1 **Decoupling seasonal and temporal dynamics of macroalgal canopy**

2 **cover in seagrass beds**

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13 **Running title:** temporal trends in seagrass habitats

14 ABSTRACT

15 Many seagrass habitats are susceptible to undesirable macroalgal overgrowth in response to

16 growing watershed development, but the mechanisms leading to overgrowth remain unresolved.

17 Partitioning the influences of intermittent seasonal cycles and directional human stressors is one

18 main challenge. We examined the dynamics of macroalgal canopies within *Halodule uninervis*

19 beds across a 10-year period in a tropical lagoon and first hypothesized that seasonal and temporal

20 variances were distinguishable. We found that cooler and dryer winter months were consistently

21 associated with blue-green algal canopies, mainly *Lyngbya* sp. and *Phormidium* sp., with an

22 inverse relationship between sea-surface temperatures and coverage. For example, given that

23 winter temperatures during the coolest month of February ranged between ±1.0 °C of the mean

24 over the past decade, the expected coverage of blue-green algae shifted by ± 15%. In contrast, the

25 warmer and wetter summer months were associated with red algae canopies, predominantly

26 *Acanthophora spicifera*, which were positively related to rainfall. Last, a weaker seasonal trend

27 existed between some green and brown algae and a tidal-height proxy to groundwater discharge

28 where karst watersheds existed. We next hypothesized that removing the variances associated with

29 seasonal growth cycles in the differing phyla would reveal temporal trends in total macroalgal

30 persistence associated with watershed development that were otherwise masked. Following

31 seasonal adjustments, we found that persistent macroalgal canopies existed in the central,

32 urbanized lagoon over the past decade; however, when moving to the north or south of the urban

33 center, significant increases in macroalgal canopies were revealed. Watershed size and

34 development were the strongest predictors of seasonally-adjusted macroalgal canopies through

35 time. No similar trends were found when using unadjusted macroalgal cover data. More

36 importantly, predictions were used to determine thresholds in watershed development associated

37 with the transition between seagrass-versus-macroalgal dominance. The results offered a novel

38 approach for ecological studies that may be limited by financial and logistical constraints to

39 partition seasonal versus temporal change, and better appreciate their differences. For our study

40 lagoon, the results unmasked a growing human footprint into seagrass beds and identified

41 predictive thresholds for management to consider.

42 *Keywords: competition, Halodule uninervis, macroalgal canopies, pollution, seagrass habitats*

43   1.0 INTRODUCTION

44   Seagrass habitats provide essential ecosystem services that support the economy, culture, and

45   livelihood of coastal states and nations (van Beukering et al. 2006, Houk et al. 2012). Productive

46   seagrass habitats are well known to support a variety of fisheries (Jackson et al. 2001, Duarte et

47   al. 2006), remove sediments and nutrients from watershed discharge, stabilize shorelines (Houk &

48   van Woesik 2008, Houk & Camacho 2010, Houk et al. 2013), and sequester globally-significant

49   levels of carbon (Duarte et al. 2005, Duarte et al. 2006). Yet, seagrass habitats remain threatened

50   by human activities such as coastal development that produces both point and non-point source

51   pollution. Excess nutrients and sediments can allow macroalgal canopies to outcompete seagrass

52   for sunlight and space, eventually diminishing or even removing many of the services provided by

53   seagrass beds (McGlathery 2001, Ferdie and Fourqurean 2004, Burkholder et al. 2007). This is

54   especially true for 'pioneering species' with limited blade height and rigidity that have faster

55   rhizome growth and turnover (e.g., *Halodule* versus *Enhalus* in the tropics, 'pioneering' versus

56   'climax' species respectively, Gallegos et al. 1994, Vermaat et al. 1995), providing less protection

57   against macroalgal canopy establishment (Houk & van Woesik 2008). While significant seagrass

58   habitat loss has been widely reported across long time periods (decades) and large spatial scales

59   (tens to hundreds of km^2), fewer studies have examined trends within seagrass beds across shorter

60   time periods (within decades) to help understand how and why loss occurs (Fourqurean et al. 2001,

61   Duarte et al. 2006). For instance, an estimated 65% of seagrass habitat has been lost globally

62   between 1879 to 2006 (Lotze et al. 2006, Short et al. 2007, Waycott et al. 2009). However, multi-

63   year trends within seagrass beds have typically focused on 'climax' species that are better defended

64   against macroalgal overgrowth, but potentially susceptible to epiphytic growth (Lobelle et al.

65   2013). Studies focused on 'pioneering' species are mostly limited to one or a few years to

66   understand seasonal cycles given the high variability associated with sunlight, temperature, and

67   rainfall that change these dynamic systems across each year (Duarte 1989, Fong & Zedler 1993,

68   Lanyon & Marsh 1995, Fourqurean et al. 2001, Keser et al. 2003, Biber & Irlandi 2006, Lirman et

69   al. 2008). In sum, temporal trends are more likely to be masked in seagrass beds composed of

70   'pioneering' species, confounding our ability to understand and manage these dynamic systems.

71

72   Seasonal cycles in seagrass habitats are associated with numerous environmental regimes; but

73   shifting rainfall, sea-surface temperature, sunlight, wave energy, and tidally-influenced

74   groundwater discharge appear to be most influential. The onset of the rainy season in Biscayne

75   Bay, Florida, decreased salinity values of nearshore marine waters and increased the proliferation

76   of mixed-species macroalgal canopies (Lirman et al. 2008). Wave energy regime influenced

77   sediment characteristics and macroalgae abundance across a 50 km region in Tampa Bay, Florida,

78   where intermittent wave energy served to remove canopies from the top of seagrass beds (Bell &

79   Hall 1997). Cooler temperatures promoted the growth of seasonal red macroalgal canopies that

80   competed with *Halodule uninervis* for sunlight in a tropical Pacific lagoon (Houk & Camacho

81   2010). Groundwater discharge has been associated with both the extent and composition of

82   macroalgal canopies growing on top of seagrass beds containing species that have relatively short

83   blades such as *Thalassia* and *Halodule* (Fourqurean et al. 1992, Kamermans et al. 2002, Slomp &

84   Van Cappellen 2004, Carruthers et al. 2005, Houk & Camacho 2010, Houk et al. 2013). Clearly

85   natural environmental cycles have profound influences to seagrass habitats, but their interaction

86   with human stressors such as land-based pollution is poorly decoupled.

87

88   Watershed drainage provides nutrients and chemicals to seagrass habitats that are processed and

89   sequestered within the marine environment (Duarte et al. 2005, Romero et al. 2006, McGlathery

90   et al. 2007). From an energetic standpoint, the metabolism of nutrients within seagrass habitats

91   serve to slow the energetic flux within the system as decomposition and consumption occur

92   (Hutchings et al. 1991, Duarte et al. 2005, Romero et al. 2006, Burkholder et al. 2007, McGlathery

93   et al. 2007). Transforming a rapid, pulsed discharge of nutrients and sediments to a slow, steady

94   discharge is beneficial for the stability of entire food webs because boom-and-bust macroalgal

95   cycles become diminished (Hutchings et al. 1991, Burkholder et al. 2007, Houk & Camacho 2010).

96   In turn, seagrass habitats with little macroalgal canopy overgrowth provide foraging habitat,

97   refuge, and nursery grounds for many (juvenile) fish and other marine biota (Unsworth et al. 2007,

98   Horinouchi 2008, Unsworth et al. 2008, Unsworth et al. 2009). In contrast, Tuya et al. (2014)

99   reported that mats of the macroalgae, *Caulerpa prolifera*, overgrowing *Cymodocea nodosa*

100 seagrass contain less density and biomass in both predatory and prey fishes, less primary

101 productivity, and less stabilization on sediments compared with seagrass beds that had little

102 macroalgal overgrowth. Thus, improving our ability to predict causes and thresholds leading to

103 seagrass-to-macroalgal transitions is necessary to mitigate continued seagrass habitat loss. Studies

104 documenting locations where seagrass-to-macroalgae transitions have occurred in the past are

105 common, however, capturing timeseries data describing how seagrass-to-macroalgal shifts occur

106 are less common (Hauxwell et al. 2001, Cardoso et al. 2004, Houk & Camacho 2010). Therefore,

107 and the causes, mechanisms, and thresholds remain unclear.

