

1 **Title:** Removal of intertidal grazers by human harvesting leads to alteration of species interactions, community
2 structure and resilience to climate change

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13
14 **ABSTRACT**

15 Extreme fluctuations in abiotic conditions can induce a biological stress response (e.g. bleaching) detrimental to an
16 organism's health. In some instances, organisms can recover if conditions are alleviated, such as through co-
17 occurrence with other species that confer protection. Biodiverse, multitrophic communities are increasingly
18 recognised as important promoters of species persistence and resilience under environmental change. On
19 intertidal shores, the role of grazers as top-down determinants of algal community structure is well recognised.
20 Similarly, the harvesting of grazers for human consumption is increasingly prevalent with potential to greatly alter
21 the community dynamics. Here, we assess how differences in harvesting pressure of grazers under three
22 management regimes (no-take; managed access; open-access) alters the trophic interactions between grazers, and
23 algal communities. Grazer density and body size frequencies were different among regimes leading to changes in
24 the photosynthetic performance and recovery of crustose coralline algae (CCA) post-bleaching, as well as their
25 presence altering the strength of interactions between species. The exclusion of grazers from patches using cages
26 led to different emergent communities and reduced negative correlations between taxa. The absence of larger
27 grazers (>9cm) at the managed access site led to macroalgal overgrowth of bleached CCA negatively affecting its
28 recovery, whereas no-take or open-access led to a moderated algal growth and a shift from competitive to
29 facilitative interactions between algal species. Given that CCA play an important role in the population growth and
30 development of other species, the choice of management measure should be carefully considered before
31 implementation, depending on objectives.

32
33 **Keywords:** environmental change; ecosystem management; MPA; conservation; herbivory

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35

36 **INTRODUCTION**

37 Climate change is expected to increase the intensity and frequency of extreme weather events (Field et al. 2012)
38 affecting marine ecosystems and the economies and societies that depend on them (Harley et al. 2006, Jones et al.
39 2010). In addition to the background of gradual ocean warming (a 'press' perturbation), temporally brief but
40 extreme departures from typical conditions ('pulse' perturbations) can lead to significant disruptive stress for
41 many organisms that may severely affect the functioning of biological systems (Russell et al. 2009). For intertidal
42 organisms, the combination of low tides, calm seas, elevated air temperatures and high solar radiation (UV) may
43 act as short-term, but extreme departures from typical conditions causing severe and widespread damage or
44 mortality (e.g. Bender et al., 1984).

45

46 Bleaching of corals (Ampou et al., 2017) and algae (Hawkins and Hartnoll, 1985; Scrosati and DeWreede, 1998;
47 Wieters et al., 2013) are particularly clear biological stress responses associated with exposure to anomalous
48 environmental conditions (Brown, 1997). Manifested as the loss of symbiotic zooxanthellae or damage to
49 photosynthetic pigments (Davison and Pearson, 1996), bleaching events are occurring worldwide at historically
50 unprecedented rates (Anthony, 2016) leading to marked reductions in primary productivity (Harley et al., 2012;
51 Irving et al., 2004; Kayanne et al., 2005), and negative impacts on food web structure and ecosystem functioning
52 (Graham et al., 2015).

53

54 Recovery following bleaching is, however, possible if stressful conditions are alleviated (Baker et al., 2008). Stress
55 may be alleviated in several ways including individual behavioural responses, such as physical relocation, that limit
56 the duration of exposure to detrimental environmental conditions (Littler, 1972), or associational defences
57 whereby other co-occurring species provide protection (Irving et al., 2004). Increasingly, the importance of
58 biologically-diverse, multitrophic communities is being recognised as a mechanism for species persistence in
59 environments that ordinarily would be stressful to an individual (Griffin et al., 2009; Steiner et al., 2006). For
60 instance, in intertidal systems, crustose coralline algae (CCA) can compete for resources with turf-forming algae or
61 macroalgal canopy species that can reduce the availability of light by shading (Irving et al., 2004). However,
62 'shading' has also been shown to limit damage to CCA from high irradiance levels by reducing the risk of
63 desiccation (Figueiredo et al., 2000; Melville and Connell, 2001). Competitors may therefore act as 'buffers' against
64 environmental change, facilitating the persistence of individuals (e.g. see Przeslawski & Benkendorff, 2005; Wahl
65 et al. 2004 and Bulleri et al. 2018 for examples in other taxa) and entire assemblages via the provision of refugia
66 from environmental stress. The role of facilitation is increasingly recognised as enhancing food web topology and
67 stability by reducing the strength of negative competitive interactions (Rooney and McCann, 2012), and enhancing
68 species fitness (Bertness and Callaway, 1994; Leonard, 2000).

69

70 On intertidal rocky shores, it has long been known that grazers can play a critical role in reducing algal biomass
71 (Steneck, 1982; Wanders, 1977), preventing recovery from a bleaching event. Grazers have been shown to prevent
72 colour restoration through the removal of epiphytes that provide shade (Figueiredo et al., 2000). The size and
73 density of grazers has also been correlated with changes in algal biomass loss, with higher densities of large grazers
74 reducing algal biomass, which in turn, reduces the abundance of healthy CCA (Cattaneo and Mousseau, 1995). In
75 many areas, intertidal grazers important in controlling the abundance and distribution of algae are removed by
76 humans for food (Espinosa et al., 2014; Moreno et al., 1984). Large-scale changes in the population structure, size
77 distributions and density of grazers can occur (Oliva and Castilla, 1986) in turn, directly affecting lower trophic
78 levels (Paine, 1980; Polis et al., 2000) and indirectly affecting the entire system by decoupling fast (small, fast
79 growing populations with high biomass turnover and strong interactions) and slow (low biomass turnover and
80 weak community interactions) energy channels (Rooney and McCann, 2012). The most profound change directly
81 mediated through harvesting is highlighted on rocky shores where the removal of grazers often leads to algal
82 proliferation (Moreno et al., 1984; Oliva and Castilla, 1986). The effect of top-down pressure from predators
83 including humans on grazer densities can therefore alter the outcome of conservation efforts that directly or
84 indirect influence grazer assemblages with knock-on consequences for primary producers including CCAs (O'Leary
85 and McClanahan, 2010; Paine, 1980; Polis et al., 2000).

86
87 Efforts to balance biodiversity conservation with sustainable harvesting practices are on-going worldwide
88 (Espinosa et al., 2014). Conservation strategies like Marine Protected Areas (MPAs) can result in altered
89 demographic structure of populations, influencing species size distributions and the density of grazers (Oliva and
90 Castilla, 1986), and indirectly influencing lower trophic levels via top-down cascading effects (O'Leary and
91 McClanahan, 2010; Paine, 1980; Polis et al., 2000), especially algae (Moreno et al., 1984; Oliva and Castilla, 1986).
92 The level of protection afforded to species and habitats within a reserve can, however, vary depending on the
93 reserve objectives (Lester and Halpern, 2008; Lester et al., 2009). In some instances, this is complete protection
94 (no-take) for all species; in others, partial protection (restrictions) for certain species or control of activities
95 considered harmful (Knights et al., 2015; Piet et al., 2015). Differences in the level of protection can result in
96 emergent communities with varying structural (biomass, density, diversity) and functional (trophic interactions)
97 properties depending on the type of reserve implemented (Lester and Halpern, 2008). It is therefore difficult to
98 differentiate the effect of conservation strategies from the natural biological structuring of communities due to
99 changes in multitrophic species interactions.

