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Seasonal regulation of herbivory and nutrient effects on macroalgal recruitment and succession in a Florida coral reef

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Herbivory and nutrient enrichment are drivers of benthic dynamics of coral reef macroalgae; however, their impact may vary seasonally. In this study we evaluated the effects of herbivore pressure, nutrient availability and potential propagule supply on seasonal recruitment and succession of macroalgal communities on a Florida coral reef. Recruitment tiles, replaced every three months, and succession tiles, kept in the field for nine months, were established in an ongoing factorial nutrient enrichment-herbivore exclusion experiment. The ongoing experiment had already created very different algal communities across the different herbivory and nutrient treatments. We tracked algal recruitment, species richness, and species abundance through time. Our results show seasonal variation in the effect of herbivory and nutrient availability on recruitment of coral reef macroalgae. In the spring, when there was higher macroalgal species richness and abundance of recruits, herbivory appeared to have more control on macroalgal community structure than did nutrients. In contrast, there was no effect of either herbivory or nutrient enrichment on macroalgal communities on recruitment tiles in cooler seasons. The abundance of recruits on tiles was positively correlated with the abundance of algal in the ongoing, established experiment, suggesting that propagule abundance is likely a strong influence on algal recruitment and early succession. Results of the present study suggest that abundant herbivorous fishes control recruitment and succession of macroalgae, particularly in the warm season when macroalgal growth is higher. However, herbivory appears less impactful on algal recruitment and community dynamics in cooler seasons. Ultimately, our data suggest that the timing of coral mortality (e.g. summer vs. winter mortality) and freeing of benthic space may strongly influence the dynamics of algae that colonize open space. [

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Abstract.

Herbivory and nutrient enrichment are drivers of benthic dynamics of coral reef macroalgae; however, their impact may vary seasonally. In this study we evaluated the effects of herbivore pressure, nutrient availability and potential propagule supply on seasonal recruitment and succession of macroalgal communities on a Florida coral reef. Recruitment tiles, replaced every three months, and succession tiles, kept in the field for nine months, were established in an ongoing factorial nutrient enrichment-herbivore exclusion experiment. The ongoing experiment had already created very different algal communities across the different herbivory and nutrient treatments. We tracked algal recruitment, species richness, and species abundance through time. Our results show seasonal variation in the effect of herbivory and nutrient availability on recruitment of coral reef macroalgae. In the spring, when there was higher macroalgal species richness and abundance of recruits, herbivory appeared to have more control on macroalgal community structure than did nutrients. In contrast, there was no effect of either herbivory or nutrient enrichment on macroalgal communities on recruitment tiles in cooler seasons. The abundance of recruits on tiles was positively correlated with the abundance of algal in the ongoing, established experiment, suggesting that propagule abundance is likely a strong influence on algal recruitment and early succession. Results of the present study suggest that abundant herbivorous fishes control recruitment and succession of macroalgae, particularly in the warm season when macroalgal growth is higher. However, herbivory appears less impactful on algal recruitment and community dynamics in cooler seasons. Ultimately, our data suggest that the timing of coral mortality (e.g. summer vs. winter mortality) and freeing of benthic space may strongly influence the dynamics of algae that colonize open space.

Introduction

On coral reefs, herbivory and nutrient availability are often considered the primary ecological drivers of macroalgal community dynamics (Littler and Littler, 1984; McCook, 1999; Burkepile and Hay, 2006). Field experiments excluding herbivores have resulted in a substantial increase of both biomass and density of some macroalgal species, generating changes in species composition at the community level (Lewis, 1986; Burkepile and Hay, 2009; Ferrari et al., 2012). Nutrient enrichment tends to have more variable effects on macroalgal communities, possibly linked to species-specific responses of macroalgae to nutrient availability (Larned, 1998; Fong et al., 2001; Dailer et al., 2012). In particular, growth rates of some small, fast-growing species quickly peak in nutrient enriched environments (Lapointe et al., 1997; McClanahan et al., 2004; Smith et al., 2005). In contrast, larger slow-growing species, typical of late stages of macroalgal community succession (e.g., *Sargassum* spp., *Amphiroa* spp.), often show weak or mixed effects in nutrient enriched areas (McClanahan et al., 2004; Burkepile and Hay, 2009). However, abundance of different macroalgal species can vary seasonally on reefs (Lirman and Biber, 2000), which could explain the variable relative effect of each driver on structuring macroalgal communities (Burkepile and Hay, 2006; Smith et al., 2010).

A number of factors may influence seasonality of algal communities on reefs including seasonal changes in abiotic conditions (e.g. temperature and light; Clifton and Clifton, 1999), the timing and intensity of disturbances (Diaz-Pulido and Garzon-Ferreria, 2000; Diaz-Pulido and McCook, 2004; Goodsell and Connell, 2005) and propagule supply and recruitment (McClanahan 1997; Diaz-Pulido and McCook, 2002). Increases in water temperature and light availability can promote macroalgal growth and trigger reproduction in some species (Clifton 2008, Collado-Vides et al., 2011). For example, both *Dictyota pulchella* and *Sargassum* spp.

show a peak of abundance during the summer and a loss of biomass in the coolest seasons (Lirman and Biber, 2000; Mumby et al., 2005; Renken et al. 2010). In contrast, *Gracilaria* spp. and *Stypopodium zonale* often exhibit higher abundance during cooler seasons (Hay and Norris, 1984; Chung et al., 2007). In addition to influencing macroalgal growth rates, temperature also influences the rate of herbivory in fishes with grazing rates often peaking during warmer periods (Smith, 2008; Lefevre and Bellwood, 2010). Thus, variation in abiotic controls of both algal growth rates and rates of herbivory across seasons could result in temporal fluctuations of bottom-up and top-down forcing.