108

109 The present study examined macroalgal canopy growth in *Halodule uninervis* seagrass beds during

110 a 10-year period to: (i) improve our understanding of potential mechanisms leading to seagrass-

111   to-macroalgal transitions, (ii) partition the variance associated with seasonal and temporal

112   dynamics in macroalgal canopy cover (i.e., intra- versus inter-annual trends, respectively), and (iii)

113   evaluate temporal trends with respect to watershed pollution to help guide management responses.

114   We first investigated seasonal canopy cover dynamics to reveal the influences of sea-surface

115   temperature, rainfall, and groundwater. These models provided a basis to remove the seasonal

116   component of variance in these dynamic systems. We then investigated trends in the residual

117   variance through time to reveal relationships between macroalgal canopy persistence and

118   watershed characteristics that were otherwise masked. The combined results provided a repeatable

119   approach to isolate patterns and mechanisms associated with undesirable macroalgal proliferation

120   through time.

121

122   2.0 METHODS

123   The present study was undertaken in the Saipan Lagoon, Commonwealth of the Northern Mariana

124   Islands (CNMI). Both *Halodule uninervis* and *Enhalus acoroides* form abundant and extensive

125   seagrass beds, but a third species also exists in low abundances, *Halophila minor*. Previous studies

126   reported that *Enhalus* seagrass beds were less prone to macroalgal overgrowth due to their large,

127   waxy blades, while macroalgal proliferation within *Halodule* beds was predicted by seasonal

128   dynamics (i.e., temperature, rainfall, groundwater, and large-wave events) and human populations

129   and watershed development in a snapshot study (Houk & van Woesik 2008, Houk & Camacho

130   2010). Here, we expand upon previous work and investigate both seasonal variability and temporal

131   trends across 10-years.

132

133   *2.1 Data collection*

134   The lagoon was divided into 6 regions differing in watershed size and human population (A – F,

135   Figure 1, watershed sizes ranging from 0.5 to 4.0 km^2, and human populations ranging between

136   209 to 3,983 people). Each region had between 1 and 3 survey sites, with a total of 11 sites within

137   the 6 regions. Sites were all situated between 200 and 400 m from the shoreline within extensive

138   *Halodule* seagrass beds (Figure 1). Depths ranged between 0.5 to 1.5 m below the mean low water

139   height. Data collection at each site followed standardized protocols since 2000, however, the

140   frequency and timing of monitoring shifted across the 2006 to 2015 study period based upon

141   logistics and funding availability. Data were collected along five 50 m transects laid parallel to

142   shore. Quadrats 0.5 m x 0.5 m were placed at 1 m intervals and the canopy cover under each of

143   five random points, either in-situ or from photographs, were assigned a pre-defined category. The

144   canopy cover categories chosen for analysis were seagrass (to genus level), corals (to genus level),

145   turf algae (less than 2 cm), macroalgae (greater than 2 cm, to genus level if abundant), crustose

146   coralline algae, sand, and other invertebrates (genus level if abundant). Means, standard deviations,

147   and standard errors for each site were calculated based on the five transects with a total of n = 250

148   points per transect, and n= 1250 data points per site. Photos were processed using the computer

149   software Coral Point Count (Kohler & Gill 2006). In sum, data for this study represented ~50,000

150   data point associated with 237 transects surveyed across 11 sites between 2006 and 2015. Not all

151   sites were surveyed in all years and the analytical design presented below describes the methods

152   used to assess both seasonal and temporal trends.

153 Fig. 1

154
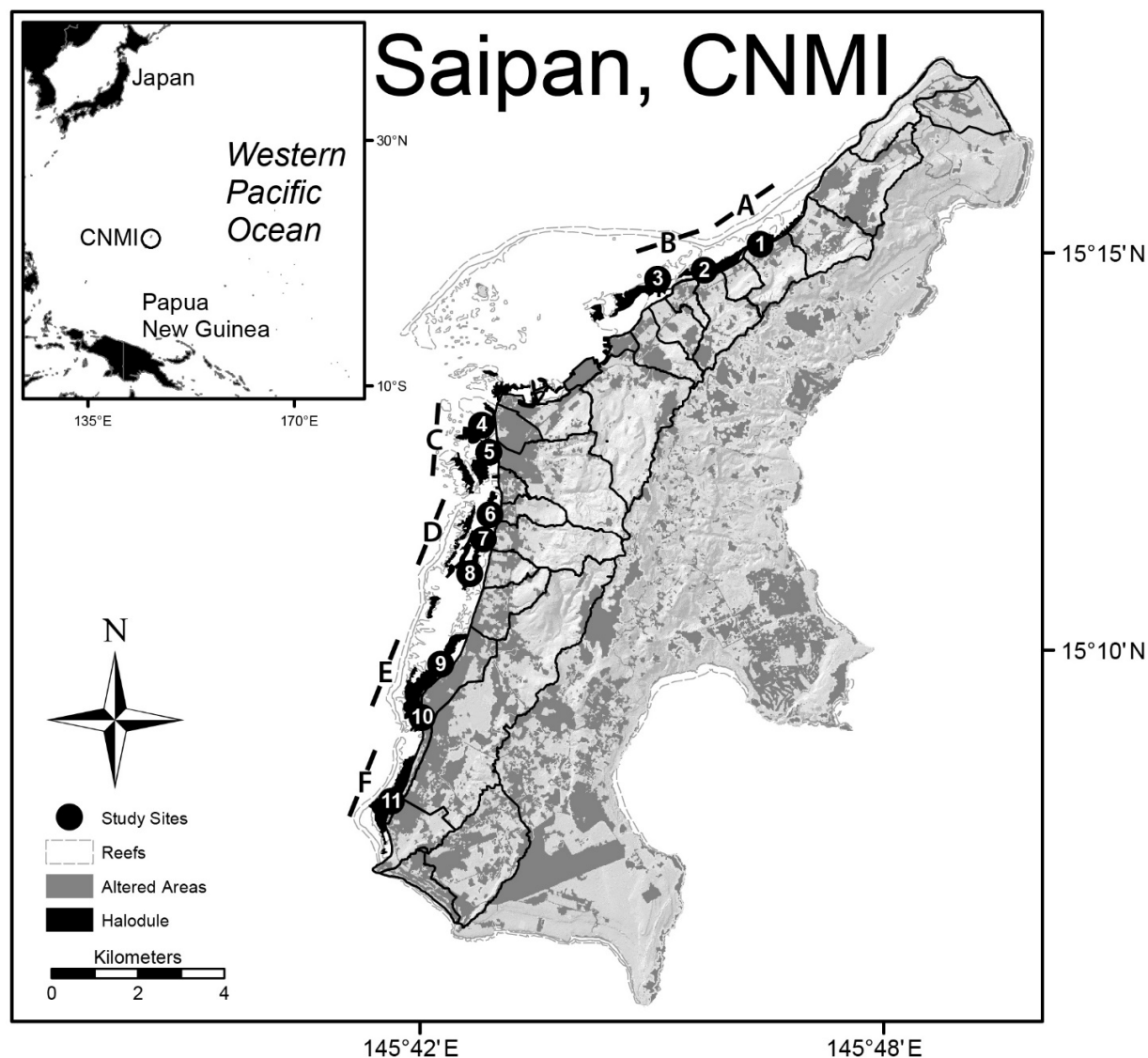
155

156

157 Figure 1. Map of the Western Pacific Ocean and the Commonwealth of the Northern Mariana

158 Islands (CNMI, inset figure). Saipan Lagoon, CNMI, was broken up into 6 regions based upon

159 physical features (A to F, based upon watershed boundaries, distances to reef crest, human

160 population, and the presence of channels in the reef crest). Within each region between 1 and 3

161 sites were examined (*methods*).