100
101 Here, we explore how different management objectives can alter multitrophic interactions among humans
102 (harvesting), grazers, macroalgae, and crustose coralline algae (CCA). We explore the extent to which changes in
103 harvesting pressure associated with different ecosystem management measures alters the structure of the grazing

104 community, and by way of a series of cage experiments, make links between the effect of harvesting and the
105 capacity for primary producers (i.e. CCA) to withstand pulse perturbations associated with intertidal living.

106

107 **MATERIALS AND METHODS**

108 *Study sites*

109 Experiments were conducted at three wave-exposed rocky intertidal sites of relatively weak upwelling along the
110 coast of central Chile (Fig. 1). Estación Costera de Investigaciones Marinas (ECIM) is a no-take marine reserve

111 established in October 1982, covering approximately 500m of rocky shore and 10 hectares of subtidal rocky reefs.

112 Immediately adjacent, Las Cruces (LC) applies seasonal closures but otherwise access and harvesting is

113 unrestricted, while, 18km north, El Quisco (EQ) is a territorial users rights fisheries management area (MA)

114 assigned by the government to the Fishermen's Union in 1993. The fishing union works alongside marine ecologists

115 to develop a management plan and conduct annual assessments to assess and set changes in the total allowable

116 catch of benthic resources and minimum size limits for harvested species (Gallardo Fernández, 2008).

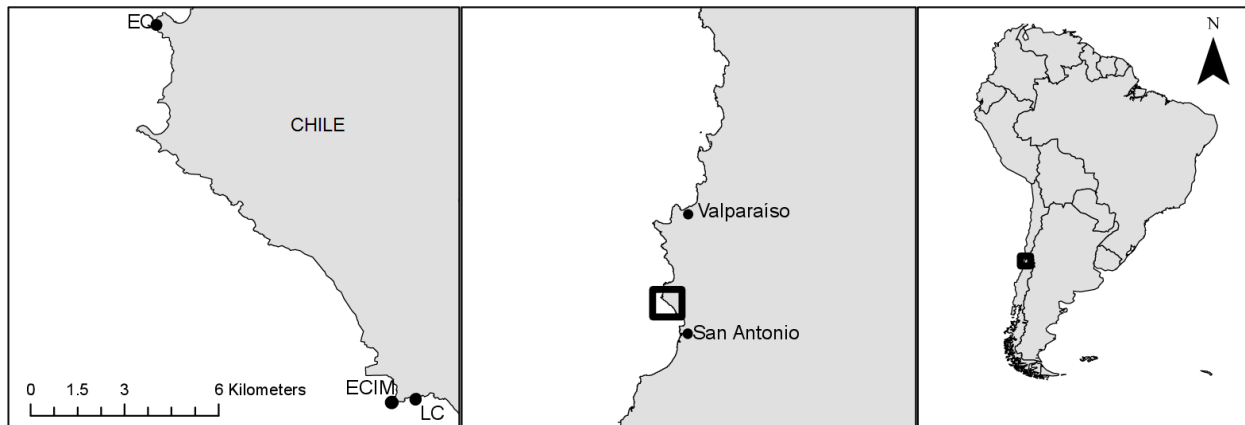
117 Across the three sites, epibenthic communities of the low intertidal zone are characterised by canopy kelp

118 (*Lessonia* and *Durvillaea antarctica*), crustose (mostly *Hildebrandia* spp.) and calcified coralline (*Lithothamnion* spp.)

119 and corticated algae (*Gelidium* spp.) as well as mobile consumers including patellid gastropods (*Scurria*), chitons

120 (predominantly *Chiton granosus*) and keyhole limpets (*Fissurella* spp.)(Broitman *et al.* 2001).

121



122

123 Fig. 1. Location of the three experimental sites: Estación Costera de Investigaciones Marinas (ECIM) - no-take

124 marine reserve; Las Cruces (LC) - open access harvest area; and El Quisco (EQ) – managed access area.

125

126 *Experimental design and set-up*

127 Biodiversity management tools, such as marine MPAs, are largely absent throughout Chile (see www.mpatlas.org

128 for a review) curtailing our ability to 'replicate' this study across management regimes. As such, this study

129 undertakes an exploratory comparison of the three locations, describing the community structure and associated

130 changes in structure and functioning in each following our experiment, rather than attempting to formally

131 compare management strategies by including 'management' as a factor in our analyses. Instead, we compare sites,
132 either in a one-factor analysis (i.e. grazer density and length), or as a random factor (photosynthetic yield and
133 percentage cover analyses) to test the null hypothesis of no difference among sites. Any differences were thus
134 inferred to be a result of management rather than direct causation.

135

136 To test the effect of grazers on CCA bleaching, cages were used to exclude potential algal grazers from patches of
137 bleached CCA (BCCA hereafter) and the recovery of the BCCA to healthy CCA (HCCA) was assessed over time. Cage
138 treatments were compared with open (full-access) and procedural controls to test for artefacts of the cage (e.g.
139 Knights et al. 2012). At each site, up to fifteen 225 cm² independent patches containing BCCA were randomly
140 assigned in equal numbers to one of three treatments (control, cage or procedural control). For the cage
141 treatment, square cages (15 x 15 x 3 cm) made of metal mesh (~1 cm diameter) were placed over each BCCA plot
142 once all grazers were removed. Control and procedural control plots, which allow full access by grazers, were
143 identified using screws and tags to indicate the corners of each experimental patch. The procedural control used
144 the same cage material, but only half of the structure was installed to allow grazer entry. The number of replicates
145 in each treatment was limited by the number of naturally-occurring BCCA plots and site restrictions, such that 3, 4
146 and 5 replicates of each treatment were established at ECIM, LC and EQ respectively (for a total of 36 plots). Cages
147 were installed in November 2015 and were monitored for up to 104 days.

148

149 *Grazer density and length*

150 Due to differences in harvesting restrictions among sites, density and sizes of individual grazers potentially
151 affecting local algal assemblages was expected to differ. To evaluate this, 25 quadrats (0.25m²) were haphazardly
152 placed in the low intertidal zone. For each quadrat, the density of all grazers, including *Fissurella* spp., *Scurria* spp.,
153 *Siphonaria* spp. and several chiton species (e.g., *Chiton* spp. and *Enoplochiton niger*) was determined, and the shell
154 length (greatest distance between anterior and posterior ends) of all individuals was measured using Vernier
155 callipers.