These seasonal differences in macroalgal growth and herbivory rates could affect how disturbances to reefs impact macroalgal community development and succession. For example, in reefs in the Florida Keys, both extreme warm water (Eakin et al., 2010) and cold water (Lirman et al., 2011) anomalies can lead to coral mortality. Given that these disturbances open up free space for macroalgal colonization during different times of the year with different abiotic conditions, different species of algae may become dominant and drive different successional trajectories depending on the timing of these disturbances and the initiation of algal succession.

Propagule abundance can also impact community dynamics by influencing the rates of recruitment in many marine organisms (Stiger and Payri, 1999; Lotze, Worm and Sommer, 2000; Grorud-Colvert and Sponaugle, 2009). The abundance of adult macroalgal individuals, the number of propagules they produce, and the distance to a suitable substrate for colonization can determine the number of macroalgal recruits in a given area (Kendrick and Walker 1991, Stiger and Payri 1999, Lotze, Worm and Sommer, 2000). Thus, abundant adult macroalgae might increase local macroalgal recruitment, especially after relatively localized disturbances such as coral mortality events (Roff and Mumby, 2012). Consequently, increases in macroalgae due to reductions in herbivory or increases in nutrient availability could lead to increased macroalgal propagule supply and a positive feedback on macroalgal abundance. Yet, no studies have directly addressed how seasonality and propagule supply interact with herbivory and nutrient availability to impact macroalgal community development and succession on coral reefs.

In the current study, we tested how both nutrient availability and herbivory varied across seasons as drivers of recruitment and succession of a coral reef macroalgal community. We used a factorial field experiment manipulating access by herbivorous fishes and nutrient availability that had been established two years prior to examine the effects of herbivory, nutrient enrichment, and macroalgal abundance on macroalgal recruitment patterns and succession on primary substrate. We established primary substrate in the different treatments multiple times across different seasons to test for the interactive effects of herbivory, nutrient availability, and seasonality on recruitment patterns. We quantified macroalgal abundance and diversity on both primary substrate and the established macroalgal communities regularly over nine months. We predicted that macroalgal recruitment would be higher in areas with greater adult macroalgal abundance and that herbivory would be the main ecological driver of macroalgal abundance. In addition, we hypothesized that the effect of both nutrient availability and herbivory would be reduced in cooler seasons when lower temperature and light availability limit macroalgal growth and rates of herbivory are typically lower. We also expected to find that in our study site, characterized by high abundance of herbivorous fish, algal community composition will vary seasonally with turf-forming and articulated-calcareous algae dominant in cooler seasons with foliose algae (e.g. *Dictyota* spp.) becoming dominant in warmer seasons.

Materials and methods

Study site and experimental design

This study was conducted on a spur and groove reef system located in the upper Florida Keys near Pickles Reef (25°00’05”N, 80°24’55”W) with the approval of the Florida Keys National Marine Sanctuary (FKNMS-2009-047 and FKNMS-2011-090). The reef is a shallow area (5-6m) where parrotfish and surgeonfish are the dominant herbivorous fishes and the long-spined urchin, *Diadema antillarum,* is present at very low densities (<1 individual per $50m^2$, pers. obs.). In June 2009, eight $9m^2$ experimental plots (3x3m) were established to examine the interactive effects of herbivory and nutrient availability on benthic community dynamics (Zaneveld et al. In Press). Plots were separated by at least 5m. Each $9m^2$ plot contained two quadrats ($1x1m^2$) for herbivore exclusion (exclosure), covered with plastic-coated wire mesh (2.5cm diameter holes) around a 0.5m high metal bar frame. Two other quadrats ($1x1m^2$) were used as herbivore exclusion controls (uncaged) that had metal bar frames with three sides covered with wire mesh but allowed access to all herbivores.

To mimic nutrient loading, four of the eight $9m^2$ experimental plots were enriched with Osmocote (19-6-12, N-P-K) slow-release garden fertilizer. The Osmocote (175g) was placed in a 15cm diameter PVC tube with 10 (1.5cm) holes drilled into it. These tubes were 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 spread evenly across each enrichment plot. Enrichment tubes were replaced every 4-6 weeks to ensure continual nutrient addition. The other four $9m^2$ plots were kept at ambient nutrient conditions. Sampling of water column nutrients in this experiment showed that this enrichment increased both dissolved inorganic nitrogen (3.91µM vs. 1.15µM in enriched vs. ambient) and soluble reactive phosphorus (0.27µM vs. 0.035µM in enriched vs. ambient) in the water column (Vega Thurber et al., 2014). Levels of both DIN and SRP in the ambient nutrient plots were within the range of concentrations for offshore reefs in the Florida Keys (Boyer & Briceño, 2010). Further, levels of DIN and SRP in the enriched treatment were similar to those reported from other anthropogenic-impacted reefs located around the world (Dinsdale et al., 2008). Additionally, nitrogen concentration in the tissues of the common alga *Dictyota menstrualis* were 20% higher in the enriched plots compared to the control plots, suggesting that the nutrients from the enrichment were consistently available to benthic organisms (Vega Thurber et al., 2014).

Fish community structure

To estimate the intensity of herbivore pressure, fish community structure was evaluated four times during the study period (September, 2011; January, 2012; April, 2012 and July 2012) using 30x2m belt transects (n=12) placed haphazardly across the study site following AGRRA methodology (Protocols Version 5.4; Lang et al., 2010). All individuals of all fish species included in the AGRRA protocol were identified and size estimated to the nearest cm. Size estimates were converted to biomass for each individual fish using published length: weight relationships (Bohnsack and Harper, 1988). We did not quantify abundances of the urchin *D. antillarum* as they are currently rare across the Florida Keys (Chiappone et al., 2002) and were very infrequently seen at our field site.

