al.*, 2012). However, the magnitude impact of each driver on macroalgae species could vary depending upon herbivore density and concentration of nutrients. Smith *et al.* (2005) reported overgrowth of *Cladophora sericea* in Hawaiian coral reef caused by eutrophication where grazing pressure, sea-urchin and fish included, was not sufficient to control it. Thus, future coral reef studies could address the

following questions: 1) what density and biomass of herbivorous fish and invertebrates are required to control macroalgal overgrowth at different levels of nutrient availability? and 2) what density and biomass of coral reef macroalgae can herbivores control? For instance, Hoey and Bellwood (2011) reported a decrease of reef fish grazing rate as macroalgae density increase. In addition, because the most studied nutrients on coral reef macroalgae, nitrogen and phosphorous, could exert different effects on growth rate and production of chemical deterrent compounds of algae, also affecting grazing rate and herbivorous preferences (Larned, 1998, Boyer *et al.*, 2004; Rasher and Hay, 2010; Hay *et al.*, 2011) an upcoming scientific research could investigate: 2) How concentration and availability, of different nutrients (e.g., nitrogen and/or phosphorous) found on coral reef common pollution sources would affect grazing rate and consumption preferences of herbivores? In this sense, some secondary metabolites have been described as chemical defense of algae (e.g., *Sargassum* sp.) against different herbivore groups (Duffy and Hay, 1994) which concentration could increase with nutrient addition (Hay *et al.*, 2011). In contrast, Boyer *et al.* (2004) reported an increase of herbivory rates as a consequence of higher nutrient content in *Acanthophora* sp. Perhaps, because of above mentioned studies analyzed different macroalgae species, opposite responses to nutrient enrichment treatment of macroalgae resistance and tolerance to herbivory were found. Furthermore, macroalgal species could response differently to nutrient enrichment depending on type and concentration of nutrient available which could also affect herbivory rate.

As a result of high macroalgal diversity and difficulties of “*in situ*” species identification, the classification system at form-functional groups, following Steneck and Dethier (1994), was used in the current study. As a first approach to characterize macroalgal assemblages, analysis of form-functional groups provides useful results, but it limits the possibility of examining

important macroalgal elements such species-specific chemical defenses, interspecific competition and herbivores preferences (Padilla and Allen, 2000). For instance, *Dictyota* spp. are known to chemically deter herbivores while benefiting not only the individual plant but also associated macroalgae species (Pereira *et al.*, 2010). Therefore, it would be convenient to use a survey method where form-functional group and genus or species composition are combined as possible, at least for most common species. In addition, conclusions emerging from present research referred to impact and magnitude of coral reef drivers as well as successional patterns are based on a single abundance metric, percent cover of macroalgae. However, grazing intensity could change depending upon density and height within macroalgal individuals of same species (Hoey, 2010; Hoey and Bellwood, 2011). Additionally, in particular macroalgal species of early-successional stages could take advantages of nutrient availability and not only cover larger areas but also increase growth rate which could be tested by using wet and dry mass as metric (Dailer *et al.*, 2012). Thus, in order to have a more truthful effect of coral reef macroalgal community ecological drivers, other metrics such as biomass and plant height and /or complexity index, or architectural index should be included.

Crustose algae (e.g., *Peyssonnelia* spp. and *Hydrolithon* spp. and *Porolithon* spp.) showed about 14% cover in recruitment tiles and approximately 4% and 8% onto permanent tiles and field established communities respectively. However, the experimental time of present study was nine months which, for this particular group of algae, could be short in order to observe long-term response to ecological drivers. For instance, in field caged experiments Burkepile and Hay (2009) reported abundance of crustose algae of nearly 15 % after 22 weeks (5th month of first year), and approximately 20% after 27 weeks (6th month of second year). However, crustose algae could cover up to 60% after a year of having placed experimental tiles on well protected

