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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. [b]

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2   succession in a Florida coral reef

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24   **Abstract.**

25   Herbivory and nutrient enrichment are drivers of benthic dynamics of coral reef

26   macroalgae; however, their impact may vary seasonally. In this study we evaluated the effects of

27   herbivore pressure, nutrient availability, and potential propagule supply on seasonal recruitment

28   and primary succession of macroalgal communities on a Florida coral reef. Recruitment tiles,

29   replaced every three months, and succession tiles, kept in the field for nine months, were

30   established in an ongoing factorial nutrient enrichment-herbivore exclusion experiment. The

31   ongoing field experiment had already created very different algal communities on the natural

32   reef benthos across the different herbivory and nutrient treatments. We tracked recruitment,

33   species richness, and species abundance of algae through time. Our results show seasonal

34   variation in the effect of herbivory and nutrient availability on recruitment of coral reef

35   macroalgae. In spring, when there was higher macroalgal species richness and abundance of

36   recruits, herbivory appeared to have more control on macroalgal community structure than did

37   nutrients. In contrast, there was no effect of either herbivory or nutrient enrichment on

38   macroalgal communities on recruitment tiles in fall and winter. The abundance of recruits on

39   tiles was positively correlated with the abundance of algae in the ongoing, established

40   experiment, suggesting that propagule abundance is likely a strong influence on algal recruitment

41   and early succession. Results of the present study suggest that abundant herbivorous fishes

42   control recruitment and succession of macroalgae in the warm season (spring and summer) when

43   there is stronger demand of nutrients and macroalgal growth is higher. However, herbivory

44   appears less impactful on algal recruitment and community dynamics in cooler seasons (fall and

45   winter). Ultimately, our data suggest that the dynamics of algae colonizing open space may be

46   strongly influenced by the timing of coral mortality (e.g. summer vs. winter mortality) and

47   freeing of benthic space.

48

49   **Introduction**

50   "Grazing ecosystems" are characterized by an herbivore-based food web where over 50%

51   of primary production is processed by aquatic or terrestrial grazers (McNauthon, 1985; Douglas

52   et al., 1998; Burkepile, 2013). Coral reefs are grazing ecosystems where herbivory and nutrient

53   availability are often considered the primary ecological drivers of macroalgal community

54   dynamics (Littler and Littler, 1984; McCook, 1999; Burkepile and Hay, 2006). Field experiments

55   excluding herbivores have resulted in a substantial increase of both biomass and density of some

56   macroalgal species, generating changes in species composition at the community level (Lewis,

57   1986; Burkepile and Hay, 2009; Ferrari et al., 2012).

58   Nutrient enrichment tends to have variable effects on macroalgal communities, possibly

59   linked to species-specific responses of macroalgae to nutrient availability (Larned, 1998; Fong et

60   al., 2001; Dailer et al., 2012). In particular, growth rates of some small, fast-growing species

61   quickly peak in nutrient enriched environments (Lapointe et al., 1997; McClanahan et al., 2004;

62   Smith et al., 2005). In contrast, larger slow-growing species, typical of late stages of macroalgal

63   community succession (e.g., *Sargassum* spp., *Amphiroa* spp.), often show weak or mixed effects

64   in nutrient enriched areas (McClanahan et al., 2004; Burkepile and Hay, 2009). However,

65   abundance of different macroalgal species can vary seasonally on reefs (Lirman and Biber, 200

66   Collado-Vides et al. 2005, 2007), which could explain the variable relative effect of herbivores

67   and nutrients on structuring macroalgal communities (Burkepile and Hay, 2006; Smith et al.,

68   2010).

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69   A number of factors may influence seasonality of algal communities on reefs including

70   seasonal changes in abiotic conditions (e.g. temperature and light; Clifton and Clifton, 1999), the

71   timing and intensity of disturbances (Diaz-Pulido and Garzon-Ferreria, 2000; Diaz-Pulido and

72   McCook, 2004; Goodsell and Connell, 2005) and propagule supply and recruitment

73   (McClanahan 1997; Diaz-Pulido and McCook, 2002, Walters et al., 2002, Vroom et al., 2003).

74   Increases in water temperature and light availability can promote macroalgal growth and trigger

75   reproduction in some species (Clifton 2008Collado-Vides et al., 2011). For example, both

76   *Dictyota pulchella* and *Sargassum* spp. show a peak of abundance during the summer and a loss

77   of biomass in the coolest seasons (Lirman and Biber, 2000; Renken et al., 2010). In contrast,

78   *Gracilaria* spp. and *Stypopodium zonale* rather exhibit higher abundance during cooler seasons

79   (Hay and Norris, 1984; Chung et al., 2007). In addition to influencing macroalgal growth rates,

80   temperature also influences the rate of herbivory in fishes with grazing rates often peaking

81   during warmer periods (Ferreira et al., 1998, Smith, 2008; Lefevre and Bellwood, 2010). Thus,

82   variation in abiotic controls of both algal growth rates and rates of herbivory across seasons

83   could result in temporal fluctuations of bottom-up and top-down forcing.

84   These seasonal differences in macroalgal growth and herbivory rates could affect how

85   disturbances to reefs impact macroalgal community development and succession. For example,

86   in reefs in the Florida Keys, both extreme warm water (Eakin et al., 2010) and cold water

87   (Lirman et al., 2011) anomalies can lead to coral mortality. Given that these disturbances open

88   up free space for macroalgal colonization during different times of the year with different abiotic

89   conditions, different species of algae may become dominant and drive different successional

90   trajectories depending on the timing of these disturbances and the initiation of algal succession.

