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**The complex net effect of reciprocal interactions and recruitment facilitation maintains
an intertidal kelp community**

Allison K. Barner^{1,*}, Sally D. Hacker¹, Bruce A. Menge¹ and Karina J. Nielsen²

¹Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis OR
97331

²Romberg Tiburon Center for Environmental Studies and Department of Biology, San Francisco
State University, Tiburon CA 94920

*Correspondence author, E-mail allison.barner@science.oregonstate.edu

Running headline: Positive interactions and coexistence in kelp community

24 **Summary**

- 25 1. Theoretical and empirical ecology has transitioned from a focus on the role of negative
26 interactions in species coexistence to a more pluralistic view that acknowledges that
27 coexistence in natural communities is more complex, and depends on species interactions
28 that vary in strength, sign, and reciprocity, and such contexts as the environment and life
29 history stage.
- 30 2. We used a whole-community approach to examine how species interactions contribute to
31 the maintenance of a rocky intertidal macroalgal canopy-understorey assemblage. We
32 determined both the types of interactions in this network, and whether interactions were
33 sensitive to environmental gradients.
- 34 3. Focusing on a structurally dominant canopy kelp *Saccharina sessilis*, and its diverse co-
35 occurring understorey assemblage, we evaluated the role of the understorey in controlling
36 *S. sessilis* recruitment and quantified the reciprocal effect of the *S. sessilis* canopy and
37 understorey on one another using a removal experiment replicated across 600 km of
38 coastline. We determined the sensitivity of interactions to natural variation in light and
39 nutrient availability (replicated among four regions on the N.E. Pacific coast), and under
40 different wave conditions (three wave regimes).
- 41 4. Surprisingly, species interactions were similar across sites and thus not context-
42 dependent. Unexpectedly, the understorey community had a strong positive effect on the
43 *S. sessilis* canopy, whereby the adult canopy decreased dramatically following
44 understorey removal. Additionally, *S. sessilis* recruitment depended on the presence of
45 understorey coralline algal turf. In turn, the canopy had a neutral effect on the coralline
46 understorey, but a negative effect on non-calcifying algal turfs, likely eventually

47 generating positive indirect canopy effects on the coralline understorey. Density-
48 dependent intra-specific competition between *S. sessilis* adults and recruits may moderate
49 this positive feedback between the *S. sessilis* canopy and coralline understorey.

50 5. *Synthesis*. Our research highlights the importance of positive interactions for coexistence
51 in natural communities, and the necessity of studying multiple life-history stages and
52 reciprocal species interactions in order to elucidate the mechanisms that maintain
53 diversity.

54 **Key-words:** aquatic plant ecology; benthic; environmental gradients; macroalgae; marine; plant-
55 plant interactions; positive interactions

56

57 **Introduction**

58 A longstanding goal of community ecologists has been to reconcile the patterns of
59 species diversity within communities with the mechanisms that promote coexistence. At local
60 scales, competition has the potential to decrease species diversity in favor of a competitive
61 dominant (Chesson 2000), but decades of research on other species interactions have illuminated
62 the role of consumers (Caswell 1978), positive interactions (Hacker & Gaines 1997; Bruno,
63 Stachowicz & Bertness 2003; Thomsen *et al.* 2010) and indirect effects (Paine 1966; Wootton
64 1994) in promoting coexistence. Positive interactions, specifically, have gained attention with the
65 recognition that they can promote coexistence in diverse communities, both empirically (Verdú
66 & Valiente-Banuet 2008; Cerfonteyn *et al.* 2011) and theoretically (Gross 2008; Kéfi *et al.*
67 2012). In practice, however, positive and negative interactions may not be easily disentangled,
68 and feedbacks between different types of interactions within a diverse network complicate our
69 understanding of species coexistence.

70 In natural communities species interactions vary in strength, sign, and reciprocity, the
71 combination of which can result in unanticipated net effects. Positive and negative species
72 interactions in natural communities can switch along environmental gradients (Bertness &
73 Callaway 1994) and under different contexts (Chamberlain, Bronstein & Rudgers 2014), and
74 vary according to life history stage (Miriti 2006; Keammerer & Hacker 2013), or have net
75 neutral effects (Callaway & Walker 1997). In combination, positive and negative direct
76 interactions can influence species coexistence in unexpected ways, and examining only
77 unidirectional effects can hide important component interactions (Levine 2000). For example,
78 even if the direct interactions in a community are all competitive, indirect positive effects can
79 counter competitive exclusion to promote coexistence (Miller 1994; Callaway 2007; Thomsen *et*
80 *al.* 2010). Hence, to understand the drivers of coexistence, the network of interactions and their
81 mechanisms need to be considered. Here we use a rocky intertidal network of species to explore
82 a complex set of reciprocal interactions in a diverse kelp canopy-algal understory community.

83 In the rocky intertidal of the northeast Pacific, the low zone is occupied primarily by
84 macrophyte communities, with the kelp *Saccharina sessilis* (C.Agardh) Kuntze (henceforth *S.*
85 *sessilis* or “kelp canopy”) often forming a dense, monospecific canopy that overlies a diverse
86 mosaic of understory algae and invertebrates (Dayton 1975). Despite the presence of several
87 other kelp species in the low intertidal, *S. sessilis* is often the “ecological dominant” (Dayton
88 1975), both in terms of its abundance and its deterministic return to dominance after disturbance
89 (Paine 1984). Despite consistent co-occurrence of these canopy and understory species across
90 environmental conditions, we know little about the biotic factors (recruitment, species
91 interactions) that allow these species to co-occur, given their seeming overlap in use of essential
92 resources (Menge *et al.* 2015). In this study we examined the reciprocal interactions between *S.*

93 *sessilis* and the understory community to understand how these interactions could promote
94 observed diversity in this system, and ultimately species coexistence.