162

163 Environmental data were collected to evaluate both seasonal cycles and temporal trends in

164 macroalgal canopies. Watershed characteristics were derived from geographic information system

165 (GIS) layers pertaining to topography, land-use, and human population. Digital elevation models

166 were first used to define watershed boundaries. Land-use data were then overlaid upon the

167 watershed boundaries (USFS 2006), and a measure of disturbed land was calculated by summing

168 the coverage of barren land, urbanized vegetation, and developed infrastructure. In addition,

169 human population data within each watershed were obtained from the 2010 US census (US Census

170 2010). *Enterococcus* bacterial violations from nearshore waters were also examined as a proxy

171 for water quality based upon the CNMI Division of Environmental Quality weekly beach water

172 quality monitoring database (DEQ 2014). The percentages of bacteria violations for each site-year

173 were calculated between 2006 and 2015, and the overall means across the years were used for

174 predictive modeling described below. A proxy for groundwater influence was determined by

175 taking the lowest minimum tide for two months prior to each ecological survey date. This

176 groundwater proxy was previously linked with continuously recorded salinity data to reveal

177 groundwater influences on macroalgal canopies in the Saipan lagoon at these tidal regimes (Houk

178 & Camacho 2010). Tide data were collected from the software Wtides (Thornton 2005). Sea-

179 surface temperature data were obtained from NOAA's OceanWatch (NOAA). Finally, rainfall data

180 were obtained from the Saipan airport weather station (NOAA).

181

182 *2.2 Data analyses*

183 We first sought to characterize potential seasonal differences using a subset of data collected

184 during sequential wet (November 2014) and dry (March 2015) seasons. This subset of data from

185 10 of the 11 sites was ideal because: (i) data were intensively collected during 1-week in both the

186 wet and dry season to minimize inter-site variation in sea surface temperature and rainfall within

187 each season and therefore focus on seasonal influences across the lagoon, and (ii) these years were

188 furthest from two typhoon disturbances that may have influenced macroalgal growth (*Kong-Rey*

189 in March 2007, *Dolphin* in December 2008). Besides typhoon disturbances, a previous study found

190 that large swell events infrequently occurred in the northern lagoon during winter and served to

191 remove some of the macroalgal canopy (Houk and Camacho 2010).

192

193 A suite of multivariate analyses were conducted to examine potential seasonal trends across the

194 lagoon from the snapshot of data described above. Multivariate analyses used Primer software

195 version 6.1.13, Permanova software version 1.0.3, and Vegan package in R version 2.4-6

196 (Anderson et al. 2008, Oksanen et al. 2008). Canopy cover data were log transformed and used to

197 create a Bray-Curtis similarity matrix. Bray-Curtis matrices described the ecological similarity

198 between each pair of sites based upon summed differences in pairwise species abundances. Given

199 homogeneous multivariate variance structures, nested permutational ANOVA tests were

200 performed to assess if seasonal differences existed in a ubiquitous or nested manner. Permutational

201 ANOVA tests provided F-statistics and t-statistics for post-hoc comparisons, both determined from

202 P-values that were assessed by a bootstrapping procedure that removed one data point at a time

203 and reassessed the results. Finally, a principal coordinate ordination (PCO) was used to depict the

204 multivariate results in two-dimensional space by minimizing the differences between actual and

205 depicted distances. In order to appreciate which species contributed most to the PCO plot structure,

206 species-based vector overlays were placed on the PCO plots with vector length describing the

207 strength of the correlation with the axes.

208

209 The seasonal trends revealed from the initial analyses corroborated similar trends reported in an

210 earlier study in the same lagoon, but at smaller scales of investigation (10 m^2 observation windows,

211 Houk and Camacho 2010). The combined information from the present and past study revealed

212 similar, key attributes of seasonal cycles that differed spatially across the lagoon that should be

213 accounted for prior to examining temporal changes. Generally, these included relationships

214 between: (i) cooler sea-surface temperatures and blue-green algae during the winter months, (ii)

215 rainfall and *Acanthophora* red algae during summer months, and (iii) minimum tidal height (i.e.,

216 our proxy to groundwater) and several brown and green algae in the karst watersheds of the

217 southern lagoon. Thus, seasonal cycles were consistent and predictable, however their nature and

218 magnitude differed spatially. Therefore, all subsequent analyses were conducted separately within

219 each region.

220

221 Next, an ordinal variable to describe temporal change was created by sequentially numbering years

222 since the start of sampling in 2006. Stepwise, multivariate regression analyses were then

223 performed to model the variation in macroalgal canopy assemblages, aggregated at the phylum

224 level, that could be explained by both seasonal variables and time (DistLM analyses, a distance-

225 based model using the ordination axes to constrain relationships between macroalgal assemblages

226 and environmental variables, software platform and version noted above). Seasonal environmental

227 variables described above were sea surface temperature, rainfall, and groundwater influence.

228 Because multivariate rather than univariate data were used, interaction terms were difficult to

229 interpret across 2-dimensional plots. We therefore used this approach to appreciate whether

230 seasonal and temporal variation existed and could be distinguished. The significance of each

231 predictor variable was assessed using a similar permutational process described above (F-statistics

232   and P-values), and effect sizes (R^2-values) were calculated by the distances between residual and

233   fitted values. This process sequentially identified predictor variables with the greatest effect size

234   and continued until all significant terms were included. One redundancy plot was included in the

235   results to depict an example of this process for study region B, while a table of results was used to

236   describe results across all regions. All temporal analyses used data from 10 of 11 sites where time

237   series existed, as noted in the results.

238

239   Given independent, significant effects due to both seasonal variation and time within study regions,

240   we performed a third analysis to derive a seasonally-adjusted, univariate metric of macroalgal

241   canopy cover that could be assessed with respect to human factors. Based upon previous studies

242   and our initial analyses described above, different phyla responded differently to seasonal

243   environmental variables. Therefore, regression models were examined between each of the

244   seasonal environmental factors and the four macroalgal phylum for each lagoon region using data

245   from all years. These included both linear models and linear mixed effects models that allowed for

246   potential random variation at the site-level within each region using the R statistical base packages

247   noted above, with random effects assessed by comparing AIC scores and ANOVA's comparing

248   the residual fits. Seasonally-adjusted macroalgal coverage values were derived by replacing the

249   percent cover of any phyla with its residual if a significant regression model existed. Subsequently,

250   the total seasonally-adjusted macroalgal cover represented the sum across all phyla. Capturing

251   residuals in this manner is useful in certain instances (Freckleton 2002), notably when there is little

252   or no covariance structure between the predictor variables. Here, our time variable had no

253   correlation with any of the seasonal environmental variables which differed randomly between the

254   years. Temporal trends were then examined using ANOVA and post-hoc pairwise comparisons

255 across differing timeframes within each site and region. For these analyses, timeframe was

256 considered as a categorical variable to allow for multiple comparisons considering the change in

257 macroalgal cover over time might not be linear. Bonferroni adjustments were made for all post-

258 hoc pairwise tests to account for the fact that several independent tests were being performed on

259 the same dataset.

260

261 We last investigated the possible causes of change in macroalgal canopies through time. For these

262 analyses, trends in macroalgal canopies were binned into logical categories to simplify the nature

263 of temporal trends observed at each site: (i) a consistent and high presence of seasonally-adjusted

264 macroalgal canopies ≥20%, (ii) an increase in adjusted macroalgal canopies through time with

265 present estimates ≥20%, and (iii) adjusted macroalgal canopies that remained <20%. The 20%

266 cutoff value was determined from a Jenk's natural breaks optimization procedure that optimized a

267 natural break in "high" macroalgal canopy estimates above 19.5% (Jenks and Coulson 1963). We

268 classified the temporal trends as either having a "high" likelihood of macroalgal canopy

269 persistence through time for situations (i) and (ii) above, or a "low" likelihood of macroalgal

270 persistence through time, situation (iii) above. We binned situations (i) and (ii) because significant

271 increases through time appeared to be related to both a gradual increase through time at sites less

272 exposed to seasonal winter swells, and a persistently high canopy cover with relatively high

273 variation that had previously been attributed to infrequent large-wave events. In sum, mechanisms

274 leading to macroalgal persistence may have differed, but the outcome remained the same.