91   Propagule abundance can also impact community dynamics by influencing the rates of

92   recruitment in marine organisms (Stiger and Payri, 1999; Lotze, Worm and Sommer, 2000;

93   Walters et al 2002, Grorud-Colvert and Sponaugle, 2009). The abundance of adult macroalgal

94   individuals, the number of propagules they produce, and the distance to a suitable substrate for

95   colonization can determine the number of macroalgal recruits in a given area (Kendrick and

96   Walker 1995, Stiger and Payri 1999, Lotze, Worm and Sommer, 2000, Yniguez *et al* 2015).

97   Thus, abundant adult macroalgae might increase local macroalgal recruitment, especially after

98   relatively localized disturbances such as coral mortality events (Walters *et al*. 2002, Roff and

99   Mumby, 2012). Consequently, increases in macroalgae due to reductions in herbivory or

100   increases in nutrient availability could lead to increased macroalgal propagule supply and a

101   positive feedback on macroalgal abundance. Yet, no studies have directly addressed how

102   seasonality and propagule supply interact with herbivory and nutrient availability to impact

103   macroalgal community development and succession on coral reefs.

104   In the current study, we tested how both nutrient availability and herbivory varied across

105   seasons as drivers of recruitment and succession of a coral reef macroalgal community. We used

106   coral limestone tiles as primary substrate in a factorial field experiment, previously established

107   for two years, manipulating access by herbivorous fishes and nutrient availability to examine the

108   effects of herbivory, nutrient enrichment, and macroalgal abundance on algal recruitment

109   patterns and primary succession across seasons. We quantified algal abundance and diversity on

110   both primary substrate and the established macroalgal communities regularly over nine months.

111   We predicted that macroalgal recruitment would be higher in areas with greater adult macroalgal

112   abundance because adult macroalgae act as propagule supply source; and because herbivores

113   consume late successional species, usually large palatable species, herbivory would be the main

114 driver of macroalgal communities at late successional stages. In addition, we hypothesized that

115 the effect of both nutrient availability and herbivory would be reduced in cooler seasons because

116 lower temperature and less light availability reduce rates of macroalgal growth and at low

117 temperature herbivory rates are typically lower.

118

119 **Materials and methods**

120 *Study site and experimental design*

121 This study was conducted from September 2011 to June 2012 on a spur and groove reef

122 system located in the upper Florida Keys near Pickles Reef (25°00'05"N, 80°24'55"W) with the

123 approval of the Florida Keys National Marine Sanctuary (FKNMS-2009-047 and FKNMS-2011-

124 090). The reef is a shallow area (5-6m) where parrotfishes and surgeonfishes are the dominant

125 herbivorous fishes and the long-spined urchin, *Diadema antillarum,* is present at very low

126 densities (<1 individual per 50m^2, authors' pers. obs.). Water temperature oscillates seasonally

127 from ~ 24 °C in winter (December and January) to over 30 °C during summer (Appendix I).

128 In June 2009, eight 9m^2 experimental plots (3x3m) were established to examine the

129 interactive effects of herbivory and nutrient availability on benthic community dynamics

130 (Zaneveld et al. 2016). Plots were separated by at least 5m. Each 9m^2 plot contained two

131 quadrats (1x1m^2) for herbivore exclusion (exclosure), covered with plastic-coated wire mesh

132 (2.5cm diameter holes) around a 0.5m high metal bar frame. Two other quadrats (1x1m^2) were

133 used as herbivore exclusion controls (uncaged) that had metal bar frames with only three sides

134 covered with wire mesh to allow access to all herbivores. As part of the ongoing experiment on

135 the benthos, a third (completely open, no sides or top) control was also used and showed no

136   differences in algal communities between the exclusion controls and completely open areas

137   (Zaneveld et al., 2016)

138   To mimic nutrient loading, four of the eight 9m^2 experimental plots were enriched with

139   Osmocote (19-6-12, N-P-K) slow-release garden fertilizer. The Osmocote (175g) was placed in 5

140   cm diameter PVC tubes with 10 (1.5cm) holes drilled into them. These tubes were wrapped in

141   fine plastic mesh to keep the fertilizer inside and attached to a metal nail within the plot for a

142   total of 25 enrichment tubes spread evenly across each enrichment plot. Enrichment tubes were

143   replaced every 4-6 weeks to ensure continual nutrient addition. The other four 9m^2 plots were

144   kept at ambient nutrient conditions. Yearly sampling of water column nutrients of each

145   experimental plots (Summer 2009, 2010 and 2011) showed that this enrichment increased both

146   dissolved inorganic nitrogen (3.91μM vs. 1.15μM in enriched vs. ambient) and soluble reactive

147   phosphorus (0.27μM vs. 0.035μM in enriched vs. ambient) in the water column (for detailed

148   methods see Vega Thurber et al., (2014)). Additionally, nitrogen concentration in the tissues of

149   the common alga *Dictyota menstrualis* collected from each plot every year (Summer 2009, 2010

150   and 2011) was 20% higher in the enriched plots compared to the control plots, suggesting that

151   the nutrients from the enrichment were consistently available to benthic organisms (Vega

152   Thurber et al., 2014). The levels of DIN and SRP in the enriched treatment were similar to those

153   reported from other anthropogenic-impacted reefs located around the world (Dinsdale et al.,

154   2008).

155   Ambient nutrient values were obtained from the SERC-FIU Water Quality Monitoring

156   Network, data from this network is open to the public (http://serc.fiu.edu/wqmnetwork/FKNMS-

157   CD/DataDL.htm). Levels of both dissolved inorganic nitrogen (DIN) and soluble reactive

158   phosphorus (SRP) in the ambient nutrient plots were within the range of concentrations for

159   offshore reefs in the Florida Keys (Boyer & Briceño, 2010). Water quality data from a nearby

160   reef (Molasses Reef) shows a high variability of nutrient concentration along the years.

161   Particularly, during the study period, ambient levels of DIN (mean 0.58 μM, max 0.87 μM) and

162   SRP (mean .038 μM, max 0.070 μM) were consistently lower than the enrichment treatments

163   (Appendix I). (The highest values of DIN, SRP and temperature were reported for the end of

164   May 2012 and lower values were detected in April 2011 for DIN and December 2011 for SRP,

165   while temperature had its lowest in December 2011 (Appendix 1).