coral reefs (McClanahan, 1997). Nonetheless, the fact that coral reef herbivorous fish are able not only to strongly control fleshy macroalgae but also promote crustose algae cover has important implications for coral reef resilience. Indeed, Vermeij and Smith (2011) showed how crustose coralline algae could induce coral recruitment whereas it is well known the negative impact of fleshy macroalgal abundance on recruitment and juvenile survival rate of corals (Kuffner *et al.*, 2006; Box and Mumby, 2007). Thus, after natural disturbance such as hurricane damages and coral bleaching events, success of coral recruitment and juvenile survival rate are key processes for coral cover recover and consequently coral reef resilience. Both mentioned process are directly impacted by herbivory pressure as it reduce fleshy macroalgal abundance while promoting crustose algae (Mumby and Steneck, 2008; Diaz-Pulido *et al.*, 2009). Although, it is recommended for future field researches to extend the study period longer than a year and if possible analyze crustose algae at lower taxonomic levels, genus or species. Also, not only fish but other coral reef herbivores such as snails, crabs and urchins should be included since they could exert significant impact on early successional species and thus contribute to control macroalgae growth (Steneck, 1983; O'leary and McClanahan, 2010; Butler and Mojica, 2012).

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Appendix 1. List of algal species identified for the study site and assigned form functional groups (FFG) following Steneck and Dethier, 1994 classification