275

276 We tested whether watershed size, development, or percentage of bacteria violations could predict

277 the macroalgal state categories using logit models available in the R base packages (R Core Team

278   2016). Logit models provided P-values to determine significance that were derived from likelihood

279   ratios tests against null models. We also conducted Hosmer-Lemeshow goodness of fit tests that

280   examined residuals against a chi-square distribution for fit using the R package ResourceSelection

281   version 0.3-2 (Lele et al. 2017). P-values significantly greater than 0.05 indicated that the model

282   provided a good fit. We used Akaike Information Criterion (AIC) scores to contrast models using

283   differing predictor variables. To provide further support for the logit modeling process, linear

284   models examined whether seasonally-adjusted macroalgal canopies from the spatially-

285   comprehensive 2014-2015 data could be predicted by the same variables used in the logit model

286   temporal examinations noted above (n=10 sites sampled during 2014-2015, see above). The

287   assumption was that present macroalgal estimates may be indicative of the described macroalgal

288   states through time if they were seasonally adjusted. Linear models were assessed for significance

289   (P-value), fit (R^2), and AIC scores.

290

291   3.0 RESULTS

292   *3.1 Seasonal and spatial dynamics*

293   Significant differences across the wet and dry seasons were found using the subset of data collected

294   during 2014 and 2015 (Pseudo-F = 55.5, P<0.001, permutational ANOVA, Figure 2a). Higher

295   cover of the red algae *Acanthophora spicifera,* the green algae *Halimeda* spp., and the brown algae

296   *Dictyota* spp. were found during the warmer, wet season (July to December, Figure 2a). In contrast,

297   mixed species of blue-green algae, *Hydroclathrus* spp., and *Padina* spp. became more prolific

298   during the cooler, dry season (January to June). These seasonal differences in macroalgal canopies

299   were found to be consistent across study regions, but their magnitude varied spatially (Figure 2b).

300   Seasonal differences were greatest where the larger watersheds existed in the central lagoon,

301   regions B, C, D, and E (Figures 1 and 2b), and decreased moving both northward and southward.

302   In support of spatially constrained seasonal differences, a nested permutational ANOVA found

303   significant differences across the lagoon regions once accounting for season (Pseudo-F = 7.4,

304   P<0.001).   During the dry season, spatial differences were primarily attributed to higher

305   abundances of blue green algae and *H. clathratus* in the central lagoon with larger watersheds,

306   with diminished presence elsewhere (Figure 2, Pseudo t-statistics >1.94, P<0.026, for regional

307   comparisons during the dry season). During the wet season, there was also clear separation across

308   regions (Pseudo t-statistics >2.36, P<0.016, for regional comparisons during the wet season). The

309   central south lagoon had the greatest presence of *Acanthophora* (regions C, D, and E), while the

310   northern lagoon had a greater presence of *Dictyota* and *Tolypiocladia* (regions A and B).

311   Interestingly, the southernmost regions were less differentiated across seasons (Figures 1 and 2b),

312   as proxies to groundwater discharge became a more significant factor in these karst watersheds

313   described below.

314

315   Multivariate regression models inclusive of all sites and years with temporal data supported that

316   both seasonal and temporal trends existed, but their magnitude differed spatially across the lagoon

317   (Figure 3, Table 1, n=10 sites with temporal data, site 7 was only surveyed during the 2014-2015

318   snapshot described above but did not have temporal data, Figure 1). Rainfall, sea surface

319   temperature, two-month minimum low tide which served as a proxy for groundwater, and time all

320   explained significant amounts of variation in the macroalgal canopy assemblages (Table 1). The

321   differing correlation structure with the first three RDA axes suggested their unique influences, and

322   most notably the unique influence of time compared to seasonal factors within 5 out of 6 regions

323   Fig.2

a)

b)
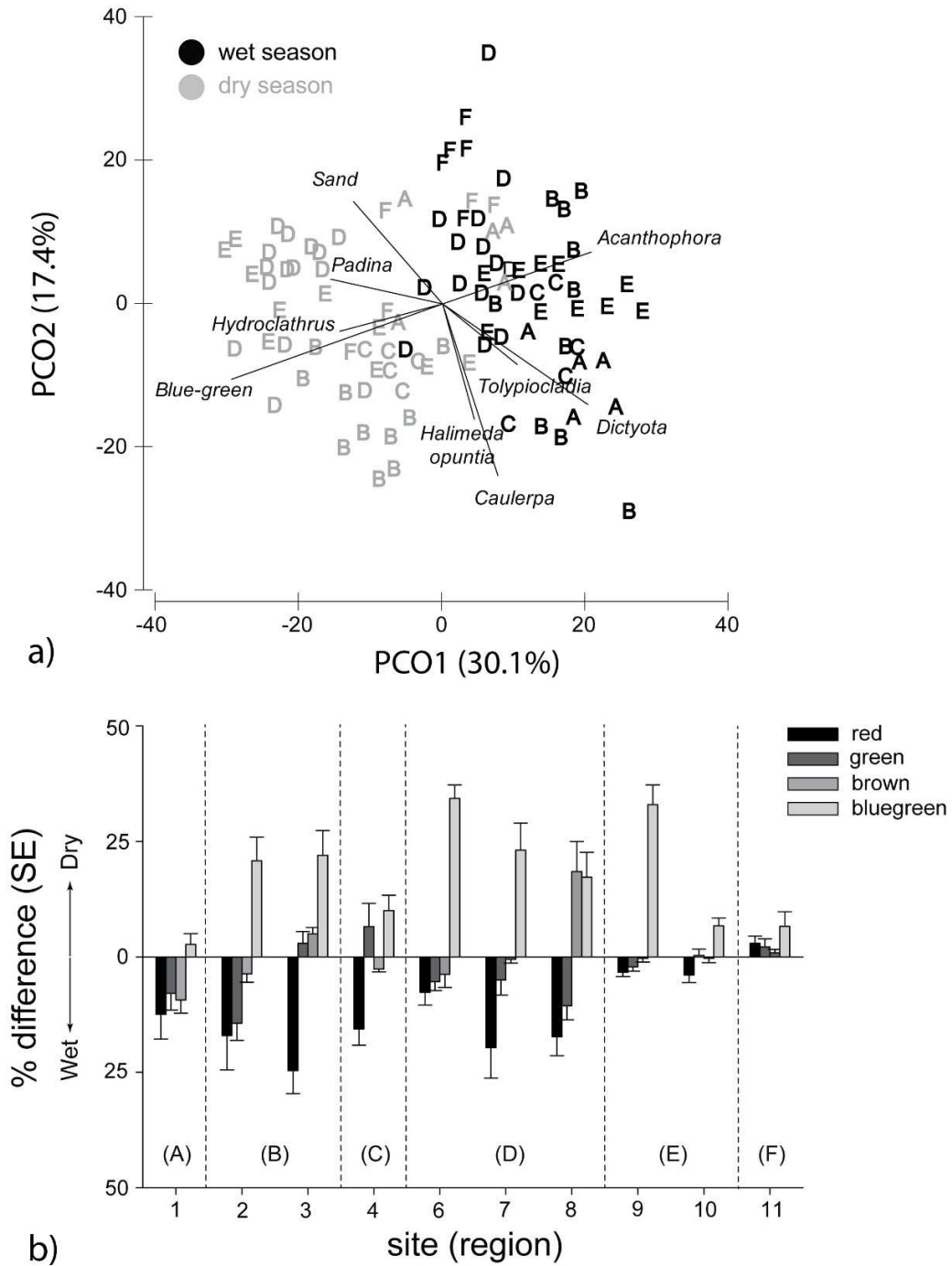
324
325
326   Figure 2. Principal component ordination plot highlighting difference in macroalgal canopy cover

327   between the wet and dry seasons for each study region (a). Percent difference between wet and dry