Recruitment of macroalgae on primary substrate

To study macroalgal recruitment across different seasons in the different treatments, we placed two settlement tiles (10x10cm from quarried Pleistocene coral limestone) in each of the two exclosure and uncaged quadrats within every 9m^2 plot (n=64 tiles total) in September 2011. We did not put tiles in completely open areas as data from the main experiment showed that the macroalgal communities in the uncaged and completely open areas did not differ (Zaneveld et al., In Press). These tiles (hereafter ‘recruitment tiles’) were collected after three months and replaced with new tiles to quantify recruitment and early succession during each season. These deployments resulted in a total of three separate sets of data on macroalgal recruitment across different seasons: fall (September-December 2011), winter (December 2011-March 2012) and spring (March- June 2012). A tropical storm in Summer 2012 removed much of the experimental infrastructure precluding data from the planned Summer period.

After three months in the field, recruitment tiles were transported to the laboratory where algae were identified to the lowest possible taxonomic level (Appendix I) and their percent cover was visually quantified. The recruitment tiles were then placed in individual separate aquaria that were prepared to replicate the field conditions as closely as possible (salinity: 35-36ppt, temperature: 25-28ºC, constant water circulation, and artificial high output white light with 12:12 day-night cycle). We kept the tiles in their corresponding aquaria for three months to promote growth of macroalgal recruits that were unidentifiable in our immediate evaluation due to their small size or lack of identifiable traits. After this period, all macroalgal species were re-identified and any new contribution was added to the species list.

Succession of macroalgal communities on primary substrate

In September 2011, we also placed a second set of two settlement tiles (10x10cm) (hereafter ‘succession tiles’) in each exclosure and uncaged quadrat (n=64 tiles total). Succession tiles were kept in the field from September 2011 to June 2012. Macroalgal abundance was visually quantified on succession tiles *in situ* in January and June 2012 using a percent cover scale of 0.1 (single individual), 0.5 (less than three sparse individuals), 1 (few individuals), and then 5 to 100 with multiples of 5 based on visually estimated percent cover. Macroalgae were identified to the lowest taxonomic level possible and also binned into form-functional groups (FFG) following Steneck and Detheir (1994).

Established macroalgal communities

Macroalgal abundance of established communities showed significant differences in the benthic macroalgal community composition across the different treatments (Zaneveld et al. In Press). These differences in the abundance and community composition of algae could have resulted in differing levels of propagule abundance across treatments, an important factor potentially affecting recruitment and succession on primary substrate in our study. To evaluate the potential propagule supply of each established community, macroalgal abundance was visually quantified using quadrats (50x50cm) in January and June 2012 using the percent cover scale and FFG classification as described above.

Statistical analyses

Biomass and density of total and herbivorous fish were compared across seasons using a one-factor ANOVA. For statistical analyses of the different macroalgal community metrics of recruitment and succession tiles, we averaged data from the two tiles located within each exclosure and uncaged quadrat. For recruitment tiles, succession tiles, and established communities we averaged metrics of the two exclosure quadrats and two uncaged quadrats of each plot such that n=4 for each treatment except for the ambient-exclosure treatment where n=3 due to losing exclosures in one plot in May 2012 during a storm.

We used a three-factor ANOVA to test for the effects of herbivores, nutrient enrichment, season, and their interactions on algal species richness and overall macroalgal abundance of recruitment tiles. When there were significant treatment X season interactions, we used a two-factor ANOVA to assess treatment effects (i.e. nutrient enrichment and herbivore exclosure) within different seasons. We used non-metric multi-dimensional scaling (nMDS) and permutational MANOVA (PERMANOVA) to assess the effects of treatments and seasonality on macroalgae community composition of recruitment tiles. We used a similarity percentage analysis (SIMPER) to assess how different species contributed to differences in community structure across treatments. To assess variability in abundance of most common species across treatments and seasons, we used three-factor ANOVAs or non-parametric tests when data did not satisfy assumptions for parametric tests.

For both successional tiles and established algal communities, we used a three-factor ANOVA to test the effects of herbivory, nutrient availability, and season on overall algal abundance and the abundance of different FFG. To test the effects of treatment on community succession, a non-metric multi-dimensional scaling (nMDS) and a PERMANOVA were performed on the abundance of all FFG analyzed seasonally. To examine how macroalgal abundance in the established communities (potential propagule supply) impacted macroalgal recruitment, we used a Pearson correlation to assess the relationship between FFG abundance of established communities and both succession tiles and recruitment tiles in both winter and spring. We performed descriptive and inferential analyses using the R program from R Development Core Team (2012), version 3.2.2.

Results

Fish community structure

Overall fish mean biomass and density at the study site were 6495.60 ± 508.10 g/100m^2, and 39.93 ± 3.20 Ind./100m^2 respectively. Herbivores (Family Scaridae and Acanthuridae) comprised 78% of overall fish biomass with an average of 5086.17 ± 569.50 g/100m^2 and 74%

of overall fish density 29.93 ± 2.10 Ind./100m^2. Total biomass of parrotfish and surgeonfish were 2771.65 ± 526.60 g/100m^2 and 2315.52 ± 570.60 g/100m^2 respectively. We saw no temporal changes in biomass or density of total and herbivorous fish as no significant differences were found among seasons (One-factor ANOVA, p>0.05 in all cases).