156

157 *Photosynthetic performance*

158 Point measurements of effective quantum yield (Ψ) from each CCA patch were carried out weekly for the duration
159 of the experiment using a DIVING-PAM fluorometer (Walz, Germany) to evaluate changes in CCA photosynthesis-II
160 between treatments over time. Effective quantum yield was determined by the following (Genty et al., 1989):

161

$$162 \Psi = (F'_m - F)/F'_m$$

163

164 where: F'_m is the maximal fluorescence yield in a light-adapted plant following saturating-light pulse and F is the
165 normal fluorescence in the light (see Harrington et al., 2005). All point measurements were collected under

166 ambient light with the main optical fibre placed at a distance of 10mm from the CCA at an angle of 60° to avoid
167 shading or darkening (Beer et al., 1998). To ensure that photosynthesis of CCA alone was measured, a small brush
168 was used to clear epiphytic growth from three small, randomly selected areas on the surface of CCA immediately
169 before measurements (Short et al., 2014).

170

171 *Percentage cover*

172 In the first 3 months of the study when algal overgrowth and density did not inhibit photographic analyses, a
173 photograph of each plot was taken weekly and the percentage cover of BCCA and HCCA along with other algae
174 present in the plot were estimated using the image analysis software ImageJ (Abramoff et al., 2004). After 3
175 months, algal overgrowth made such image analyses difficult and therefore percentage cover was estimated in the
176 field using point sampling. Percentage covers of habitat/species were pooled into one of 11 functional groups
177 based on morphology and resource-use strategies (see Broitman et al., 2001). Estimates of bleaching intensity
178 were calculated as the percentage of CCA cover that was visually bleached and thus was independent of local
179 abundance.

180

181 *Data analysis*

182 *Grazer density and body size*

183 All data analyses described were performed using the open source software, R (R Development Core Team, 2017).
184 Grazer densities and body size among sites were compared using one-way ANOVA and Kruskal-Wallis tests
185 respectively. For ANOVA tests, homogeneity of variance was tested using Levene's test and data square-root
186 transformed where relevant to remove heterogeneity. Where significant differences were identified, Tukey HSD
187 *post-hoc* pairwise comparisons were used to identify significant differences between groups.

188

189 *Change in photosynthetic performance and percent cover of CCA*

190 A linear mixed effects model testing change in (i) photosynthetic yield, and (ii, iii and iv) percentage cover of
191 bleached, healthy and total cover of CCA in different treatments (control; procedural control; cage) with site
192 included as a random factor was developed. Model reduction was undertaken (using AIC goodness of fit
193 comparisons) to reveal the best-fitting model. For photosynthetic yield, this was a generalised least squares (GLS)
194 additive model with an autoregression-moving average correlation structure (AR1) excluding site as a factor, and
195 for percentage cover, this was the maximal (lme) model including site as a factor and also updated to include an
196 autoregression-moving average correlation structure (AR1). Linear regression was used to test for significance of
197 model fit slopes and intercepts for each percent cover estimate of HCCA and BCCA (Fig. 4). Moving-average
198 (localised regression) was used to illustrate change in total percentage cover of CCA over time by site and
199 treatment (Fig. 5)

200

201 If CCA recovers, a negative correlation in the percent cover of CCA classified as 'bleached' or 'healthy' was
202 predicted. However, overgrowth by other algae may also occur on the surface of BCCA, so that the percentage
203 cover of HCCA may not return to pre-bleached levels. Using data from the last time point, percentage cover of
204 BCCA was correlated against the percentage cover of HCCA and functional algal groups to assess if BCCA is
205 replaced by other algal species in the presence or absence of grazing pressure. Pearson's correlations are
206 presented using correlation matrices (*corrplot* package; Friendly, 2002).

207

208 To test if local consumer treatment affects the composition of algal communities, permutational multivariate
209 analysis of variance (PERMANOVA; McArdle and Anderson, 2001) and non-metric multidimensional scaling (nMDS)
210 was used with functional groups as variables. PERMANOVA was conducted using the *adonis* function (*vegan*
211 package; see Oksanen et al., 2016), and where significant results were found, similarity of percentages analysis
212 (Clarke and Warwick, 1998) was used to determine the functional groups most responsible for dissimilarity in
213 community composition. nMDS (conducted using *vegdist* with the Bray-Curtis index of similarity) was used to
214 graphically portray similarity/dissimilarity function in the *vegan* package. Environmental fitting (*envfit* procedure in
215 *vegan*) was used to indicate correlation between the time vector and factor centroids.

216

217 **Results**

218 *Grazer density and length*

219 Grazer density was significantly different among sites ($F_{2,72} = 7.23$, $p < 0.001$) with post-hoc pairwise comparisons
220 revealing a significantly higher grazer density (2.5 x greater) at the open access site (LC), compared with the
221 managed access sites of ECIM and EQ (Fig. 2a). While densities were marginally higher at the no-take reserve site
222 (ECIM) than the fisher-managed MA site (EQ), the difference in total grazer density was not statistically significant.
223 There was no significant difference in median grazer body length at different sites ($F_{2,377} = 1.95$, $p = 0.15$, Fig. 2b)
224 although at the no take site (ECIM), a number of considerably larger individuals were recorded that were not
225 present at the open-access and managed-access sites (Fig. 2b). The maximum recorded size at ECIM was 17.5cm,
226 largely contributed by *Fissurella* spp., whereas largest sizes in the managed access and open access sites were 6
227 and 9 cm respectively.

228

229 *CCA Recovery of Photosynthetic capacity*

230 Changes in photosynthetic yield over time were dependent on treatment and time ($F_{2,302} = 3.2$, $p < 0.05$). There
231 were significant differences in the rate of increase in quantum yield over time between 'cage' treatments
232 excluding grazers, and 'control' or 'procedural control' treatments ($p < 0.05$) allowing access to grazers (Fig. 3).
233 Quantum yield increased 2.3x faster in caged treatments (a rate of 1.8×10^{-3} μ mol per day) than in the control
234 treatments (7.7×10^{-4} μ mol per day). There was no significant difference in quantum yield over time between control

235 and procedural control treatments, nor any difference in initial quantum yield between treatments (mean yield at
236 Day 0 for all treatments = 0.19 ± 0.07).

237

238 *Change in ratio of healthy and bleached CCA over time*

239 The percentage of CCA that was bleached was dependent on site (AIC fit), treatment ($F_{2,266} = 3.92$, $p < 0.05$; Fig. 4),
240 and time ($F_{1,266} = 267$, $p < 0.001$; Fig. 4). Analysis and subsequent *post-hoc* tests revealed that the percent of
241 bleached CCA at the managed access site (EQ; 42%) was approximately 2.5x and 1.7x greater than at the open
242 access site (LC; 16%) and no-take site (ECIM; 25%) respectively (Fig. 4). The percentage of CCA bleached was ~1.5x
243 greater at the no take site than the open access site. The percentage of bleached CCA decreased significantly over
244 time at a mean rate of $4.3\% \text{ day}^{-1}$, irrespective of treatment ($F_{1,266} = 267.2$, $p < 0.0001$; Fig. 4).