328   seasons were also summarized by algal phylum highlighting variation across both study regions
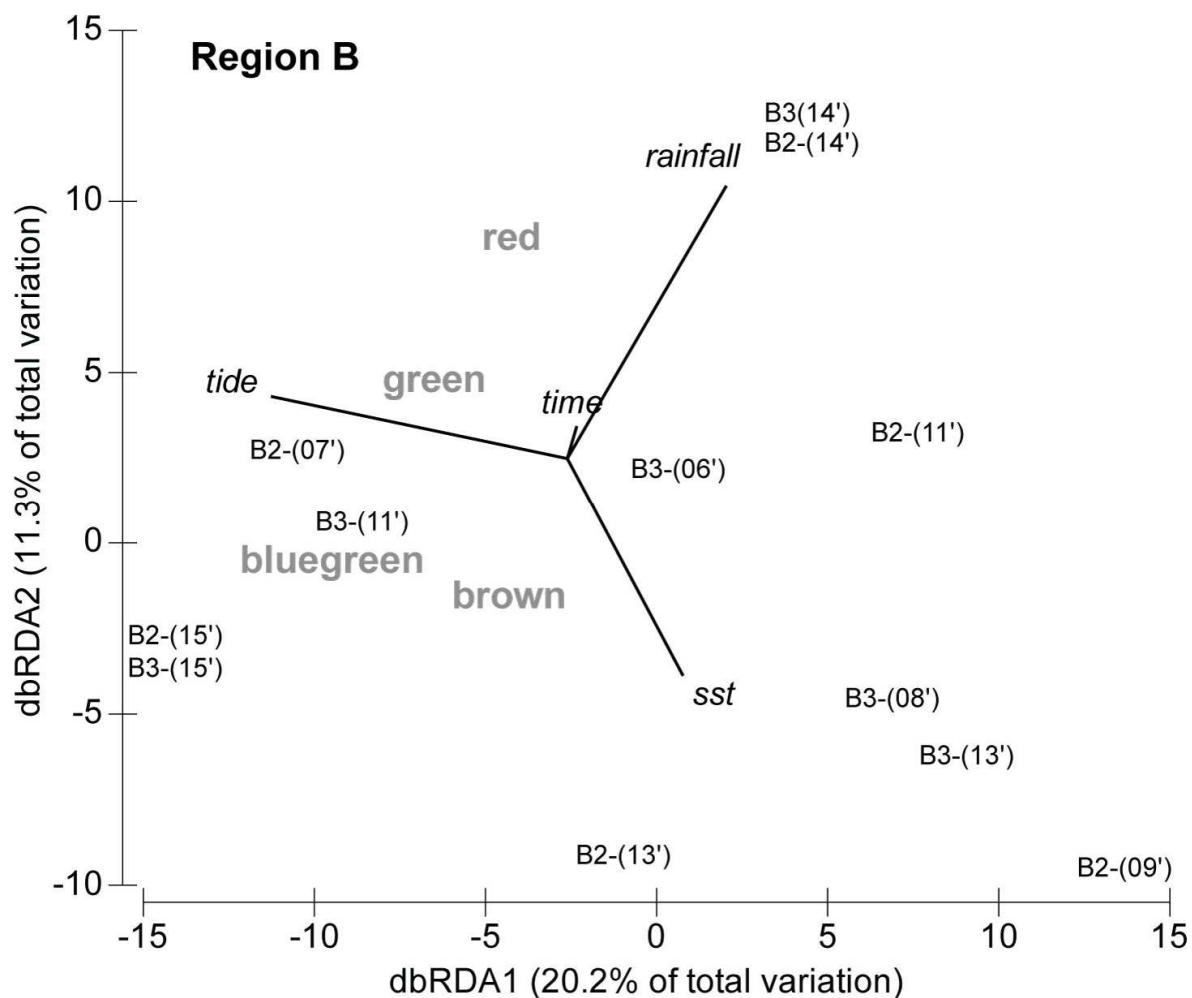
329   and sites within each region (b). Note site 5 was not surveyed in the 2014-2015 snapshots of data

330   used in this preliminary analysis, and standard errors were associated with replicate transects

331   (*Methods*).

332

333

334   Fig. 3

335

336

337

338   Figure 3. An example of one redundancy analysis (RDA) output plot for study region B showing

339   the influence of both seasonal environmental variables and time in driving the macroalgal canopy

340   assemblages. Labels indicate the two sites within study region B followed by the sampling year

341   (see Fig. 1). Each label is associated with 5 transects surveyed during any year subjected to the

342   same environmental conditions. The length of the black lines indicates the degree of correlation

343   between each environmental predictor variable (black italics) and the two RDA axes. The

344   placement of the four macroalgal phyla on the plot indicate their correlation with the RDA axes

345   (grey, bold). Note that seasonal and temporal relationships differed significantly by region (see

346   Table 1).

347

348 Table 1. Results from distance-based multivariate regressions and redundancy analysis plots

349 (RDA) describing how both temporal and seasonal factors were significant drivers of macroalgal

350 canopy assemblages (see Fig. 3 for a depiction of region B). RDA fit refers to the total amount of

351 variation in macroalgal assemblages that was accounted for in the ordination process. Predictor

352 variables are listed sequentially based upon their associated AIC scores, and all variables with

353 significant fits were included (*P<0.05, **P<0.01, ***P<0.001). Axis 1 to 3 refer to partial

354 correlations between each variable and the respective RDA axis to highlight potential difference

355 among the predictor variables. RDA were conducted on data aggregated to the site-year level to

356 match environmental predictors. Sample sizes were 5, 10, 5, 6, 9, and 5 respectively for study

357 regions A to F.

358

Region (RDA fit)	*variable*	*F-statistic*	*cumulative R^2 (AIC)*	*axis 1*	*axis 2*	*axis 3*
A (63.8%)	rain	5.5**	0.20 (130.8)	0.29	0.79	-0.23
	sst	6.6***	0.39 (126.2)	0.73	-0.28	0.57
	time	4.7*	0.51 (123.1)	-0.17	-0.51	-0.38
	tide	6.8***	0.64 (117.8)	0.59	-0.2	-0.70
B (30.3%)	rain	6.3**	0.10 (335.4)	0.45	0.77	0.33
	tide	8.2**	0.23 (329.3)	-0.83	0.18	0.43
	sst	3.7*	0.28 (327.5)	0.33	-0.61	0.62
C (54.2%)	sst	9.7***	0.26 (167.8)	0.49	0.48	-0.08
	tide	5.5**	0.38 (164.2)	-0.42	0.54	-0.72
	rain	3.8*	0.46 (162.1)	0.40	0.58	0.34
	time	4.4*	0.54 (159.2)	-0.65	0.38	0.61
D (54.9%)	rain	13.8***	0.25 (247.2)	0.19	0.98	0.03
	tide	17.5***	0.48 (233.6)	-0.98	0.19	0.01
	time	4.1*	0.53 (231.3)	0.01	-0.04	0.98
E (41.8%)	time	6.8**	0.10 (368.2)	-0.24	-0.87	0.20
	rain	7.8***	0.21 (362.6)	0.22	-0.17	-0.93
	tide	8.7***	0.32 (355.9)	-0.82	0.37	-0.16
	sst	9.4***	0.42 (348.4)	-0.48	-0.28	-0.25
F (49.7%)	tide	4.4**	0.17 (148.2)	-0.92	0.33	0.22
	rain	6.5***	0.36 (143.6)	0.30	0.83	0.37
	time	4.0**	0.47 (141.3)	-0.27	-0.05	-0.36

359

360 (Table 1, right three columns). Seasonal factors typically predicted the most variation among the

361 first two RDA axes, suggesting their primary role in determining what types of macroalgal canopy

362 would be expected during any sampling event. Rainfall had a greater contribution to the northern

363 lagoon (region A and B), while the tidal proxy to groundwater grew in importance moving

364 southward (Table 1, hierarchical ordering of explanatory variables within each region).

365 Meanwhile sea surface temperature had a spatially inconsistent influence. Beyond seasonal factors,

366 the multivariate regressions also suggested macroalgal assemblages have shifted through time.

367 Visualizing and quantifying the differences between stochastic seasonal variation and directional

368 temporal change was difficult to interpret in n-dimensional analyses. Instead, univariate

369 seasonally-adjusted macroalgal abundances were calculated.