Recruitment of macroalgae on primary substrate (recruitment tiles)

We identified 101 macroalgal taxa (Appendix I) including field and laboratory observations. Macroalgal species richness on recruitment tiles increased across seasons, averaging 9.73 species per tile in fall, 12.13 in winter, and 14.40 in spring (three-factor ANOVA, Season: F=6.09, p=0.006). Neither nutrient enrichment nor herbivore exclosure had an independent or interactive effect on species richness of recruitment tiles (Appendix II). Overall abundance of macroalgae on recruitment tiles was twofold higher in spring (116.12 ± 9.50%) compared with fall (60.00 ± 7.48%) and winter (51.77 ± 6.31%) regardless of treatment (Figure 1, three-factor ANOVA, Season: F=30.54, p<0.001). Across seasons the combination of herbivore exclosure and nutrient enrichment had significant impact with noticeable increase in macroalgal abundance (Figure 1; Appendix II).

Macroalgal assemblages on recruitment tiles were different across seasons (nMDS, Figure 2, PERMANOVA, Season: pseudo F= 7.68, p=0.01). Only four groups were present in all seasons (CCA, Cyanobacteria, *Jania capillacea* and *Peyssonnelia* spp.) but with dissimilar abundances (Table 1). There was a peak of cyanobacteria in spring while the abundance of *Peyssonnelia* spp. was four times higher during fall and spring compared to winter (Table 1). Other species such as *Ectocarpus* sp., *Gelidiella* sp. and *Heterosiphonia* sp. increased their abundance in winter although abundance of both *Laurencia* species peaked in spring (Table 1). There was an effect of herbivore exclosure and a significant interaction between herbivore exclosure and season in driving differences in community composition on recruitment tiles (PERMANOVA, Herbivore: pseudo F= 3.94.67 $p=0.01$ and Herbivory:Season interaction: pseudo F= 2.15, $p=0.01$, respectively). Analyses within season showed a clear effect of herbivore exclosure and nutrient enrichment in spring which seems to be stronger when both are combined as shown in the nMDS analyses (Figure 2; PERMANOVA, Herbivory: pseudo F= 6.16, $p=0.01$ and Nutrient: pseudo F= 3.08, $p=0.04$, respectively).

Succession of macroalgae on primary substrate (succession tiles)

Excluding herbivores from succession tiles led to almost double overall macroalgal cover (77.29±7.29%) compared to uncaged tiles (40.84 ± 5.22%; three-factor ANOVA, Herbivory: F=16.52, $p<0.001$), while no other factors showed significant effects (Figure 3; Appendix II). Filamentous algae increased abundance in June with 33.83±4.58% (Figure 3, three-factor ANOVA, Season: F=6.09, $p=0.02$) and was negatively affected by nutrient enrichment (Figure 3, three-factor ANOVA, Nutrient: F=13.23, $p=0.01$) but not by herbivore exclosure (three-factor ANOVA, Herbivory: F=0.12, $p=0.74$). Abundance of foliose macroalgae (e.g. *Dictyota* spp.) increased when herbivores where excluded (Figure 3; three-factor ANOVA, Herbivory: F=7.84, $p=0.01$) with stronger effect within ambient nutrient treatments where abundance doubled compared to other treatments (Figure 3; three-factor ANOVA, Herbivory:Nutrient interaction: F=10.55, $p=0.004$). Articulated calcareous algae (e.g. *Jania* spp. and *Amphiroa* spp.) showed higher abundance when herbivores were excluded (three-factor ANOVA, Herbivory: F=12.15, $p=0.002$), particularly when combined with nutrient enrichment, resulting in over three times the abundance compared to other treatments (Figure 3, three-factor ANOVA, Herbivory:Nutrient interaction: F=6.77, $p=0.02$). There was a trend towards herbivore exclosure increasing the abundance of leathery algae (e.g. *Sargassum* spp.) (three-factor ANOVA, Herbivory: F=3.22, *p*=0.09), but these species were quite variable. There was also a trend towards herbivore exclosure decreasing abundance of crustose algae (e.g. *Peyssonnelia* spp. and crustose coralline algae) (three-factor ANOVA, Herbivory: F=3.31, *p*=0.08).

Some observations suggest that macroalgal assemblages go through different successional patterns depending upon treatment. For instance, in both January and June, the nMDS analysis showed herbivore exclosure had significant effects on the FFG composition of macroalgal communities (Figure 4, PERMANOVA, Herbivory: pseudo F = 8.96; *p*=0.01, pseudo F = 3.46, *p*=0.03 respectively). However, there was an effect of nutrient enrichment only in January (Figure 4, PERMANOVA, Nutrient: pseudo F = 2.84; *p*=0.03). The significant effect of herbivore exclosure in the nMDS was not surprising given that some species of articulated calcareous algae (*Jania* spp. and *Amphiroa* spp.) and leathery algae (*Sargassum* spp.) were present almost exclusively within exclosures.

Established macroalgal communities

Overall macroalgal abundance of established communities was over twofold higher in June with 84.3 ± 7.76% compared to January 39.36 ± 7.55% (Figure 5, three-factor ANOVA, Season: F=59.65, *p*<0.001). Herbivore exclosures had two fold higher algal cover (Figure 5, three-factor ANOVA, Herbivory: F=65.49, *p*<0.001) while there was no effect of nutrient enrichment (Figure 5, Appendix II). Filamentous and crustose algae were the only macroalgal groups that showed a seasonal increase from January to June on established communities (Figure 5, three-factor ANOVA, Season: F=70.46, *p*<0.001; F=10.05, *p*=0.004, respectively). The three groups of upright macroalgae: foliose, leathery and articulated calcareous algae were more abundant in herbivore exclosures (Figure 5). Leathery macroalgae were practically only found in herbivory exclosure treatments regardless of nutrient treatment (Figure 5). Furthermore, articulated calcareous algae (e.g. *Jania* spp. and *Amphiroa* spp.) were much more abundant inside exclosures when combined with nutrient enrichment in both January and June (Figure 5, three-factor ANOVA, Herbivory:Nutrient interaction, F=10.00, *p*=0.005).