166   *Fish community structure*

167   To estimate the intensity of herbivore pressure, fish community structure was evaluated

168   four times during the study period (September, 2011; January, 2012; April, 2012 and July 2012)

169   using 30x2m belt transects (n=12) placed haphazardly across the study site following AGRRA

170   methodology (Protocols Version 5.4; Lang et al., 2010). All individuals of all fish species

171   included in the AGRRA protocol were identified and size estimated to the nearest cm by same

172   diver. Size estimates were converted to biomass for each individual fish using published length:

173   weight relationships (Bohnsack and Harper, 1988). We did not quantify abundances of the urchin

174   *D. antillarum* as they have been rare across the Florida Keys (Chiappone et al., 2002; 2008) and

175   they have been very infrequently seen at our field site since the establishment of the experiment

176   in 2009 (D. Burkepile *pers. obs.)*.

177   *Recruitment of macroalgae on primary substrate*

178   To study macroalgal recruitment across different seasons in the different treatments, we

179   placed two coral limestone settlement tiles (10x10cm; cut from quarried South Florida

180   Pleistocene limestone) in each of the two exclosure and uncaged quadrats within every 9m^2 plot

181   (n=64 tiles total) in September 2011. We did not put tiles in completely open areas as data from

182　the main experiment showed that the macroalgal communities in the uncaged and completely

183　open areas did not differ (Zaneveld et al., 2016). The tiles were attached to plastic mesh with

184　cable ties and anchored to the benthos using 1.9 cm galvanized staples. These tiles (hereafter

185　'recruitment tiles') were collected after three months and replaced with new tiles to quantify

186　recruitment and early succession during each season. These deployments resulted in a total of

187　three separate sets of data on macroalgal recruitment across different seasons: fall (September-

188　December 2011), winter (December 2011-March 2012) and spring (March-June, 2012). A

189　tropical storm in summer 2012 removed much of the experimental infrastructure precluding data

190　from the planned summer period.

191　　　After three months in the field, recruitment tiles were transported to the laboratory where

192　algae were identified to the lowest possible taxonomic level (Appendix II). Their percent cover

193　was visually quantified using a rule to measure percent cover of each algal individual.

194　Abundance of each species was classified from 0.1 (single individual < 0.5% cover), 0.5 (less

195　than three sparse individuals and < 1% cover), 1 (few individuals and <5% cover), and then 5 to

196　100 with multiples of 5 by the same trained specialist. If a single individual covered 10% of the

197　tile, then that individual got a 10% cover. If a single individual was present but below 1% cover,

198　it was scored as 0.1 or 0.5 % cover depending upon size. The recruitment tiles were then placed

199　in individual separate aquaria to avoid possible propagule contamination. Each tank was

200　prepared to replicate the field conditions as closely as possible (salinity: 35-36 ppt using artificial

201　seawater, temperature: 25-28ºC, constant water circulation, and artificial high output white light

202　with 12:12 day-night cycle). Initial water was filtered and then the tanks were re-fill with

203　artificial water (Instant ocean) to avoid propagule contamination from the ocean. We kept the

204　tiles in their corresponding aquaria for three months to promote growth of macroalgal recruits

205   that were unidentifiable in our immediate evaluation due to their small size or lack of identifiable

206   traits. After this period, all macroalgal species were re-identified and any new contribution was

207   added to the species list.

Succession of macroalgal communities on primary substrate

209   In September 2011, we also placed a second set of two coral limestone settlement tiles

210   (10x10cm) (hereafter 'succession tiles') in each exclosure and uncaged quadrat (n=64 tiles total).

211   Succession tiles were kept in the field from September 2011 to June 2012. Macroalgal

212   abundance was visually quantified on succession tiles *in situ* in January and June 2012 using the

213   same method described above. Macroalgae were identified to the lowest taxonomic level

214   possible and also binned into form-functional groups (FFG) following Steneck and Detheir

215   (1994).

Established macroalgal communities

217   Algal abundance of established communities showed significant differences in the

218   benthic macroalgal community composition across the different treatments (Zaneveld et al.

219   2016). These differences in the abundance and community composition of algae could have

220   resulted in differing levels of propagule abundance across treatments, an important factor

221   potentially affecting recruitment and succession on primary substrate in our study. To evaluate

222   the potential propagule supply of each established community, macroalgal abundance was

223   visually quantified within each exclosure and uncaged quadrat in January and June 2012 using

224   the percent cover scale and FFG classification as described above.

Statistical analyses

226   Average values of biomass, density and percent cover are followed by calculated

227   standard error. Biomass and density of total and herbivorous fish were compared across seasons

228   using a one-factor ANOVA. For statistical analyses of the different macroalgal community

229   metrics of recruitment and succession tiles, we averaged data from the two tiles located within

230   each exclosure and uncaged quadrat. For recruitment tiles, succession tiles, and established

231   communities we averaged metrics of the two exclosure quadrats and two uncaged quadrats of

232   each plot such that n=4 for each treatment except for the ambient-exclosure treatment where n=3

233   due to losing exclosures in one plot in May 2012 during a storm.

234   To test for the effects of herbivores, nutrient enrichment, season, and their interactions on

235   algal species richness and overall macroalgal abundance of recruitment tiles, we used a split plot

236   ANOVA with herbivory treatments as subplots nested within nutrient treatment plots, when there

237   were significant treatment X season interactions, we used split plot ANOVA to assess treatment

238   effects (i.e. nutrient enrichment and herbivore exclosure) within different seasons. Post-hoc

239   analysis Tukey HSD was used to test for differences across season. We used non-metric multi-

240   dimensional scaling (nMDS) and permutational MANOVA (PERMANOVA) to assess the

241   effects of treatments and seasonality on macroalgae community composition of recruitment tiles.

242   We used a similarity percentage analysis (SIMPER) to assess how different species contributed

243   to differences in community structure across treatments. To assess variability in abundance of

244   most common species across treatments and seasons, we used split plot ANOVAs or non-

245   parametric tests when data did not satisfy assumptions for parametric tests.