370

371 Next, univariate regression models were used to predict seasonal variation associated with

372 temporal data for each site and region of the lagoon (Table 2). Blue-green canopy cover

373 consistently responded positively to cooler sea surface temperatures. The largest slopes associated

374 with *blue-green~sst* models were found in the center of the lagoon, and gradually decreased

375 moving both north and south (Table 2). These findings resonated with the multivariate results from

376 the initial analysis of the 2014-2015 data only described above. Red algae had a consistent and

377 positive relationship with rainfall for regions A-D (north to central lagoon), but no relationship

378 with rainfall existed in the southern lagoon. Instead, groundwater influence, as estimated by the

379 two-month minimum low tide, had a consistent but weak influence on *Acanthophora* and *Dictyota*

380 in regions E and F, whereby lower minimum tide heights predicted greater algal cover (Table 2).

381 The residuals from significant models depicting seasonal influences in the temporal data were

382 extracted and represented a seasonally-adjusted macroalgal abundance estimate. The removed

383 components of seasonal macroalgal canopies ranged between 16% and 48% (Figure 4).

384

385 *3.2 Temporal trends*

386 Seasonally-adjusted macroalgal canopies remained above 20% for all sampling events in region C

387 and increased through time (Figure 4, Table 3, mean values above 20% remained between 2012

388 and 2015, but limited historical data existed for this region compared to others). Thus, the central

389 lagoon was classified as having a "high" and persistent macroalgal canopy. Moving southward,

390 region D had macroalgal canopies that were either persistently high or increasing through time and

391 not differentiated from the 20% threshold. In contrast, the southernmost regions of the lagoon had

392 limited macroalgal canopies that were slightly decreased during the disturbance years with a

393 subsequent increase of similar magnitude (regions E and F). The southern regions were classified

394 as "low" given these coverage estimates. Moving northward from the central lagoon, region B

395 appeared to be influenced by typhoon disturbance years and annual winter swells (Figure 4, grey

396 box indicates typhoon disturbance years). Adjusted macroalgal canopies dropped by ~30% across

397 the typhoon years, but subsequently increased by the same amount and now remain above the 20%

398 threshold, and therefore classified as "high" (Table 2). The northernmost region A was similarly

399 influenced during disturbance years but remained in a persistently "high" state. In contrast with

400 the temporal trends based upon seasonally-adjusted macroalgal cover, varying and often opposite

401 trends were found when using non-adjusted raw macroalgal cover data (Figure 4).

402

403 The binary "high" and "low" macroalgal canopy states were last evaluated with respect to

404 environmental data to approach causation. Watershed size and disturbed land were the only

405 Table 2. Best-fit regression models describing the relationship between seasonal environmental

406 factors and algal canopy cover estimates (*red* – Rhodophyta, *bg* – Cyanobacteria, *brown* –

407 Phaeophyta, and *green* - Chlorophyta). Seasonal factors were rainfall, sea surface temperature

408 (sst), and the tidal proxy to groundwater discharge (gw). Statistical analyses used either linear

409 models (lm) or linear mixed-effects models (lme) depending on the presence of significant site-

410 level variability within each region (*methods*). P-values indicated by *, **, and ***, respectively

411 for $P < 0.05$, 0.005, and 0.001. The residuals associated with these models were used as seasonally-

412 adjusted macroalgal canopy cover values that were further examined (*methods*). Residuals were

413 captured at the transect level within each site, and means were taken for seasonal adjustments.

414 Sample sizes based upon transect-site-years were 25, 50, 25, 30, 45, and 25 respectively for

415 regional A to F.

416

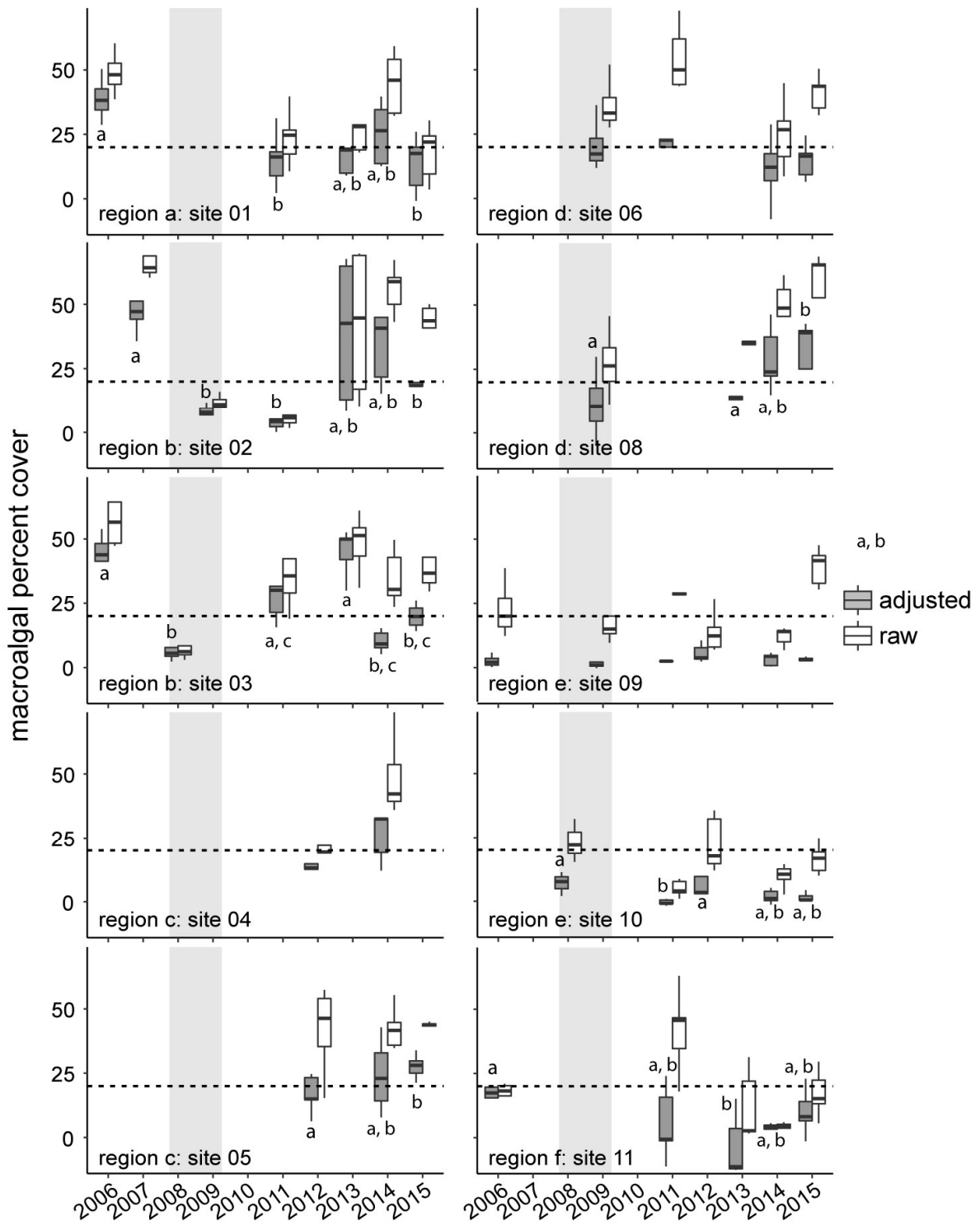| Region	Site	Model	Slope (SE)	R^2
A	1	lm(*red*~rainfall)	0.02 (0.008)	0.277**
B	2, 3	lme(log(*red*+1)~rainfall, random= ~1|site)	$2.0e^{-3}$ ($1.0e^{-3}$)	0.14*
C	4, 5	lme(log(*bg*+1)~sst, random= ~1|site)	-0.69 (0.14)	0.464***
		lme(log(*red*+1)~rainfall, random= ~1|site)	$3.0e^{-3}$ ($1.0e^{-4}$)	0.346**
D	6, 8	lm(*bg*~sst)	-11.33 (1.96)	0.438***
		lm(log(*red*+1)~rainfall	$3.0e^{-3}$ ($5.0e^{-4}$)	0.439***
E	9, 10	lme(log(*green*+1)~gw, random= ~1|site)	-0.06 (0.11)	0.287***
		lme(log(*brown*+1)~gw, random= ~1|site)	-0.23 (0.11)	0.17*
		lm(log(*bg*+1)~sst)	-0.63 (0.18)	0.172**
F	11	lm(*green*~rain x gw)	4.19 (0.75)	0.57***
		lm(log(*brown*+1)~rain x gw)	0.27 (0.06)	0.535***

417

418 Table 3. Summary temporal trends for seasonally-adjusted macroalgal canopy changes between

419 2006 and 2015 (see Fig. 4). Predicted canopy states, defined in methods, characterized sites as

420 supporting either 'high' or 'low' macroalgal canopy cover through time based upon seasonally-

421 adjusted values above or below 20%. For ANOVA F-statistic and post-hoc trends, P-values

422 indicated by *, **, and ***, respectively for $P < 0.05$, 0.005, and 0.001.