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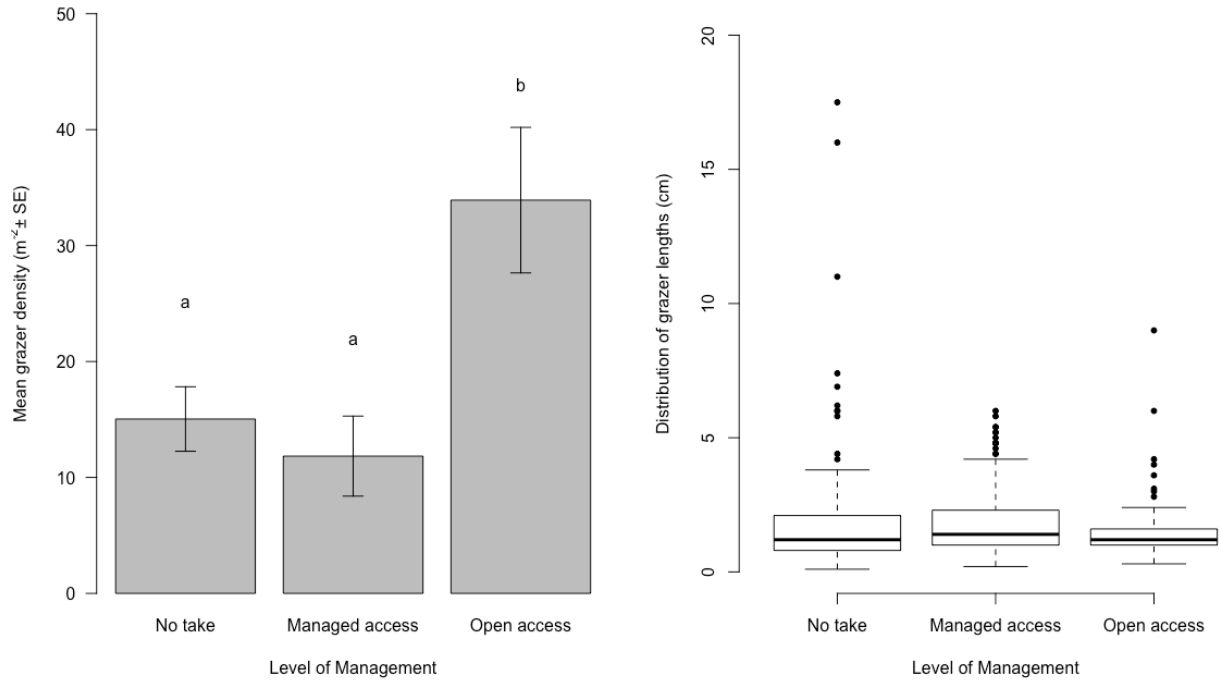
246 Change in percentage cover of healthy CCA was dependent on site, and varied among treatments over time ($F_{2,268}$
247 = 5.18 , $p < 0.01$) and varied idiosyncratically. The percentage cover of HCCA increased in the control treatment at
248 the no-take and managed access sites only (Fig. 4a, d). In three other treatments (control, procedural control and
249 cage depending on site), percentage cover of HCCA declined (Fig. 4b, g & i) at a mean rate of ~0.3% cover per day.
250 In the remaining four treatments (Fig. 4c, e, f & h), there was no change in the percentage cover of HCCA over
251 time.

252

253 In all plots, there was a reduction in the total areal extent of CCA at all sites over time depending on treatment
254 ($F_{2,534} = 3.40$, $p < 0.05$)(Fig. 5). At the managed site, the exclusion of grazers led to greater reductions in cover (e.g.
255 mean loss of 73% at the managed access site, Fig. 5f), in comparison to plots with grazers (e.g. mean loss of 49% at
256 the managed access site, Fig. 5d). Change in extent over time at the no-take site was more variable among plots
257 than at the managed and open access sites, irrespective of treatment. This was especially true in the cage
258 treatment where individual plots displayed significant reductions or little change in cover over time (Fig. 5c).

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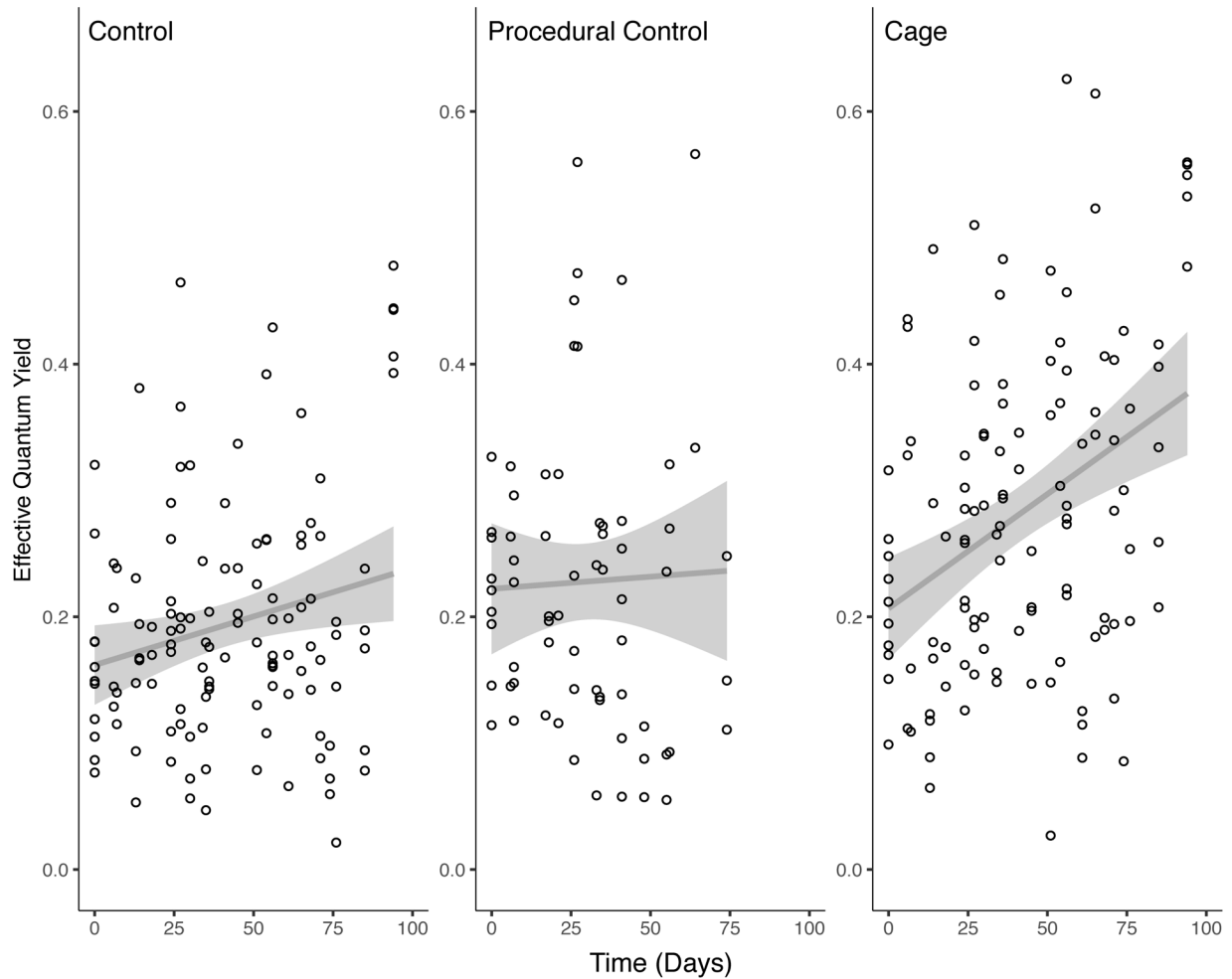
Managing human harvesting enhances multitrophic marine communities



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261 Fig. 2. (a) Mean (\pm S.E.) grazer density, and (b) distribution of body lengths of intertidal grazers at three sites with
262 differing management regimes. Different letters above bars indicate significant differences ($p < 0.05$) between
263 groups as revealed by Tukey *post-hoc* tests.