246   To test the effects of herbivory, nutrient availability, and season on overall algal

247   abundance and the abundance of different FFG or both successional tiles and established algal

248   communities, we used a split plot ANOVA, with herbivory treatments as subplots nested within

249   nutrient treatment plots. To test the effects of treatment on community succession, a non-metric

250   multi-dimensional scaling (nMDS) and a PERMANOVA were performed on the abundance of

251   all FFG analyzed seasonally. To examine how macroalgal abundance in the established

252   communities (potential propagule supply) impacted macroalgal recruitment, we used a Pearson

253   correlation to assess the relationship between FFG abundance of established communities and

254   both, succession tiles and recruitment tiles, in both winter and spring. We performed descriptive

255   and inferential analyses using packages Vegan, doBy, MASS and ggplot2 from R program

256   created by R Development Core Team (2012), version 3.2.2.

257

258   **Results**

259   *Fish community structure*

260   Overall fish mean biomass and density at the study site were 6495.60 ± 508.10 g/100m^2

261   (mean $\pm$ SE; data presented as such hereafter) and 39.93 ± 3.20 Ind./100m^2, respectively.

262   Herbivores (family Scaridae and Acanthuridae) comprised 78% of overall fish biomass with an

263   average of 5087.17 ± 569.50 g/100m^2 and 74% of overall fish density 29.93 ± 2.10 Ind./100m^2.

264   Total biomass of parrotfish and surgeonfish were 2771.65 ± 526.60 g/100m^2 and $2315.52 \pm$

265   370.60 g/100m^2, respectively. We saw no temporal changes in biomass or density of total and

266   herbivorous fish as no significant differences were found among seasons (One-factor ANOVA,

267    $p>0.05$ in all cases, Appendix III).

268   *Recruitment of macroalgae on primary substrate (recruitment tiles)*

269   We identified 101 macroalgal taxa (Appendix II) including field and laboratory

270   observations. Macroalgal species richness on recruitment tiles increased across seasons,

271   averaging 9.73 ± 0.63 species per tile in fall, 12.13 ± 0.79 in winter, and 14.40 ± 1.19 in spring

272   (split plot ANOVA, Season, $p=0.003$). Neither nutrient enrichment nor herbivore exclosure had

273   an independent or interactive effect on species richness of recruitment tiles (Appendix II).

274 Overall abundance of macroalgae on recruitment tiles was twofold higher in spring (116.12 ±

275 9.50%) compared with fall (60.00 ± 7.48%) and winter (51.77 ± 6.31%) regardless of treatment

276 (Figure 1, split plot ANOVA, Season, p=0.02). Across seasons the combination of herbivore

277 exclosure and nutrient enrichment had significant impact with noticeable increase in macroalgal

278 abundance compared to other treatments (Figure 1; Appendix III).

279 Macroalgal assemblages on recruitment tiles were different across seasons (nMDS,

280 Figure 2, PERMANOVA, Season: pseudo F= 7.68, p=0.01). Only four groups were present in all

281 seasons (crustose coralline algae (CCA), Cyanobacteria, *Jania capillacea* and *Peyssonnelia* spp.)

282 but with dissimilar abundances (Table 1). There was a peak of cyanobacteria in spring while the

283 abundance of *Peyssonnelia* spp. was four times higher during fall and spring compared to winter

284 (Table 1). Other species such as *Ectocarpus* sp., *Gelidiella* sp. and *Heterosiphonia* sp. increased

285 their abundance in winter although abundance of both *Laurencia* species peaked in spring (Table

286 1). There was an effect of herbivore exclosure and a significant interaction between herbivore

287 exclosure and season in driving differences in community composition on recruitment tiles

288 (PERMANOVA, Herbivore: pseudo F= 3.94, p=0.01 and Herbivory:Season interaction: pseudo

289 F= 2.15, p=0.01, respectively). Analyses within season showed a clear effect of herbivore

290 exclosure and nutrient enrichment in spring which seems to be stronger when both are combined

291 as shown in the nMDS analyses (Figure 2; PERMANOVA, Herbivory: pseudo F= 6.16, p=0.01

292 and Nutrient: pseudo F= 3.08, p=0.04, respectively).

293 *Succession of macroalgae on primary substrate (succession tiles)*

294 Excluding herbivores from succession tiles during the study period led to almost double

295 overall macroalgal cover (77.29±7.29%) compared to uncaged tiles (40.84 ± 5.22%; split plot

296 ANOVA, Herbivory, p=0.03), while no other factors showed significant effects (Figure 3;

297 Appendix II). Filamentous algae increased abundance in spring with 33.83±4.58% and was

298 negatively affected by nutrient enrichment (Figure 3, split plot ANOVA, Nutrient, *p*=0.05).

299 Herbivory exclusion in ambient nutrient plots increased abundance of filamentous algae in

300 winter while decreased it in spring (Figure 3, split plot ANOVA, Herbivory:Nutrient:Season

301 interaction, *p*=0.03). Abundance of foliose macroalgae (e.g. *Dictyota* spp.) increased when

302 herbivores where excluded (Figure 3; split plot ANOVA, Herbivory, *p*=0.03), there was a trend

303 towards nutrient enrichment decreasing foliose macroalgae (Figure 3; split plot ANOVA,

304 Nutrient interaction, *p*=0.08). Leathery algae (e.g. *Sargassum* spp.) increased in June (Figure 3,

305 split plot ANOVA, Season, *p=0.05*) and were almost exclusively present in herbivore

306 exclosures, although their abundance was variable and we did not detect any significant

307 statistical effect of exclosures (Figure 3). Articulated calcareous algae (e.g. *Jania* spp. and

308 *Amphiroa* spp.) were only present in exclosure treatments (Figure 3) showing a strong effect of

309 herbivore exclusion (the split plot ANOVA did not pick up this signal likely due to all zeros in

310 the uncaged areas). Nutrient enrichment also facilitated articulated calcareous algae with a trend

311 towards higher abundance in nutrient enriched herbivore exclosures (Figure 3, split plot

312 ANOVA, Herbivory:Nutrient interaction, *p*=0.06). In both winter and spring, the nMDS analysis

313 showed herbivore exclosure had significant effects on the FFG composition of macroalgal

314 communities (Figure 4, PERMANOVA, Herbivory: pseudo F = 8.96; *p*=0.01, pseudo F = 3.46,

315 *p*=0.03 respectively). However, there was an effect of nutrient enrichment only in January

316 (Figure 4, PERMANOVA, Nutrient: pseudo F = 2.84; *p*=0.03).