423

Region	Site	F-statistic	Trends	Predicted canopy state
A	1	3.636*	Decrease from 2006 to 2011 (*). Non-significant increase in 2014 and non-significant decrease in 2015. High, persistent canopy existed and recent variability may be due to large-wave disturbances affecting the northern portion of the lagoon intermittently (see Houk and Camacho, 2010).	High
B	2	11.54***	Decrease from 2007 to 2011 (**). Non-significant increase in 2014 and non-significant decrease in 2015. Increasing canopy cover now remains high and recent variability may be due to large-wave disturbances.	High
	3	4.301*	Significant decrease from 2006 to 2008 (***), significant increases from 2008 to 2013 (*), and then a significant decrease from 2013 to 2015 (***).High, persistent canopy existed and recent variability may be due to large-wave disturbances	High
C	4	2.677	Non-significant increase from 2012 to present with persistently-high macroalgal cover.	High
	5	2.964	Significant increase from 2012 to 2015 (*) with persistently-high macroalgal cover.	High
D	6	3.308	Non-significant change over the years, but persistently-high macroalgal cover.	High
	8	4.108*	Steady increase in macroalgal cover over the years with a significant increase between 2009 and 2015 (*).	High
E	9	2.086	Non-significant changes and persistently-low macroalgal cover	Low
	10	4.359**	Decrease in macroalgal cover from 2008 to 2011 (*) and a significant increase from 2011 to 2012 (*). Non-significant decrease between 2012 to 2015, cover persistently low.	Low
F	11	2.937*	Decreased from 2006 to 2013 (*) and stable in subsequent years. Cover persistently low.	Low

424　Fig. 4

macroalgal percent cover

region a: site 01
region b: site 02
region b: site 03
region c: site 04
region c: site 05
region d: site 06
region d: site 08
region e: site 09
region e: site 10
region f: site 11

adjusted
raw

425

426   Figure 4. Paired boxplots of adjusted and raw macroalgal canopy coverage estimates across all

427   sites and study years. Statistical differences in adjusted macroalgal canopy cover at differing time

428   periods noted by small lowercase letters (adjusted P<0.05, multiple comparisons of adjusted data

429   in dark grey, Table 1). Vertical light-grey box in all plots indicates the disturbance years when two

430   typhoons passed. Dashed lines indicate the threshold for high (above) and low (below) adjusted

431   macroalgal canopy states (*methods*).

432

433   significant predictors of macroalgal canopy states across the lagoon. Larger watersheds and more

434   disturbed land both predicted the presence of persistently "high" macroalgal canopies, with cutoff

435   values of 0.6 and 0.37 km^2, respectively (AIC scores 4.0 and 7.4 respectively for logit models with

436   watershed size and disturbed land, P>0.05 Hosmer-Lemeshow goodness-of-fit tests for both

437   models, P<0.001 for comparisons against null model, Figure 5a-b). Expectedly, there was a

438   moderate correlation between watershed size and disturbed land (r = 0.62), suggesting improved

439   water quality data can better address pollution loading into the future. These findings were further

440   supported by linear models that also described both watershed size and disturbed land as the only

441   significant predictors of modern macroalgal canopy cover (R^2 values = 0.62 and 0.61 respectively

442   for watershed size and disturbed land, AIC scores 61.18 and 59.95, P<0.001 for both, Figure 5c-

443   d). The confidence intervals associated with the parameters of these models overlapped, likely

444   driven by their correlation as well. In contrast, similar regression models using non-adjusted

445   macroalgal canopy cover data resulted in weakly or non-significant relationships with watershed

446   size and altered land (Figure 5e and 5f).

447

448   Fig. 5
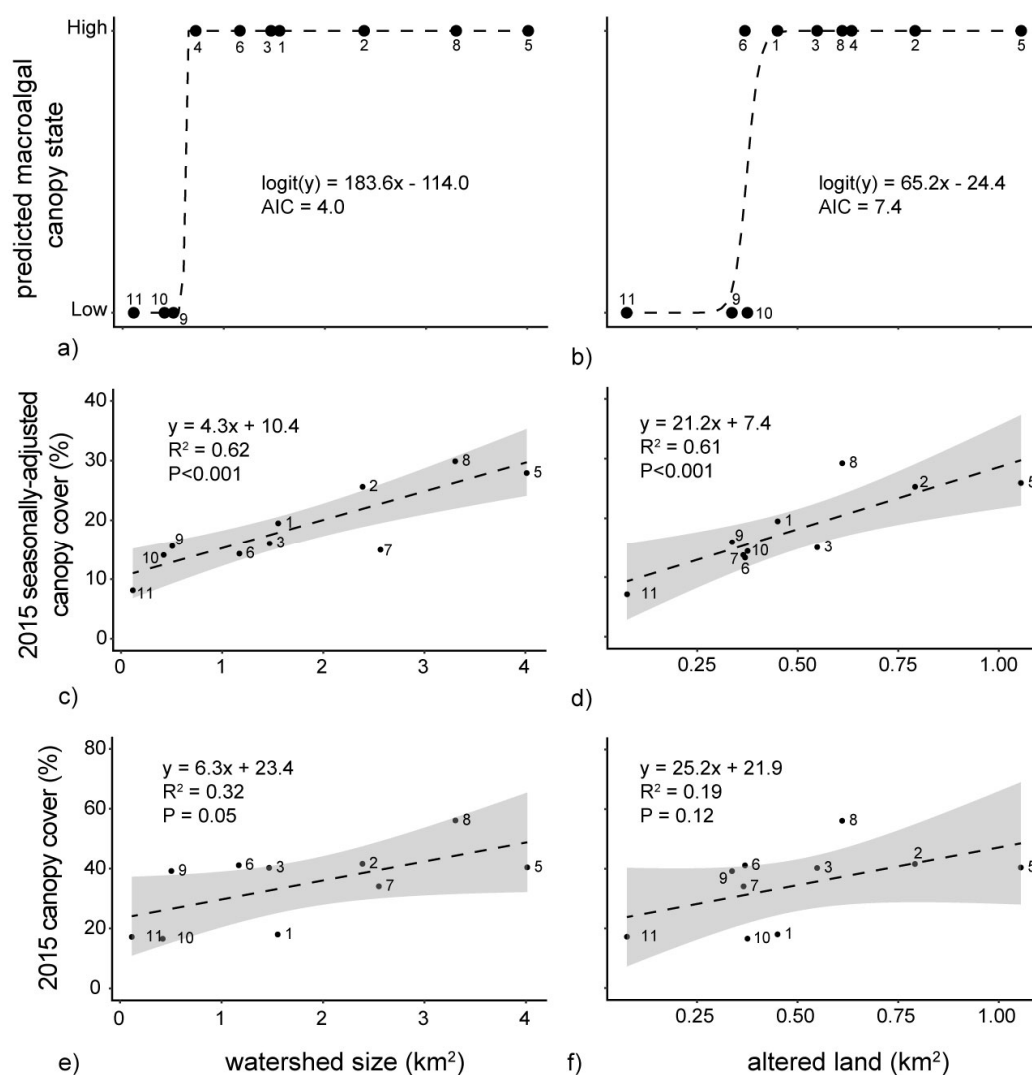
449
450
451
452   Figure 5. Logit models described how both watershed size and altered land predicted high or low

453   seasonally-adjusted macroalgal canopy states (*see methods for classifications*). Both variables

454   provided nearly perfect fits (a and b) and were correlated with each other (r = 0.62). Similarly,

455   linear models described how both watershed size and altered land also predicted present estimates

456   of seasonally-adjusted macroalgal canopy cover (c and d). Site numbers were placed next to each

457   data point. Last, unadjusted macroalgal canopy cover was poorly or not predicted by watershed

458   size and altered land (e and f).