There were significant positive correlations of algal abundance of established communities with algal abundance found on recruitment and succession tiles for some algal groups (Table 2). The abundance of leathery macroalgae on established communities was correlated with the corresponding abundances found on recruitment tiles in January (Pearson correlation, r=0.97, *p*=0.03) and with abundance of succession tiles in June (Pearson correlation, r=0.95, *p*=0.05). Articulated calcareous algae was the only algal group that showed correlations between established communities and corresponding recruitment and succession tiles in both seasons (Table 2).

Discussion

The results of this study provide evidence of the seasonal regulation of herbivory and nutrient availability effects on recruitment of coral reef macroalgae. We observed an increase in species richness and abundance of macroalgal recruits towards the warmer season (spring), with recruit abundance noticeably higher when combining reduced herbivory and nutrient enrichment. However, herbivory primarily drove macroalgal abundance and the trajectory of succession over longer time periods, with higher algal abundance for some groups of macroalgae (e.g. articulated calcareous algae) under elevated nutrient conditions. We also found positive correlations between algal abundance in established communities and abundance on both recruitment and successional tiles. These data suggest an important role of propagule supply in influencing algal recruitment and succession. These results show that the impact of herbivores and nutrient availability on macroalgal recruitment and succession varies across seasons and functional groups of algae. Herbivory was a driving force across seasons, but strongest in warmer seasons, while nutrient availability showed the strongest effects in cooler seasons.

Macroalgal communities on coral reefs can show noticeable temporal changes in species composition and abundance, associated with abiotic (e.g. temperature, light) and biotic factors (Tsai et al., 2005; Renken et al., 2010; Page-Albins et al., 2012). Some Caribbean species such as *Dictyota* spp. increase in abundance during summer, often covering over 50 % of the benthos, while others (e.g. *Halimeda* and turf-forming species) are more abundant during cooler periods of the year (Lirman and Biber, 2000; Renken et al., 2010; Ferreira et al. 2012). In our study we found an increase in overall abundance of macroalgal recruits towards spring with distinct species flourishing within treatments. For instance, recruitment of *Jania capillacea* and *Hypnea spinella* was higher in spring but mostly within exclosures which suggests the strong control of herbivory of both species during spring. Both *Laurencia cervicornis* and *L. intricata* increased in abundance in spring. However, *L. cervicornis* was abundant in uncaged treatments while *L. intricata* was abundant in exclosure treatments. Some species of *Laurencia* are chemically defended against herbivores (Nagle and Paul, 1998; Pereira, Cavalcanti and Texeira, 2000), which could explain the proliferation of *L. cervicornis* in the presence of herbivores. In contrast, the abundance of small filamentous algal species commonly consumed by herbivorous fish (e.g. *Ectocarpus* sp., *Gelidiella* sp. and *Heterosiphonia* sp.) increased in winter when other studies have shown that grazing rates often decline (Ferreira et al., 1998; Lefevre and Bellwood, 2010). Indeed, we saw an interaction between herbivory and season on community composition suggesting that herbivores have stronger effects on algal recruitment during warmer periods (spring and summer). Since recruitment of corals is often higher during spring and summe

(Green and Edmund, 2011), the strong top-down control of algal recruitment during this period could indirectly enhance coral recruitment by freeing space for corals. Herbivory may have been less important in colder seasons due to lower grazing rates combined with lower recruitment rates and slower growth rates of algae.

Succession in the absence of herbivores is expected to follow a trajectory characterized by replacement of early, fast growing species (e.g., *Enteromorpha* sp. *Ceramium* sp., *Felmania* sp.) by late successional species such as leathery and calcareous articulated species (McClanahan, 1997). Our results show that nutrient enrichment and herbivore exclosure interact to drive macroalgal succession at early stages (four months), while herbivory appears more important at later stages. After four months, filamentous and foliose algae increased inside exclosures with ambient nutrient levels, while leathery and articulated calcareous flourished in exclosures with nutrient enrichment. After nine months, species considered later successional species (e.g. *Sargassum* sp. and *Amphiroa* sp.) were present almost exclusively on succession tiles in exclosures regardless of nutrient enrichment. These results suggest that nutrient availability facilitates the rapid colonization and growth of leathery and articulated calcareous algae. But, over the long term, herbivory is the primary driver of their abundance. Other studies have shown that nutrient loading does not affect macroalgal species composition at late successional stages but facilitates abundance of early successional species such as turf forming algae and cyanobacteria (McClanahan et al., 2007). In our study we found that both nutrient availability and herbivory are significant drivers at early successional stages, whereas nutrient showed significant effect over later successional stages only when herbivores were excluded.

Competition among algae may also be important for determining successional trajectories, especially when herbivory is low. Macroalgal communities on succession tiles within herbivore exclosures were dominated by calcareous articulated and leathery species by the end of the experiment. These species appeared to replace *Dictyota* spp. and other foliose and filamentous algae, especially under nutrient enrichment, suggesting that these late successional species are better competitors in absence of herbivores. Thus, selective grazing by herbivores on more palatable species (e.g. articulated calcareous) might facilitate the colonization and establishment of less palatable foliose algae. Coral reef herbivores often consume 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.) (Lobel and Ogden, 1981; Burkepile and Hay, 2008; Hoey and Bellwood, 2011), keeping macroalgal communities in stages of early succession. Hixon and Bostroff (1996) found similar results where removal of grazers led to a rapid shift from green and brown filamentous algae to finely branched filaments followed by species forming thicker filaments (e.g. *Tolypoicladia glomerulata*). Similarly, Thacker et al. (2001) reported a community shift from unpalatable to palatable species of algae when herbivores were excluded from coral reefs on Guam. This pattern is also common in terrestrial ecosystems where selective herbivores target palatable, but often competitively superior plant species, and release unpalatable species from competition (Briske and Hendrickson, 1998; Torrano and Valderrabano, 2004).