317 *Established macroalgal communities*

318   Overall macroalgal abundance of established communities was over twofold higher in

319 spring with 84.3 ± 7.76% compared to winter 39.36 ± 7.55% (Figure 5, split plot ANOVA,

320   Season, $p=0.05$). Herbivore exclosures had two fold higher algal cover (Figure 5, split plot

321   ANOVA, Herbivory, $p=0.006$) than uncaged treatment while there was no effect of nutrient

322   enrichment (Figure 5, Appendix III). Filamentous algae were the only macroalgal group that

323   showed a seasonal increase from winter to spring on established communities (Figure 5, split

324   plot ANOVA, Season, $p=0.04$). The three groups of upright macroalgae: foliose, leathery and

325   articulated calcareous algae were more abundant in herbivore exclosures (Figure 5). Leathery

326   macroalgae were practically only found in herbivory exclosure treatments regardless of nutrient

327   treatment (Figure 5). Furthermore, articulated calcareous algae (e.g. *Jania* spp. and *Amphiroa*

328   spp.) were much more abundant inside exclosures when combined with nutrient enrichment in

329   both winter and spring compared to ambient nutrient levels (Figure 5, split plot ANOVA,

330   Herbivory:Nutrient interaction, $p=0.056$).

331   There were significant positive correlations of algal abundance of established

332   communities with algal abundance found on recruitment and succession tiles for some algal

333   groups (Table 2). The abundance of leathery macroalgae on established communities was

334   correlated with the corresponding abundances of each treatment found on recruitment tiles in

335   winter (Pearson correlation, $r=0.97$, $p=0.03$) and with abundance of succession tiles in spring

336   (Pearson correlation, $r=0.95$, $p=0.05$). Articulated calcareous algae was the only algal group that

337   showed correlations between established communities and corresponding recruitment and

338   succession tiles in both seasons (Table 2).

339

340   **Discussion**

341   Here, we show that the impact of herbivory and nutrient availability on recruitment of

342   coral reef algae changes across seasons. We observed an increase in species richness and

343   abundance of macroalgal recruits towards the warmer (appendix I) season (spring), with recruit

344   abundance noticeably higher when combining reduced herbivory and nutrient enrichment.

345   However, herbivory primarily drove macroalgal abundance and the trajectory of succession over

346   longer time periods, with higher algal abundance for some groups of macroalgae (e.g. articulated

347   calcareous algae) under elevated nutrient conditions. We also found positive correlations

348   between algal abundance in established communities and algal abundance on both recruitment

349   and successional tiles. These data suggest an important role of propagule supply in influencing

350   algal recruitment and succession. Ultimately, the impact of herbivores and nutrient availability

351   on macroalgal recruitment and succession varied across functional groups of algae and seasons,

352   with herbivory the strongest force in warmer seasons while nutrient availability showed the

353   strongest effects in cooler seasons.

354   Macroalgal communities on coral reefs can show noticeable temporal changes in species

355   composition and abundance, associated with abiotic (e.g. temperature, light) and biotic factors

356   (Tsai et al., 2005; Renken et al., 2010; Page-Albins et al., 2012). Some common species in the

357   Caribbean such as *Dictyota* spp. and *Halimeda* spp. increase in abundance during summer, often

358   covering over 50% of the benthos, while others (e.g. turf-forming species) are more abundant

359   during cooler periods of the year (Lirman and Biber, 2000; Renken et al., 2010; Ferrari et al.

360   2012). In our study we found an increase in overall abundance of macroalgal recruits towards

361   spring with distinct species flourishing within treatments. For instance, recruitment of *Jania*

362   *capillacea* and *Hypnea spinella* was higher in spring but mostly within exclosures, which

363   suggests the strong control of herbivory of both species. Both *Laurencia cervicornis* and *L.*

364   *intricata* increased in abundance in spring. However, *L. cervicornis* was abundant in uncaged

365   treatments while *L. intricata* was abundant in exclosure treatments. Some species of *Laurencia*

366   are chemically defended against herbivores (Nagle and Paul, 1998; Pereira, Cavalcanti and

367   Texeira, 2000), which could explain the proliferation of some *Laurencia* spp. in the presence of

368   herbivores. In contrast, the abundance of small filamentous algal species commonly consumed

369   by herbivorous fish (e.g. *Ectocarpus* sp., *Gelidiella* sp. and *Heterosiphonia* sp.) increased in

370   winter when other studies have shown that grazing rates often decline (Ferreira et al., 1998;

371   Lefevre and Bellwood, 2010). Indeed, we saw an interaction between herbivory and season on

372   community composition suggesting that herbivores have stronger effects on algal recruitment

373   during warmer periods (spring and summer). Since recruitment of corals is often higher during

374   spring and summer (van Woesik et al., 2006), the strong top-down control of algal recruitment

375   during this period could indirectly enhance coral recruitment by freeing space for corals.

376   Herbivory may have been less important in colder seasons due to lower grazing rates combined

377   with lower recruitment rates and slower growth rates of algae.

378   Succession in the absence of herbivores is expected to follow a trajectory characterized

379   by replacement of early, fast growing species (e.g., *Enteromorpha* sp. *Ceramium* sp., *Felmania*

380   sp.) by late successional species such as leathery and calcareous articulated species

381   (McClanahan, 1997). Our results show that nutrient enrichment and herbivore exclosure interact

382   to drive macroalgal succession at early stages (four months), while herbivory appears more

383   important at later stages. After four months, filamentous and foliose algae increased inside

384   exclosures with ambient nutrient levels, while leathery and articulated calcareous flourished in

385   exclosures with nutrient enrichment. After nine months, species considered later successional

386   species (e.g. *Sargassum* sp. and *Amphiroa* sp.) were present almost exclusively on succession

387   tiles in exclosures regardless of nutrient enrichment. These results suggest that nutrient

388   availability facilitates the rapid colonization and growth of leathery and articulated calcareous

389   algae. But, over the long term, herbivory is the primary driver of their abundance. Other studies

390   have shown that nutrient loading does not affect macroalgal species composition at late

391   successional stages but facilitates abundance of early successional species such as turf forming

392   algae and cyanobacteria (McClanahan et al., 2007). In our study we found that both nutrient

393   availability and herbivory are significant drivers at early successional stages, whereas nutrient

394   showed significant effect over later successional stages only when herbivores were excluded.