264



265
 266 Fig. 3. Change in effective quantum yield (Y) from CCA over time grouped by cage treatment. Significant linear
 267 regressions are shown as solid lines. Shading indicates 95% confidence interval. Regression line equations are:
 268 Control ($Y_{\text{control}} = 0.00077x + 0.16$), Procedural Control ($Y_{\text{cage}} = 0.0001x + 0.22$), and Cage ($Y_{\text{cage}} = 0.0018x + 0.21$).
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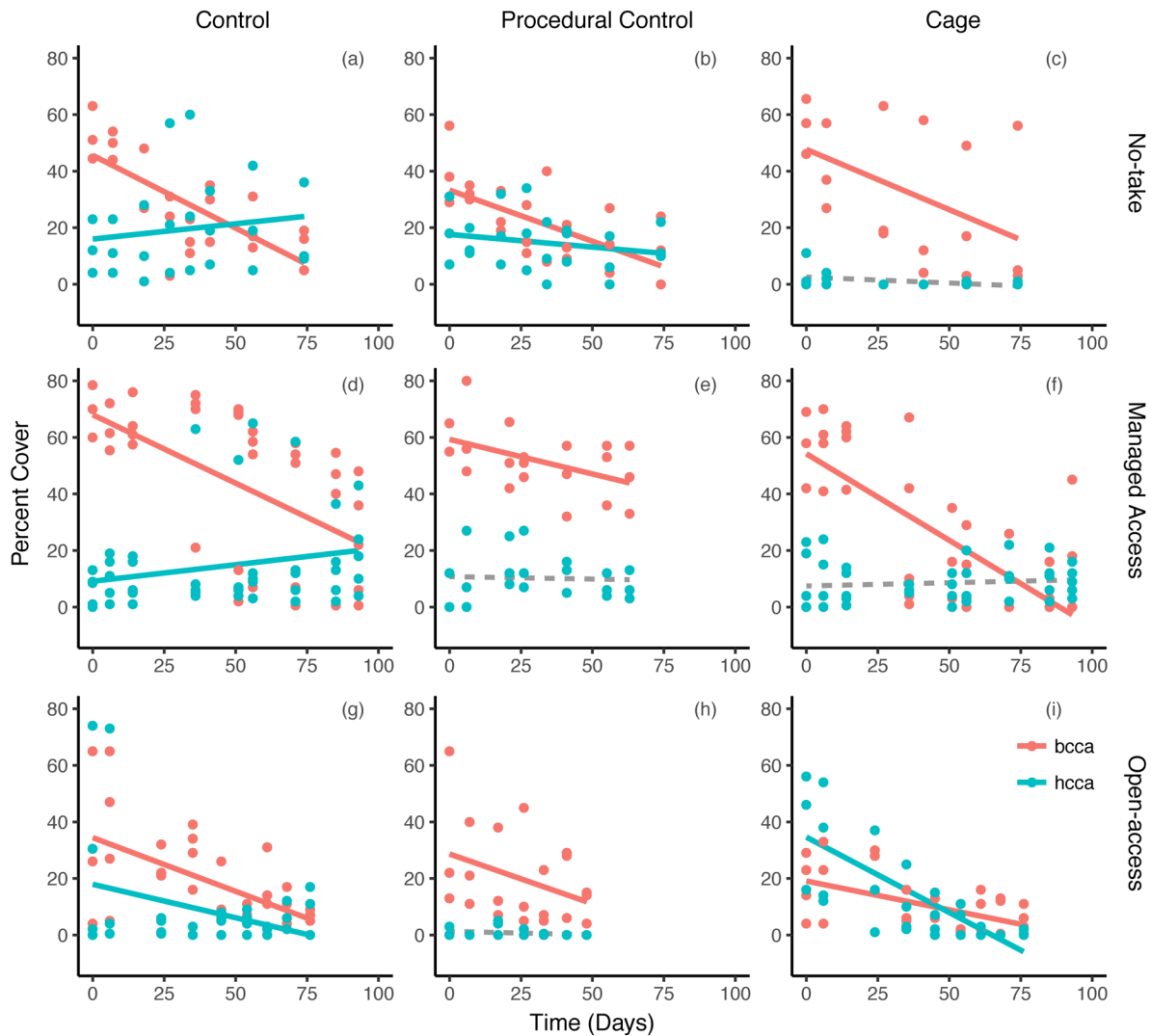
270 *Community analyses*

271 Both positive and negative correlations were found between HCCA, BCCA and other sessile functional groups at
 272 each site (Fig. 6), although relatively weak relationships were observed at the open access LC site. At all sites, HCCA
 273 and especially, BCCA, were negatively correlated with the abundance of corticated, ephemeral and/or fleshy
 274 crustose algae. The most consistent and distinctive pattern of relationships was observed where consumers were
 275 excluded: here, strongest negative correlations of BCCA and HCCA were associated with ephemeral algae at all
 276 sites. In contrast, where consumers were present (control and procedural control treatments), relationships were
 277 more variable among sites and strong negative correlations of BCCA and/or HCCA were associated with either
 278 fleshy crusts and filter feeders (no-take, ECIM), corticated and ephemeral macroalgae (managed access, EQ), or
 279 filter feeders (open-access, LC) (Fig. 6). There was only a weak negative correlation between HCCA and BCCA
 280 suggesting limited evidence of recovery of BCCA at all sites.

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The emergent communities were different among sites, treatments and time (3-way interaction term, $F\text{-perm}_{4,251} = 2.25$, $p < 0.01$) (Fig. 7). Adding terms sequentially, site accounted for the greatest variability in composition (15%), followed by treatment explaining a further 5% of the variance (Fig. 7). Time (R^2 , $p < 0.001$) played was a relatively important determinant of emergent community structure at each site, explaining ~21% of the variation in composition. SIMPER analysis revealed differences in algal functional groups between cage and control treatments (65.5% overall dissimilarity) driven by differences in ephemeral (cage plots (Δ) at all sites showed a transition toward a prevalence of ephemeral algae over time), BCCA and corticated algae (Table S1, Fig. 7). Procedural control and control plots showed broadly similar communities. The communities at each site were characteristically different in terms of composition. The no-take site (ECIM) were 61% different from those at the managed site (EQ), and 76% different from the open access site (LC), with certain functional groups more strongly associated with each site (Fig. 7). Biggest differences were driven by the presence/absence of non-calcareous crustose algae and BCCA at the managed site, and by corticated and non-calcareous crustose algae at the open access site. Communities at EQ and LC were 69% different, driven by differences in BCCA and corticated algal abundance (Table S1).