We found that macroalgal abundance on recruitment and succession tiles was correlated with abundance of algae in established communities, which suggests that local propagule supply from the established community likely impacted early community development. In temperate marine communities, particularly for fast-growing species of macroalgae (e.g. *Cladophora* sp., *Polysiphonia* sp. and *Ceramium* sp.), propagule abundance has been proposed as one of the main drivers of macroalgal population growth (Worm and Lotze, 2006; Karez et al., 2004). Worm et al. (1999) proposed that a combination of increased propagule supply and nutrient loading could overwhelm grazing rates and consequently increase the abundance of macroalgae in temperate benthic communities. Our results are consistent with Roff and Mumby (2012) who proposed that Caribbean coral reefs have lower resilience compared to Indo-Pacific reefs because they experience higher rates of macroalgal recruitment. However, further studies are needed to evaluate spatial and temporal variation of algal propagule supply and subsequent algal settlement in relation to herbivory and nutrient levels. For instance, since herbivores feed on adult macroalgae as well as recruits they might be controlling algal recruitment and abundance at multiple stages of the algal life cycle. Further, different species of herbivores could be important for controlling the same algal species at different life stages as some herbivorous fishes tend to focus more on early successional algae and would be more likely to consumer algal recruits while other herbivorous species focus on late-successional algae (Burkepile and Hay 2010).

The combined effects of herbivore exclosure and nutrient enrichment showed strong effects on abundance of macroalgae on recruitment tiles. This result suggests that reefs that are both overfished and have high nutrient loading will have higher recruitment of algae. These higher recruitment rates may mean that these reefs are more likely to undergo regime shifts or state changes to algal abundant communities when corals die back. These impacts could be magnified if coral mortality occurs primarily in warmer seasons when herbivorous fishes are the most important for impacting algal recruitment. Once algal recruits have settled, succession can be modified by both nutrient availability and herbivores, often depending on season and successional stage. While overfished reefs can quickly undergo algal succession with rapid dominance of foliose and filamentous algae, overfished and nutrient enriched reefs can rapidly increase abundance of leathery and articulated calcareous algae when space is available. While filamentous and foliose algae can reduce coral recruitment and harm small adult colonies, leathery and articulated calcareous algae can in addition shade and physically harm colonies by abrasion (McCook et al., 2001). Thus, overfishing herbivores and eutrophication can have strong impact on algal succession and, ultimately, their interactions with corals.

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Table 1. Abundance of dominant macroalgal taxa found on recruitment tiles per season. Statistics column refers to analysis performed to compare abundance of specific taxa across season (F and *p* from one-factor ANOVA and N/A and *p* from Friedman test). Letters indicate post hoc analysis (SNK or Wilcoxon pair analysis) when abundance differed across seasons.

Species	**Fall (Sep-Dec)**	**Winter (Jan-Mar)**	**Spring (Mar-Jun)**	**Statistical sign.**	
	Percent cover (%)	**Percent cover (%)**	**Percent cover (%)**	**F**	***p***
Peyssonnelia sp.	12.28 (A)	3.43 (B)	12.36 (A)	11.405	**.001**
Crustose coralline algae (CCA)	11.24	7.41	6.40	2.157	.124
Jania capillacea	4.68	2.20	10.44	N/A	.173
Neosiphonia howei	3.90 (A)	0.00 (B)	2.86 (A)	N/A	**.001**
Cyanobacteria	6.6 (B)	3.56 (B)	37.84 (A)	N/A	**.001**
Heterosiphonia sp.	0.00 (B)	1.27 (A)	0.00 (B)	N/A	**.001**
Ectocarpus sp.	0.00 (B)	12.20 (A)	0.00 (B)	N/A	**.001**
Laurencia cervicornis	2.28 (B)	0.33 (B)	6.48 (A)	N/A	**.001**
Hypnea spinella	1.56 (A)	0.82 (A)	4.30 (B)	N/A	**.001**
Gelidiella sp.	0.00 (B)	1.16 (A)	0.00 (B)	N/A	**.001**
Laurencia intricata	0.00 (A)	0.00 (A)	3.42 (B)	N/A	**.001**

Table 2. Pearson correlation between algal FFG abundance on recruitment or succession tiles and abundance of algal FFG in established communities for winter and spring. Bolded values show significant effects.

Season	**Form-Functional group**	**Recruitment tiles**		**Succession tiles**	
		Coef. Corr (r)	***p***	**Coef. Corr (r)**	***p***
Winter (January)	Overall	**0.59**	**0.002**	**0.86**	**0.001**
	Filamentous	0.89	0.11	0.35	0.65
	Foliose	0.49	0.51	0.44	0.56
	Leathery	**0.97**	**0.03**	0.28	0.72
	Articulated-Calcareous	**1.00**	**0.004**	**0.99**	**0.01**
	Crustose	**-0.94**	**0.04**	-0.77	0.23
Spring (June)	Overall	**0.53**	**0.01**	**0.43**	**0.03**
	Filamentous	-0.33	0.67	-0.51	0.49
	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

Figure 1. Overall abundance of macroalgae on recruitment tiles by treatments within each season. Bars represent means ± SEM. Probability values (*p*) come from three-factor ANOVA of main treatment effects.