395   Competition among algae may also be important for determining successional

396   trajectories, especially when herbivory is low. Macroalgal communities on succession tiles

397   within herbivore exclosures were dominated by calcareous articulated and leathery species by the

398   end of the experiment. These species appeared to replace *Dictyota* spp. and other foliose and

399   filamentous algae, especially under nutrient enrichment, suggesting that these late successional

400   species are better competitors in absence of herbivores. Thus, selective grazing by herbivores on

401   more palatable species (e.g. articulated calcareous) might facilitate the colonization and

402   establishment of less palatable foliose algae. Coral reef herbivores often consume macroalgal

403   species of late successional stages such as leathery (e.g. *Sargassum* spp. and *Turbinaria* spp.)

404   and calcareous articulated (e.g. *Amphiroa* spp., *Halimeda* spp. and *Jania* spp.) (Lobel and

405   Ogden, 1981; Burkepile and Hay, 2008; Hoey and Bellwood, 2011), keeping macroalgal

406   communities in stages of early succession. Hixon and Bostroff (1996) found similar results

407   where removal of grazers led to a rapid shift from green and brown filamentous algae to finely

408   branched filaments followed by species forming thicker filaments (e.g. *Tolypocladia*

409   *glomerulata*). Similarly, Thacker et al. (2001) reported a community shift from unpalatable to

410   palatable species of algae when herbivores were excluded from coral reefs on Guam. This

411   pattern is also common in terrestrial ecosystems where selective herbivores target palatable, but

412   often competitively superior plant species, and release unpalatable species from competition

413   (Briske and Hendrickson, 1998; Torrano and Valderrabano, 2004).

414   We found that macroalgal abundance on recruitment and succession tiles was correlated

415   with abundance of algae in established communities, which suggests that local propagule supply

416   from the established community may impact early community development. However, we could

417   not conclusively say that recruits were from local sources (i.e. from algae within exclosures) as

418   opposed to from sources from greater distance. In temperate marine communities, particularly

419   for fast-growing species of macroalgae (e.g. *Cladophora* sp., *Polysiphonia* sp. and *Ceramium*

420   sp.), propagule abundance has been proposed as one of the main drivers of macroalgal

421   population growth (Worm and Lotze, 2006; Karez et al., 2004). However, further studies are

422   needed to evaluate spatial and temporal variation of algal propagule supply and subsequent algal

423   settlement in relation to herbivory and nutrient levels. For instance, since herbivores feed on

424   adult macroalgae as well as recruits they might be controlling algal recruitment and abundance at

425   multiple stages of the algal life cycle. Further, different species of herbivores could be important

426   for controlling the same algal species at different life stages as some herbivorous fishes tend to

427   focus more on early successional algae and would be more likely to consumer algal recruits

428   while other herbivorous species focus on late-successional algae (Burkepile and Hay, 2010).

429   The combined effects of herbivore exclosure and nutrient enrichment showed strong

430   effects on abundance of macroalgae on recruitment tiles, particularly during the warmer seasons.

431   This result suggests that reefs that are both overfished (low herbivorous fish biomass) and have

432   high nutrient loading will have higher recruitment of algae during spring and summer. These

433   higher recruitment rates may mean that these reefs are more likely to undergo regime shifts or

434   state changes to communities with abundant algae when corals die. The impacts could be

435   magnified if coral mortality occurs primarily in warmer seasons when herbivorous fishes are the

436   most important for impacting algal recruitment. It is expected that bleaching events caused by

437   increasing water temperature in the Florida Keys will increase in intensity and frequency

438   (Manzello, 2015). Severely bleached corals can be quickly colonized by algae (Diaz-Pulido and

439   McCook, 2002) that once settled can used existing higher nutrient availability to growth and

440   develop. Thus, protecting herbivores is crucial to facilitate control of macroalgal recruits that can

441   settle on recently dead corals during these summer events. In addition, warmer seasons of the

442   Florida Keys coincide with increases in both DIN and SRP (Appendix I) which might exacerbate

443   the impact of other ecological stressors during warmest seasons (Vega et al., 2014). Increases of

444   nitrogen and phosphorus can enhance growth rate of algae and consequently facilitate algal

445   dominance in low herbivory reef. Thus, overfished reef can quickly undergo algal succession

446   with rapid dominance of foliose and filamentous algae, overfished and nutrient enriched reefs

447   can rapidly increase abundance of leathery and articulated calcareous algae when space is

448   available. While filamentous and foliose algae can reduce coral recruitment and harm small adult

449   colonies, leathery and articulated calcareous algae can in addition shade and physically harm

450   colonies by abrasion (McCook et al., 2001). Thus, overfishing herbivores and nutrient pollution

451   can have strong impact on algal succession and, ultimately, their interactions with corals.

452

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459

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663   pollution, and thermal stress interact to disrupt coral reefs to microbial scales. Nature
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666 Table 1. Abundance of dominant macroalgal taxa found on recruitment tiles per season. Statistics
667 column refers to analysis performed to compare abundance of specific taxa across season (F and
668 *p* from one-factor ANOVA and N/A and *p* from Friedman test). Different letters indicate post
669 hoc analysis (SNK or Wilcoxon pair analysis) when abundance differed across seasons.
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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

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686 Table 2. Pearson correlation between algal form functional group (FFG) abundance on
687 recruitment or succession tiles and abundance of algal FFG in established communities for
688 winter and spring. Bolded values show significant effects.
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Season	FFG	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