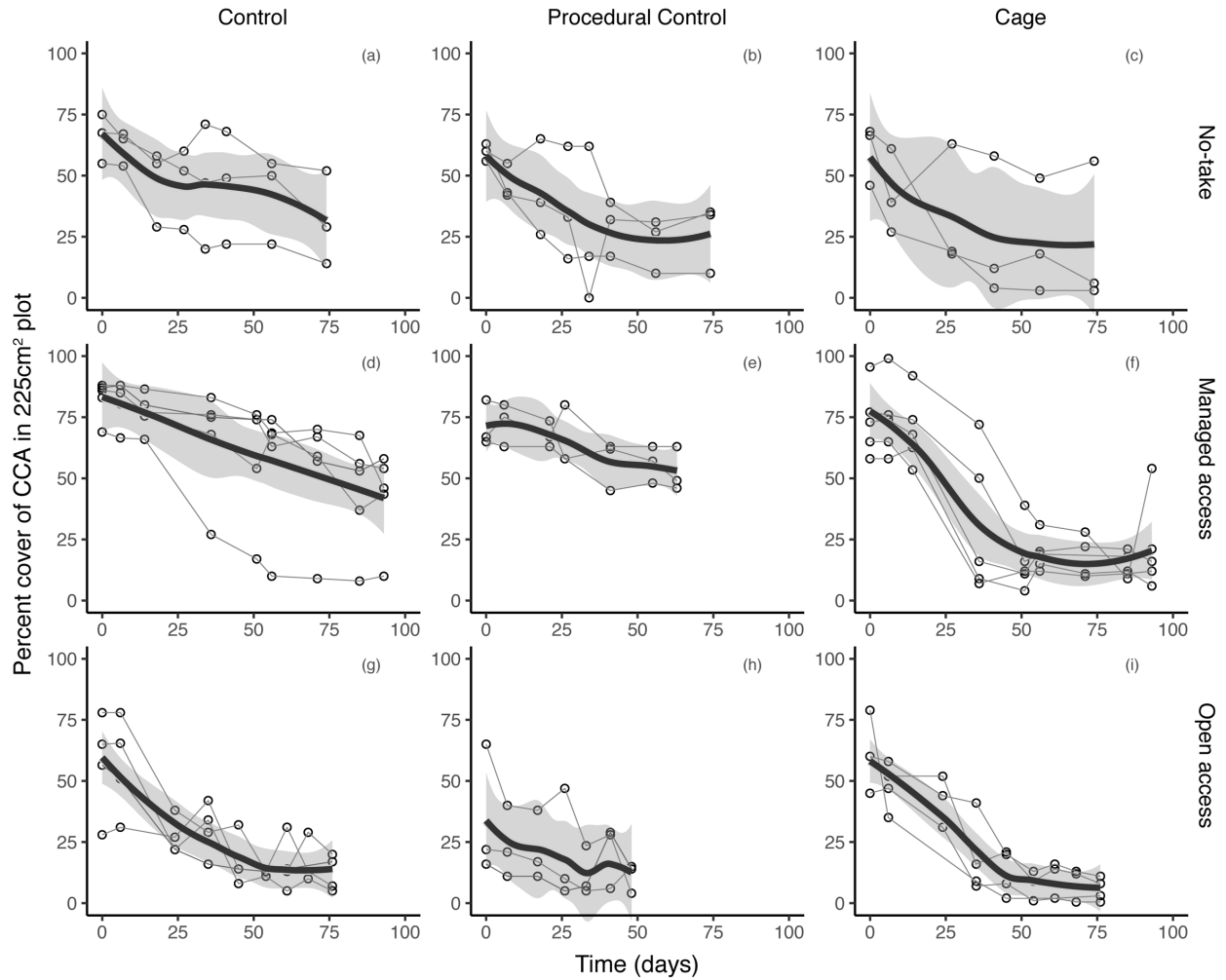
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299 Fig. 4. Percentage of CCA that is healthy (green) or bleached (red) over time (days) in control, procedural control,
 300 and cage treatments at sites with different management. Significant linear regressions are shown as solid lines ($p <$
 301 0.05).

302



303

304 Fig. 5. Change in total percent cover of CCA per 225 cm² plot in control, procedural control and caged treatment
 305 plots over time. Regressions lines show moving-average with an AR1 correlation structure and associated 95%
 306 confidence intervals (shaded area). Light grey lines trace change in percent cover of individual CCA plots.