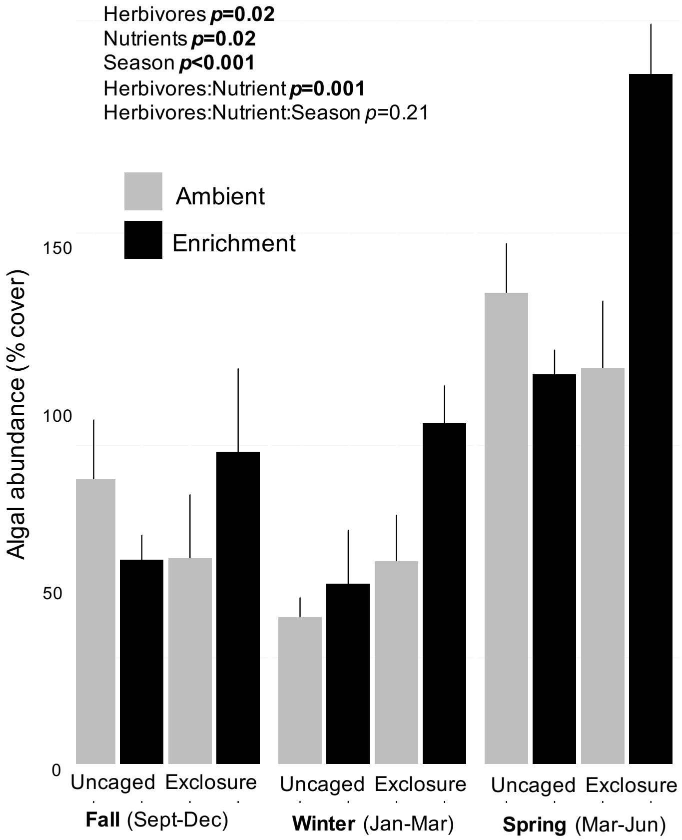

Figure 2. Non-metric Multidimensional Scaling analysis of algal abundance in communities on recruitment tiles across seasons (A) and in each treatment by season (B-D).

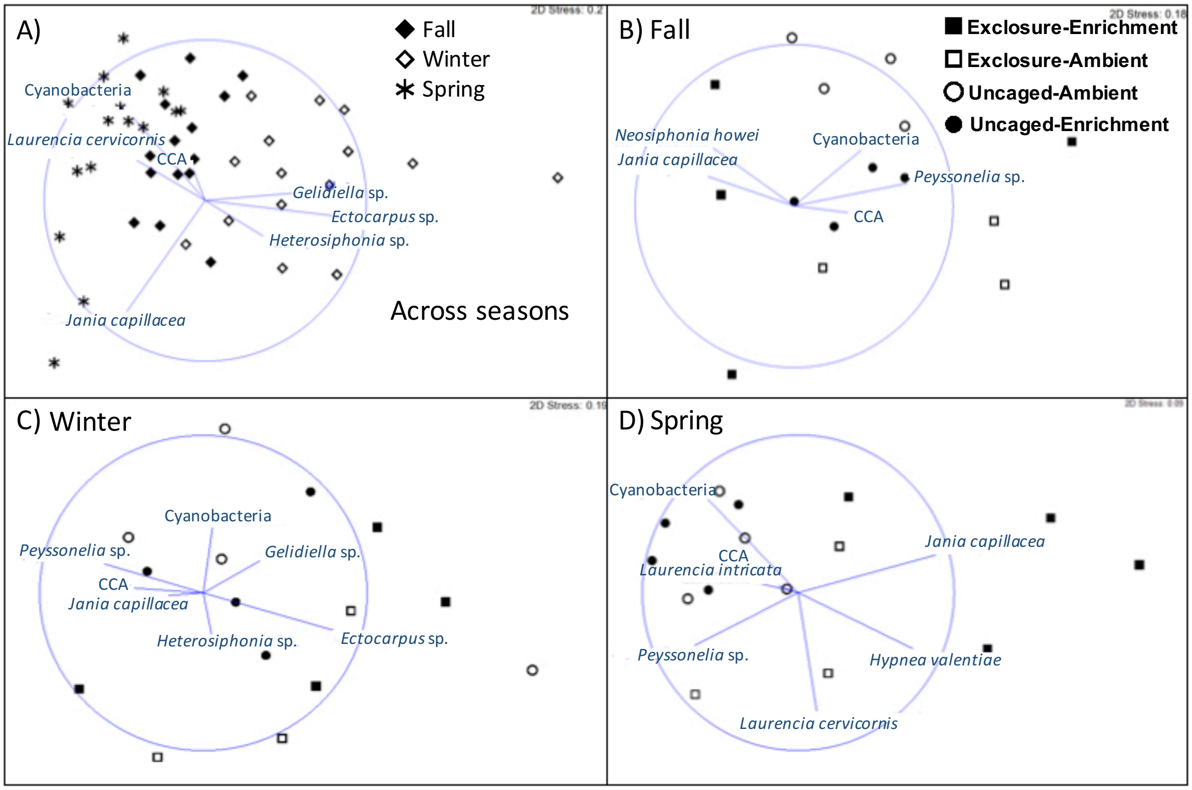

Figure 3. Abundance of macroalgal FFG on succession tiles by treatment in Winter (January) and Spring (June). Bars represent means ± SEM. Probability values (p) come from three-factor ANOVA for main treatment effects and significant interactions.