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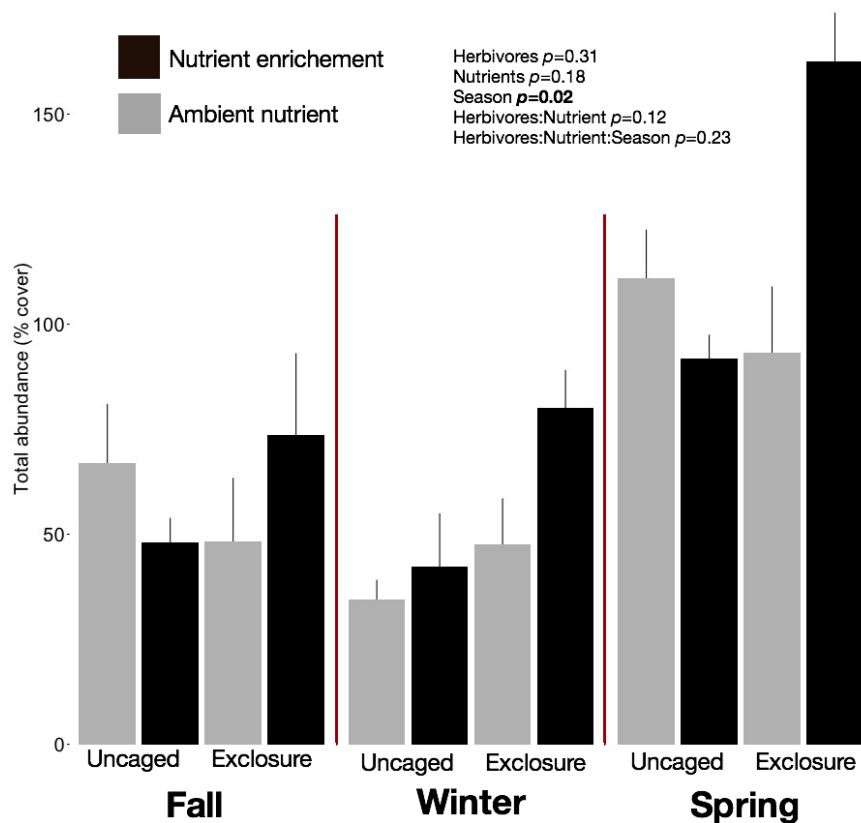696
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Figure 1. Overall abundance of macroalgae on recruitment tiles by treatments within each season. Bars represent means ± SEM. Probability values (*p*) come from Split plot ANOVA of main treatment effects. Red lines help to distinguish bars across seasons. With right side for winter and left side for spring
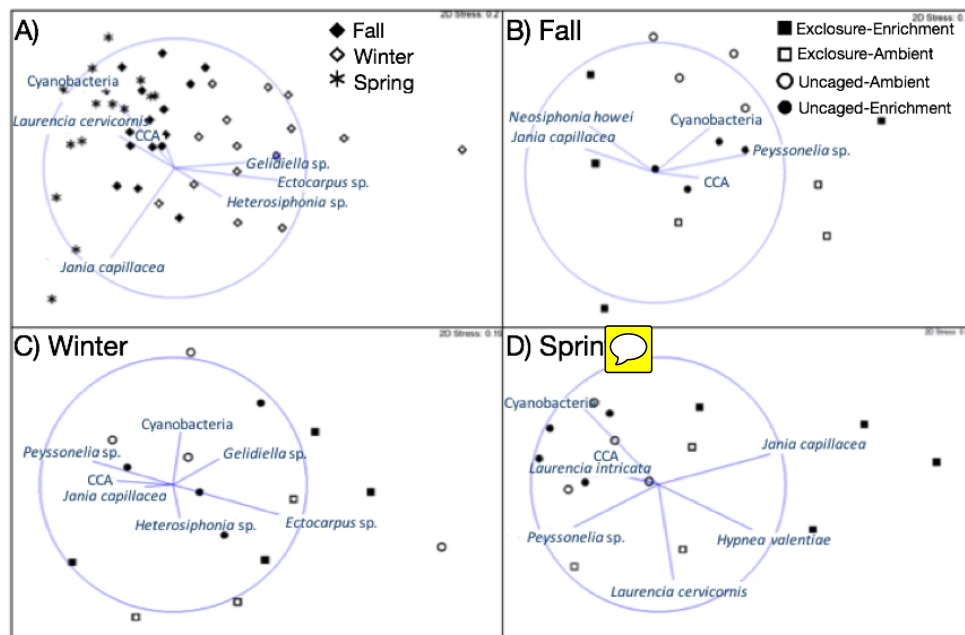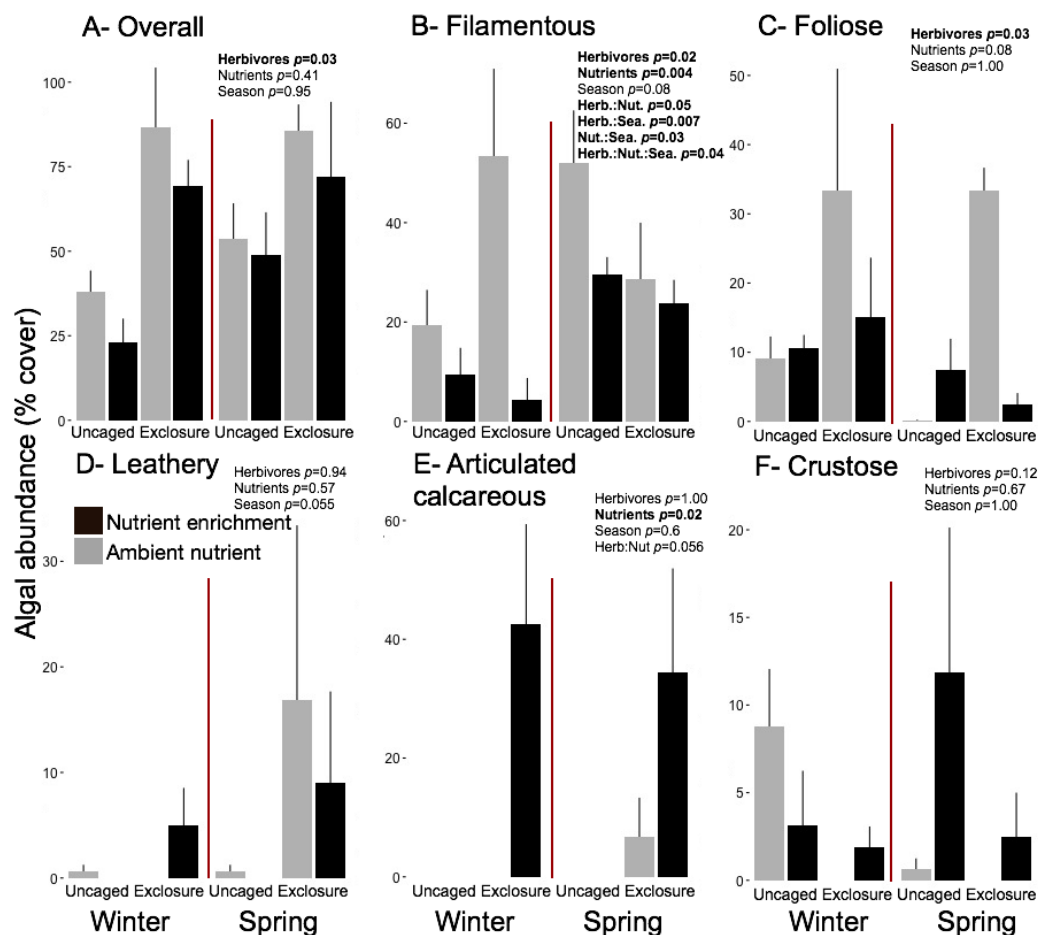
Figure 2. Non-metric Multidimensional Scaling analysis of algal abundance in communities on recruitment tiles across seasons (A) and in each treatment by season (B-D).