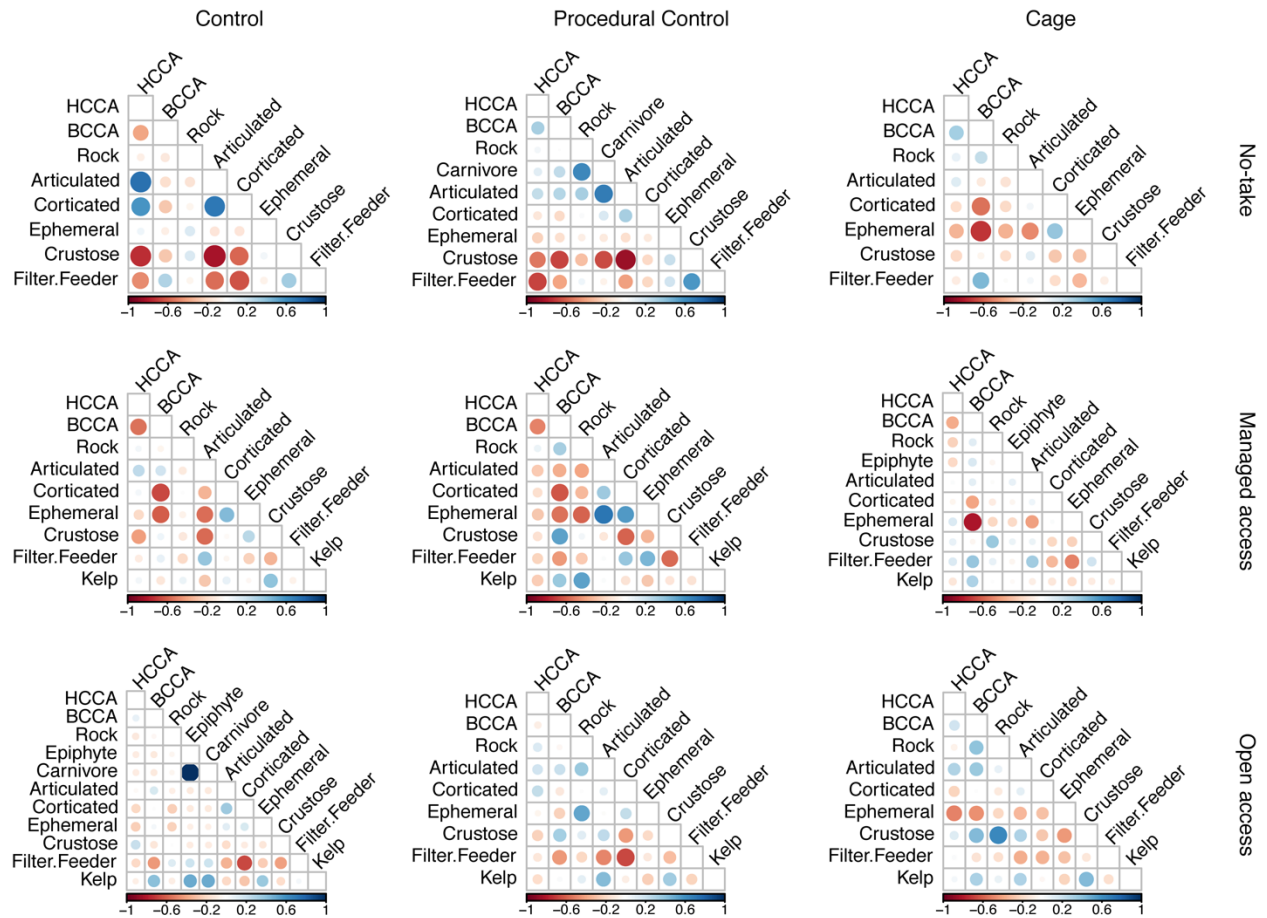
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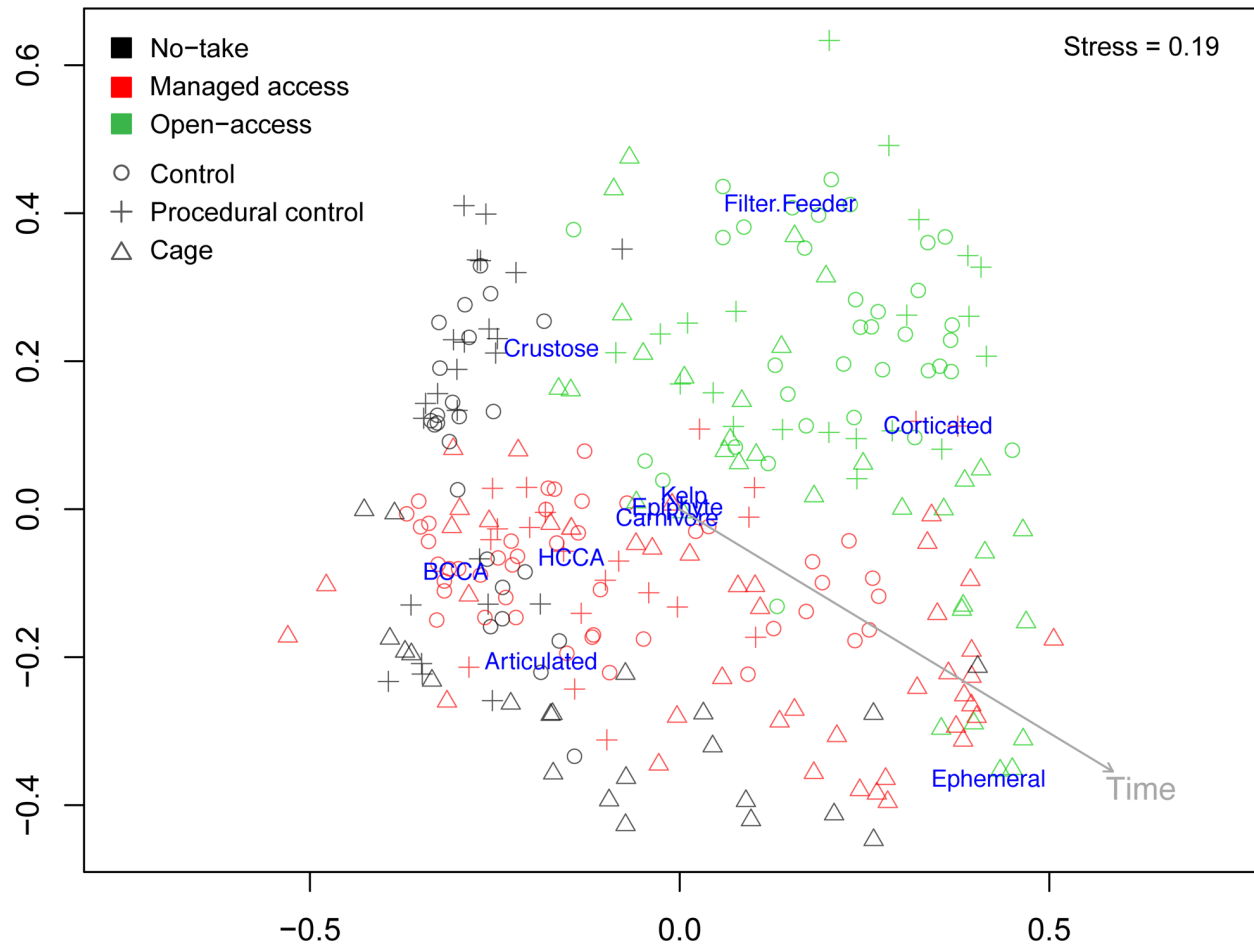
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 312 Fig. 6. Correlation between functional groups at the no-take (ECIM; top row), managed access (EQ; middle row)
 313 and open access (LC; bottom row) sites. Colour (positive or negative) and circle size (numeric value) indicates the
 314 strength of correlation. Only functional groups recorded at each site are shown.

315



316
 317 Fig. 7. Dissimilarity in community assemblages based on percentage cover data at each site (indicated by colour
 318 points). Text labels indicate the centroid for each taxon and the arrow indicates the strength and direction of
 319 correlation between community composition over time ($R^2 = 0.21$, $p < 0.001$).
 320

321 **DISCUSSION**

322 Current rates of resource exploitation are widely considered unsustainable (Airoldi and Beck, 2007; Halpern et al.,
 323 2008) and efforts to find conservation/sustainable solutions ever increasing (Fernandes et al., 2005). The
 324 application of no-take areas that set aside areas of the marine environment in which extraction activities are
 325 prevented (Hughes et al., 2003) are advocated but when implemented have shown limited success (Airame et al.,
 326 2003). Alternatively, the use of ‘customary practice’ management (Johannes, 2002) that is utilitarian in aim, is also
 327 common place using approaches such as the temporary closure of areas to restrict harvesting (Aswani and Weiant,
 328 2004) in an effort to improve yields (Cinner et al., 2006). In Chile, there is a notable absence of biodiversity
 329 conservation measures, like MPAs (www.mpatlas.org), and consequently, a paucity of studies describing their
 330 potential value to conservation objectives. Here, we examined differences in the structure of marine communities,
 331 and in particular, change in the health of crustose coralline algae at three locations where three different

332 management regimes have been employed (no-take, managed access (i.e. customary management), and open
333 access) to restrict human harvesting of a variety of benthic resources, particularly gastropods.