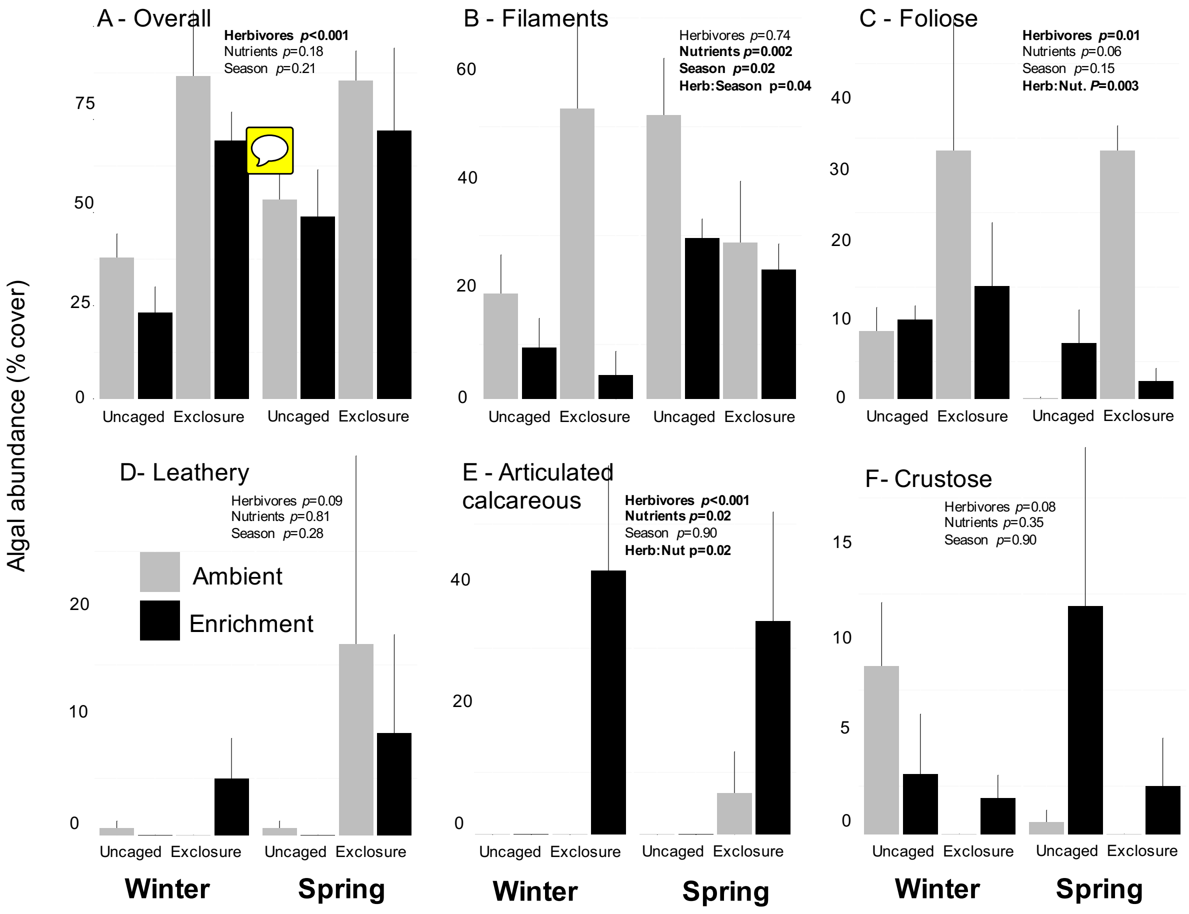

Figure 4. Non-metric Multidimensional Scaling analysis of algal cover on successional tiles using percent cover of form-functional groups among treatments in Winter and Spring.

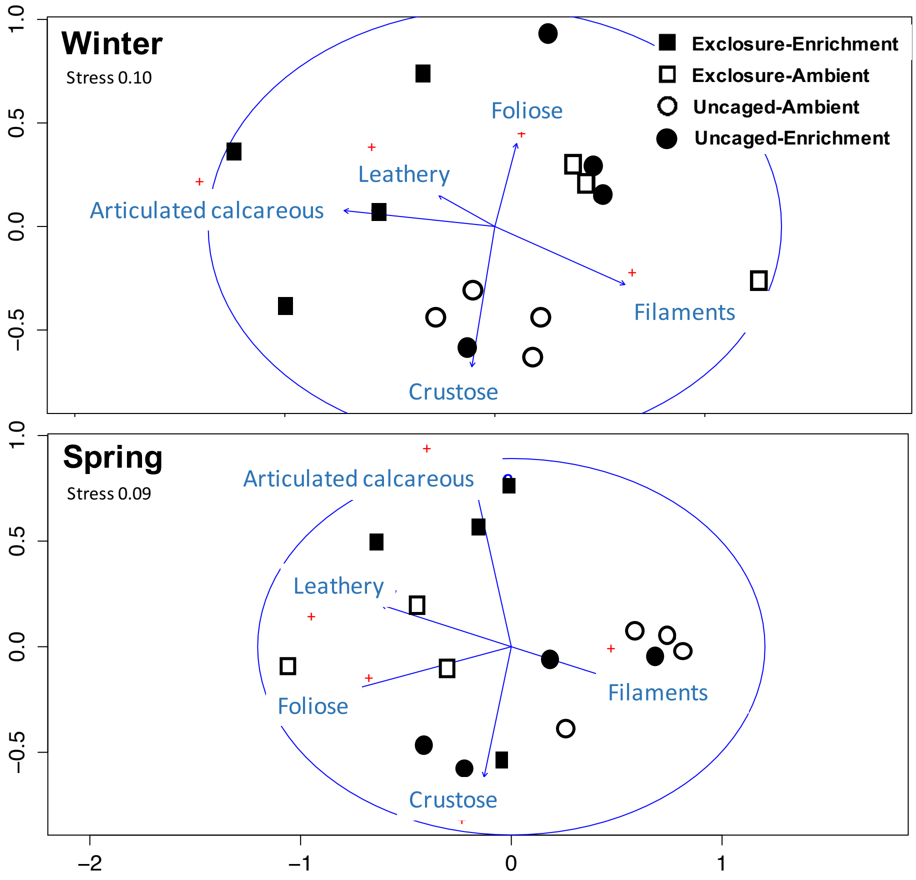

Figure 5. Abundance of macroalgal form-functional group on established communities by treatment in Winter and Spring. Bars represent means ± SEM. Probability values (*p*) come from three-factor ANOVA of main treatment effects and significant interactions.