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736　Figure 3. Abundance of macroalgal FFG on succession tiles by treatment in Winter (January)
737　and Spring (June). Bars represent means ± SEM. Probability values (*p*) come from Split plot
738　ANOVA for main treatment effects and significant interactions. Red lines help to distinguish
739　bars across seasons with right side for winter and left side spring
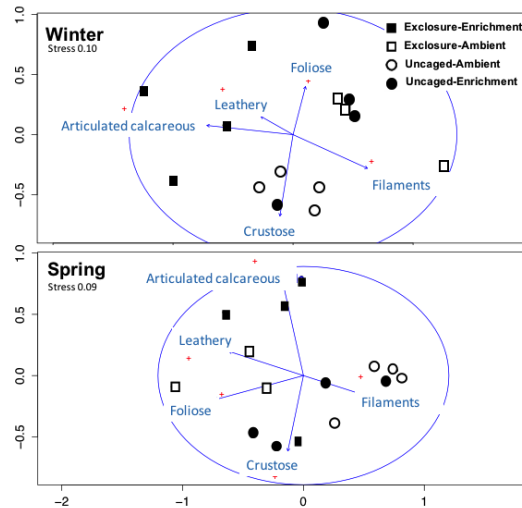740
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749   Figure 4. Non-metric Multidimensional Scaling analysis of algal cover on successional tiles
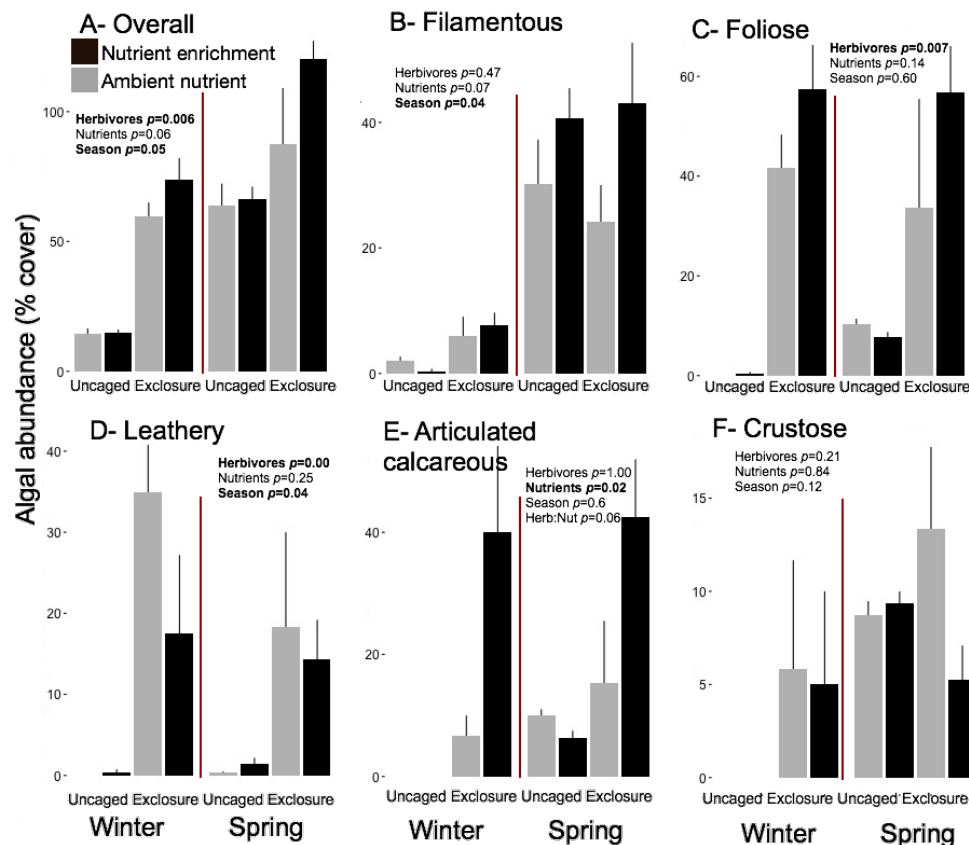750   using percent cover of form-functional groups among treatments in Winter and Spring.
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754 Figure 5. Abundance of macroalgal form-functional group on established communities by
755 treatment in Winter and Spring. Bars represent means ± SEM. Probability values (p) come from
756 Split plot ANOVA of main treatment effects and significant interactions. Red lines help to
757 distinguish bars across seasons with right side for winter and left side for spring
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