334
335 Unexpectedly, we found that grazer densities in no-take and managed access sites were considerably lower than at
336 the open-access site despite management restrictions. While the median size was not significantly different among
337 locations, a number of larger individuals were apparent at the no-take site while smallest individuals were
338 recorded at the open-access site. An inverse relationship between size and abundance is well documented in a
339 range of taxa (Damuth, 1981; White et al., 2007) although this relationship is often not shown in no-take reserves.
340 For instance, in fish, reserves have been shown to increase both abundance and biomass (Aburto-Oropeza et al.,
341 2011; Williamson et al., 2004) whereas in invertebrates, reserves have been shown to lower size and have little
342 effect on biomass (Halpern, 2003). Our results fit neither of these 'reserve' models, instead suggesting deviation
343 from energetic equivalence in the local-size density relationships (White et al., 2007); patterns that could be driven
344 by size asymmetries in competition for resources (e.g. Munger and Brown, 1981; Russo et al., 2003) or differences
345 in the availability of resources to different size species (Ernest, 2005; Holling, 1992).

346
347 Over the course of the study, photosynthetic yield (ϕ) was found to increase in all treatments at all sites over time
348 and at a faster rate in areas where grazers were excluded suggesting herbivory is playing a direct role in
349 suppressing photosynthesis (Nabity et al., 2009; Qiang and Richmond, 1996). Analysis of the algal community
350 composition indicated that the exclusion of grazers supported increased algal colonization, especially that of
351 ephemeral algae, most likely due to their release from direct grazing pressure (Steneck, 1982; Wanders, 1977).
352 Previous studies have shown that overgrowth of bleached CCA by other algal species when grazers are removed
353 can facilitate colour restoration and photosynthesis by providing shade (Figueiredo et al., 2000; Irving et al., 2004).
354 Wetherbee & Verbruggen (2016) argue that this allows the re-distribution of metabolites from uncovered to
355 shaded portions of the thallus. Improvement in photosynthetic capacity, was not however, linked to an increase in
356 areal extent of healthy CCA despite a decrease in the percent cover of bleached CCA (which occurred at a similar
357 rate irrespective of location or treatment) suggesting a temporal increase in photosynthetic yield, perhaps driven
358 by a seasonal increase in light intensity (Qiang and Richmond, 1996). In fact, the extent of healthy CCA was shown
359 to decline at the open access site when predators were excluded. The presence of macroalgal stands can create a
360 photosynthetic deficit caused by light attenuation, resulting in a lack of energetic capacity to drive calcification,
361 pigmentation and maintain levels of defence production. This can mean a physical disconnect between the
362 photosynthetically-active portions of the thallus, leading to a decrease in spatial extent when compared to patches
363 left connected to unshaded (not overgrown) thalli (Bulleri, 2006). Here, the failure of bleached CCA to transition
364 back to healthy CCA coupled with a reduction in the overall spatial extent of patches despite some recovery of
365 photosynthetic potential suggests that photosynthetic performance and its role in sustaining tissue metabolic
366 activity is not a principal constraint upon spatial dominance.

367

368 The density and size of grazers has been recognised as an important determinant of algal community composition
369 on these shores (Cattaneo and Mousseau, 1995) and is not a new concept having been shown in numerous studies
370 (e.g. Kordas et al., 2017; Sousa, 1979). Here, differences in grazer assemblage structure among sites likely
371 contributed to the change in spatial dominance of CCA over time and ultimately change in community
372 composition. Relationships among sessile functional groups were stronger in the presence of grazers (Bertness and
373 Callaway, 1994; Cavieres and Badano, 2009), especially at the no-take and managed access site where grazer
374 densities were lower. The absence of large grazers and/or increase in density of small grazers at the open access
375 site led to a general weakening of these relationships. Indeed, change or reversal of competitive hierarchies
376 mediated by herbivores has been shown in a number of previous studies (e.g. Lubchenco and Menge, 1978;
377 Steneck et al., 1991) and is reinforced here. In this system, the presence of grazers seems to have a particularly
378 strong role in ensuring a positive correlation between bleached CCA and healthy CCA cover with both articulated
379 and corticated species of algae and avoiding overgrowth by ephemeral algae. Grazer-induced bioerosion has been
380 also shown to reduce percent cover of CCA (O'Leary and McClanahan, 2010), although here, the exclusion of
381 grazers using cages has had no impact on preventing the loss of CCA cover over time suggesting bio-erosion is not
382 influencing CCA areal extent here. When grazers were excluded, there were marked shifts toward a few strong
383 negative correlations, particularly between bleached CCA and corticated and ephemeral algae, and reduction in
384 relative importance of crustose algae and filter-feeding organisms (non-calcareous crustose algae is often
385 prevalent in areas of high grazing pressure; Duffy and Hay, 1990; Jara and Moreno, 1984).

386

387 It is well known that CCA plays an important role in the population growth and development of species that
388 depend on CCA as a substrate for colonisation (Huggett et al., 2005; Tahil and Dy, 2016) and as part of their diets
389 (Asnaghi et al., 2015; Maneveldt et al., 2006). The persistence of healthy CCA is likely to underpin the persistence
390 of higher trophic levels and species important to humans. Activities that lead to the removal of canopy-forming
391 algae that protect CCA from harmful UV radiation, or grazers that prevent overgrowth by ephemeral algal growth,
392 should be carefully considered (Ojeda and Santelices, 1984). Here, persistence of CCA was observed only at the
393 managed access site (EQ), where grazers played an important role in preventing overgrowth. Surprisingly, similar
394 facilitation by grazers was not observed in the adjacent no-take marine reserve, where fleshy crustose algae
395 (predominantly *Hildenbrandtia*) appeared to obtain greater benefits. At the open access site, it could be argued
396 that large grazers are removed by humans to the extent that they are in such critically low abundance that they are
397 unable to prevent overgrowth of CCA by other algal species. Elsewhere, the removal of grazers by humans when
398 sufficiently widespread can lead to species becoming critically endangered (e.g. *Patella ferruginea*, Coppa et al.,
399 2016). However, differences in grazer population structure among sites defined by different levels of management
400 led to the emergence of different communities, especially when grazers were excluded. Interestingly, it was at the
401 managed access site (El Quisco) where the greatest percentage cover of bleached CCA occurred which suggests a

402 disproportionately important role of larger grazers (rather than density) in algal herbivory and structuring of
403 intertidal communities.

404

405 This study supports the proposition that under certain conditions, interactions that are typically considered
406 competitive (negative) may become facilitative (Bertness and Callaway, 1994). Specifically, ephemeral and
407 corticate algae that often compete with CCA appear to positively influence colour restoration of bleached CCA. The
408 health of CCA in areas of pulse environmental perturbations may therefore be reliant on the buffering capacity of
409 certain macroalgal species to mitigate environmental stress. Those interactions, however, appear strongly
410 mediated by the population structure of grazers (Lindberg et al., 1998). Unlike other studies, our results show that
411 an absence of large grazers can lead to overgrowth and shading of CCA by macroalgae leading to a decrease in
412 percent cover and replacement by other species. This balance is likely determined by the density, and probably,
413 species-specific size distributions of grazing species which may be influenced by the level of harvesting. Given that
414 CCA plays an important role in the population growth and development of species that depend on CCA as
415 substrate or food (Asnaghi et al., 2015; Huggett et al., 2005; Maneveldt et al., 2006; Tahil and Dy, 2016),
416 consideration of how harvesting might change the population structure (density and size) of grazers and the
417 consequential changes in the functioning of lower trophic levels is needed in any decision to implement
418 conservation management tools such as MPAs.

419

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424

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