459   4.0 DISCUSSION

460   This study reported on the ecology of macroalgal canopy cover within 'pioneering' *Halodule*

461   seagrass habitats over a 10-year period by first accounting for expected seasonal variation, and

462   then examining temporal trends. Predictable seasonal cycles existed with respect to sea surface

463   temperatures, rainfall, and groundwater discharge. After accounting for seasonal influences, the

464   temporal trends were well predicted by watershed sizes and disturbed land. For instance, February

465   temperatures deviated from the mean by ±1.0 °C across our study years, while September rainfall

466   deviated by ±139 mm. These differences would shift macroalgal canopy estimates by ± 15% and

467   lead to non-significant temporal trends if not accounted for. Combined with previous studies that

468   reported similar seasonal and temporal trends at smaller spatial scales (Houk and Camacho 2010),

469   the results highlighted how seagrass-to-macroalgal transitions and persistent macroalgal canopies

470   within *Halodule* beds appeared to be a consequence of: 1) extended and expanded seasonal

471   dynamics in areas adjacent to large watersheds with high coastal development, and 2) direct,

472   positive influences of watershed pollution on some macroalgae that was not predicted by seasons.

473   In sum, seasonal abundances of various macroalgae persisted for longer periods of time and the

474   extent of macroalgal canopy coverage was larger than could be predicted by seasonal factors alone.

475   In turn, macroalgal canopies are known to limit the amount of sunlight available for seagrass

476   growth and eventually decrease seagrass habitat (Bell & Hall 1997, Hauxwell et al. 2001,

477   Schaffelke et al. 2005).

478

479   The strongest seasonal cycle was associated with emergence of blue-green algae during the winter,

480   cooler months based on the seasonal comparison of 2014-2015 data, and comparisons between

481   seasons across all study years. Blue-green algae were grouped for analyses, but mainly consisted

482   of *Lyngbya* sp.*,* with secondary contributions from *Phormidium* sp. (previously identified as

483   *Schizothrix* sp.), and small contributions from *Calothrix* sp. These findings resonated with a

484   previous study in Guam that reported *Lyngbya* sp. to be most abundant starting in January with

485   cooler temperatures, with a localized presence remaining until June (Palmer 2003). Elsewhere,

486   studies from both freshwater (McQueen & Lean 1987) and marine ecosystems (Fong & Zedler

487   1993, Kanoshina et al. 2003, Watkinson et al. 2005) have concluded that water temperature is one

488   key factor promoting the growth of blue-green algae. Alternatively, studies in temperate regions

489   (Lake St. George and Baltic Sea) found that blue-green algal emergence was associated with

490   warmer spring and summer temperatures, ranging between 19-22°C, alongside nutrient

491   contributions from freshwater inputs (McQueen & Lean 1987, Kanoshina et al. 2003). In our study

492   region, cooler waters during the dry winter months have higher nutrient concentrations,

493   particularly dissolved N and P (Eldredge & Center 1983), which would differ from expected

494   nutrient contributions during the rainy season by having higher salinity and greater contributions

495   of inorganic, but not necessarily organic nitrogen. Houk and Camacho (2010) showed these

496   expected differences in salinity but nutrient studies remain lacking and desirable. Thus, cooler

497   water temperatures and associated nutrient concentrations may act individually or in combination

498   to promote blue-green algal growth, with differences across temperate and tropical regions

499   attributed to the characteristics of seasonal cycles. Increased abundances of brown algae were also

500   observed during winter months, with *Hydroclathrus clathratus* being the most dominant species.

501   This also resonated with a local study on Guam where brown algae were present throughout most

502   of the year but most abundant during winter months (Tsuda 1974).

503

504 Rainfall and tidal proxies to groundwater contribution also had predictable seasonal influences on

505 macroalgal canopies in our study lagoon based on the present and past studies (Houk and van

506 Woesik 2008, Houk and Camacho 2010). Rainfall ranged between 23 to 58 mm month^{-1} during

507 the dry, cool seasons, and more than doubled to 86 to 163 mm month^{-1} during the wet seasons

508 when red macroalgal growth peaked. Previous studies have demonstrated links between salinity,

509 surface runoff, nutrients, and algal growth (McGlathery 2001, Ferdie & Fourqurean 2004, Biber

510 & Irlandi 2006, Burkholder et al. 2007, Lirman et al. 2008), but the rate/ability at which algae can

511 assimilate available nutrients differs between species (Biber et al. 2004). *Acanthophora spicifera*

512 was most abundant with rainfall in our study, but *Halimeda macroloba*, *Caulerpa* spp., and

513 *Dictyota* spp. responded positively as well. Past studies done in Hawaii, where *A. spicifera* is an

514 invasive species, have also shown a strong response in growth with increased rainfall discharged

515 through storm-drains and sewage leaks (Eldredge & Smith 2001, Smith et al. 2002, Lapointe &

516 Bedford 2011, Dailer et al. 2012). Though *A. spicifera* was abundant throughout most of the lagoon

517 during the wet season, there was a notable absence or decreased abundance of this alga in the

518 southern lagoon where karst aquifers and groundwater discharge existed. Thus, karst aquifers may

519 serve to filter storm-water runoff during large rain events and/or reduce pulsed contributions of

520 runoff and sediment.

521

522 Monitoring programs might inherently account for seasonal cycles by sampling during the same

523 month(s) each year to detect trends in macroalgal canopy dynamics. Yet, annual differences in

524 rainfall and sea surface temperature would still exist as quantified above. Thus, accounting for

525 inter-annual seasonal variation in statistical models was necessary prior to interpreting seagrass-

526 to-macroalgal transitions. Watersheds larger than 0.6 km^2 and development footprints beyond 0.37

527 km^2 resulted in larger-than-predicted seasonal blooms of macroalgae that persisted for longer

528 periods of time (Houk and Camacho 2010 coupled with the present results). In turn, continuous

529 exposure to larger and more persistent macroalgal canopies eventually reduces the density of

530 seagrass roots, diminishes growth, and eventually leads to habitat loss. We highlight that trends in

531 seasonally-adjusted macroalgal canopies can be used to predict future habitat loss before it occurs,

532 and reveal the potential for undesirable seagrass-to-macroalgal transitions (i.e., study regions D

533 and B).

534

535 Watershed management in our study lagoon requires all permitted development to limit nutrient

536 runoff through best management practices. However, previously permitted development and their

537 contribution to non-point source pollution are not well addressed. We posit this situation led to the

538 negative relationships between watersheds and macroalgal persistence, and also to the collinearity

539 between watershed development and size. Ideally, further studies could examine nutrient data or

540 stable isotopic data to help disentangle the difference between watershed sizes (i.e., natural factor)

541 and disturbed land (i.e., human factor) to better link watershed development activities with

542 ecological trends (Fourqurean et al. 2015). Focusing management efforts on the lagoon regions

543 with persistently high macroalgal canopies may seem most appealing, however these regions also

544 represent the most urbanized watersheds with greatest economic development interests. Thus, the

545 cost of watershed management and restoration may be very high and socially contentious.

546 Alternatively, watershed projects in lagoon regions where macroalgal canopies have been

547 increasing over the years might gain more ecological value for less economic cost and have less

548 social conflict.

549

550   *4.2 Conclusions*

551   Seagrass beds provide critical habitat for fisheries, absorb nutrients from watershed runoff, and

552   have roots that stabilize coastal shorelines. However, when inundated with excess sedimentation

553   and nutrients from uncontrolled watershed development, seagrass beds and the benefits they

554   provide to society erode. The global decline in seagrass habitats has been partially attributed to

555   watershed and coastal development. Yet, seasonal dynamics complicate our understanding of

556   causation with human factors that can be managed. This study offered one approach to partition

557   the seasonal variance in macroalgal canopy cover and focus on causal relations with watershed

558   size and urban development. The results provided guidance for improved management strategies

559   in our study lagoon and improved our understanding of how seasonal and temporal trends emerge

560   in these complex ecological systems.

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