List of algae species by season (set) of Pickles reef (field and laboratory observations) S=101												
Red				Brown				Green				
	FFG	Set I	Set II	Set III		FFG	Set I	Set II	Set III			
1	<i>Amphiroa brasiliiana</i> **	6	0	0	1	1	<i>Dictyota cervicornis</i>	3.5	0	1	1	
2	<i>Amphiroa fragilissima</i>	6	1	1	1	2	<i>Dictyota menstrualis</i>	3.5	0	0	1	
3	<i>Amphiroa rigida</i>	6	1	1	1	3	<i>Dictyota pulchella</i>	3.5	0	1	1	
4	<i>Amphiroa</i> sp.**	6	1	0	0	4	<i>Dictyota</i> sp.	3.5	1	1	1	
5	<i>Amphiroa tribulus</i>	6	1	1	1	5	<i>Ectocarpus</i> sp.	2	0	1	0	
6	<i>Apoglossum rustifolium</i> **	3	0	0	1	6	<i>Fernania</i> sp.	2	0	1	0	
7	<i>Asparagopsis taxiformis</i> (falkenbergia)	2	0	1	1	7	<i>Sargassum</i> sp.	5	1	1	1	
8	<i>Ceramium clavulatum</i> **	2	0	0	1	8	<i>Sphacelaria</i> sp.	2	0	1	0	
9	<i>Ceramium curvicolatum</i> **	2	0	0	1	9	<i>Sphacelaria tribuloides</i>	2	0	0	1	
10	<i>Ceramium flaccidum</i> **	2	1	0	1	10	<i>Styopodium zonale</i>	3.5	0	0	1	
11	<i>Ceramium cimbricum</i> **	2	0	0	1	11	<i>Turbinaria turbinata</i>	5	1	0	0	
12	<i>Ceramium nitens</i> **	2	0	1	0	Total number of species				3	7	7
13	<i>Champia parvula</i> **	2	0	1	1	Green						
14	<i>Champia</i> sp.**	2	0	1	0	1	<i>Acetabularia myriospora</i>	6	0	1	1	
15	<i>Chodria</i> sp. 1**	4	0	0	1	2	<i>Acetabularia pusilla</i>	6	1	1	1	
16	<i>Chodria</i> sp. 2 (aff. <i>Polyrhiza</i>)	4	0	1	0	3	<i>Acetabularia</i> sp.**	6	0	0	1	
17	<i>Chondria</i> sp. 3 (aff. <i>Leptocremone</i>)	4	0	1	0	4	<i>Bryobesia johanne</i>	2	1	1	1	
18	<i>Chrysmenia ventricosa</i> **	4	0	0	1	5	<i>Chaetomorpha</i> sp.	2	0	1	0	
19	<i>Gelidiella acerosa</i> **	4	1	0	0	6	<i>Cladophora albida</i>	2	1	1	0	
20	<i>Gelidiella sanctarum</i> **	4	0	1	1	7	<i>Cladophora catenata</i> **	2	1	0	1	
21	<i>Gelidiella</i> sp.	4	0	1	0	8	<i>Cladophora laetevirens</i>	2	0	1	0	
22	<i>Gelidiopsis intricata</i> **	4	0	0	1	9	<i>Cladophora prolifera</i>	2	0	1	1	
23	<i>Gelidiopsis planicaulis</i>	4	0	1	0	10	<i>Cladophora</i> sp.	2	1	0	0	
24	<i>Gelidiopsis</i> sp.	4	0	1	0	11	<i>Derbesia marina</i>	2	1	1	1	
25	<i>Gelidium americanum</i> **	4	1	0	0	12	<i>Derbesia osterhoutii</i> (Halisysis stage)	2	0	1	0	
26	<i>Gelidium</i> sp.**	4	0	1	0	13	<i>Derbesia</i> sp.**	2	0	1	0	
27	<i>Gracilariopsis lemaneiformes</i> **	4	0	1	0	14	<i>Dictyosphaeria cavernosa</i>	3	0	1	0	
28	<i>Griffithsia globulifera</i> **	2	0	0	1	15	<i>Enteromorpha chaetomorphaeoides</i> **	2	1	0	0	
29	<i>Griffithsia</i> sp.**	2	0	1	1	16	<i>Enteromorpha prolifera</i> **	2	0	0	1	
30	<i>Herposiphonia secunda</i>	2	0	1	0	17	<i>Enteromorpha</i> sp.	2	1	1	0	
31	<i>Herposiphonia</i> sp.**	2	1	1	1	18	<i>Halimeda opuntia</i> *	6	0	0	0	
32	<i>Heterosiphonia gibbesi</i>	2	1	1	1	19	<i>Halimeda tuna</i> *	6	0	0	0	
33	<i>Heterosiphonia</i> sp.**	2	0	1	0	20	<i>Neomeris</i> sp.*	5	1	0	0	
34	<i>Hildenbrandia rubra</i> **	7	0	0	1	21	<i>Neomeris annulata</i> **	5	0	0	1	
35	<i>Hypnea</i> sp.**	4	1	1	0	22	<i>Penicillus capitatus</i> *	6	0	0	0	
36	<i>Hypnea spinella</i>	4	1	1	1	23	<i>Ulva flexuosa</i> **	3	0	0	1	
37	<i>Hypnea valentiae</i> **	4	1	1	1	24	<i>Ulva</i> sp.**	3	1	0	0	
38	<i>Jania adhaerens</i>	6	1	1	1	25	<i>Valonia macrophysa</i>	3	0	1	0	
39	<i>Jania capillacea</i>	6	1	1	1	26	<i>Ventricaria ventricosa</i>	3	0	1	1	
40	<i>Jania</i> sp.**	6	1	1	1	Total number of species				10	14	11
41	<i>Laurencia cervicornis</i>	4	1	1	1	Blue-green algae						
42	<i>Laurencia intricata</i> **	4	0	0	1	1	<i>Lynbya</i> sp.**	1	N/A	N/A	N/A	
43	<i>Laurencia poiteau</i> **	4	0	0	1	2	<i>Symploca</i> sp.**	1	N/A	N/A	N/A	
44	<i>Laurencia</i> sp. 1	4	1	1	1	3	<i>Calothrix</i> sp.**	1	N/A	N/A	N/A	
45	<i>Laurencia</i> sp. 2	4	0	1	0	4	<i>Rivularia</i> sp.**	1	N/A	N/A	N/A	
46	<i>Laurencia</i> sp. 3**	4	0	0	1	Total number of species				1	1	1
47	<i>Meristiella schrammii</i> **	4	0	0	1							
48	<i>Neosiphonia howei</i>	2	1	1	1							
49	<i>Peyssonelia</i> spp.	7	1	1	1							
50	<i>Plenosporium flexuosum</i> **	2	0	1	0	FFG-Steneck and Dethier form-functional groups (1994)						
51	<i>Polysiphonia atlantica</i>	2	0	1	0	1-	Microalgae					
52	<i>Polysiphonia scopulorum</i> **	2	0	0	1	2-	Filamentous algae					
53	<i>Polysiphonia</i> sp. 2	2	0	1	0	3-	Foliose algae					
54	<i>Polysiphonia</i> sp. 3	2	0	1	0	3.5-	Corticated foliose					
55	<i>Polysiphonia</i> sp.1	2	1	1	0	4-	Corticated macrophytes					
56	<i>Pterocladia capillacea</i> **	4	0	0	1	5-	Leathery macrophytes					
57	<i>Rhodomenia pseudopalmata</i> **	2	0	0	1	6-	Articulates calcareous algae					
58	<i>Spyridia clavata</i> *	2	0	0	1	7-	Crustose algae					
59	<i>Wurdemannia miniata</i> **	4	0	0	1							
60	Crustose Coraline Algae	7	1	1	1							
Total number of species			21	37	39							