95 The effect of plant canopy species on their understory community has been variably
96 characterized, from positive recruitment facilitation by canopy nurse plants (Valiente-Banuet &
97 Verdú 2007) to negative light limitation by the canopy (Holmgren, Scheffer & Huston 1997).
98 Studies of kelp canopy-understorey systems have largely focused on the unidirectional effect of
99 the canopy on the understory, given consistently strong effects of canopies (Irving & Connell
100 2006). Competitive release of understory algae following kelp removal has been demonstrated
101 many times in intertidal and subtidal systems, with competition for light strongly structuring
102 these communities (Dayton 1975; Ojeda & Santelices 1984; Kennelly 1987; Benedetti-Cecchi &
103 Cinelli 1992; Lilley & Schiel 2006; Arkema, Reed & Schroeter 2009). However, in a few studies
104 kelp canopies have been shown to facilitate the understory via amelioration of thermal or
105 desiccation stress (Dayton 1975; Paine 1984; Bennett & Wernberg 2014) or modification of the
106 light environment (Benes & Carpenter 2015).

107 The reciprocal effect of the understory on kelp canopies is less well understood, and few
108 studies have attempted to fully characterize reciprocal interactions in vertically-structured
109 communities given the often obvious importance of the canopy for community structure. Strong
110 negative interactions characterize some subtidal kelp canopy systems, with canopy recruitment
111 inhibition by algal turfs (Graham 1997; Okamoto, Stekoll & Eckert 2013). However, in
112 terrestrial plant communities, understories can facilitate the recruitment of other plant species by
113 ameliorating stressful conditions (Arroyo *et al.* 2003; McIntire & Fajardo 2014; Holmgren *et al.*
114 2015). Similarly, some intertidal understory turf algae has been found to facilitate the
115 recruitment of canopy species (Johnson & Brawley 1998). For example, *S. sessilis* recruits have

116 been found on articulated coralline algae, a functional subgroup of the understory consisting of
117 calcified algal turfs (Milligan & DeWreede 2000), suggesting that recruitment facilitation is a
118 potential mechanism of coexistence in this system (e.g., Gouhier, Menge & Hacker 2011).

119 Some of the inconsistencies in the role of facilitation and competition in canopy-
120 understory interactions may be attributable to the sensitivity of interactions to environmental
121 gradients. The strength and relative importance of competition and facilitation are hypothesized
122 to vary with environmental gradients, by altering the availability of limiting resources and the
123 influence of abiotic stress (Stress Gradient Hypothesis [Bertness & Callaway 1994] and
124 Environmental Stress Models [Bruno *et al.* 2003]). In the rocky intertidal, interactions may
125 change among sites that differ in light and nutrient availability, a consequence in the northeast
126 Pacific of regional variation in the strength of upwelling and nearshore bathymetry (Pfister,
127 Altabet & Post 2014; Menge *et al.* 2015). Gradients in local wave conditions may also drive
128 changes to the interactions among macroalgae. High wave energy can increase competition by
129 increasing the capacity of macroalgae to harness light and nutrients (Leigh *et al.* 1987; Nielsen
130 2003) and increase kelp whiplash on understory species (Dayton 1975). However, low wave
131 splash can also increase desiccation stress during low tide and thereby may increase the positive
132 effect of canopy shade on the understory.

133 To determine the role of facilitation and competition in structuring kelp canopy-
134 understory communities and the influence of the environment on these interactions, we ask the
135 following questions: (1) What are the reciprocal, component interactions that characterize the *S.*
136 *sessilis* canopy and understory community? (2) Does the strength and/or sign of these
137 interactions change along an environmental gradient in wave action or with the availability of
138 light and nutrients? We experimentally determined the interactions between the *S. sessilis*

139 canopy and major functional groups of the understory assemblage and specifically explored
140 whether these interactions were sensitive to differences in nutrient/light conditions or wave
141 regimes. We tested whether the strength of species interactions varied with the availability of
142 light and nutrients by conducting the same experimental manipulations at 10 sites (4 regions)
143 across a 600 kilometer coastline that varied in environmental conditions. We examined the
144 sensitivity of species interactions to wave stress by replicating the experiment across three levels
145 of wave exposure at a single site. We coupled these experimental data with large-scale
146 observational surveys of *S. sessilis* recruitment to fully account for the role of dispersal in
147 perpetuating this community assembly. We expected strong negative species interactions to
148 dominate in this community, given previous evidence of strong competitive interactions among
149 canopy and understory macrophytes in subtidal, intertidal and terrestrial ecosystems.

150

151 **Materials and Methods**

152 ***Study System***

153 Our study system was the low zone of the rocky intertidal of the northeast Pacific, which
154 is dominated by the perennial canopy kelp, *S. sessilis* (Dayton 1975). Sites in the N.E. Pacific
155 vary in environmental conditions (temperature, light, and nutrients) as the result of regional
156 upwelling and coastal geomorphology (Menge *et al.* 2015, Fig. 1, Appendix A Table A1 in
157 Supporting Information). Varying abiotic conditions along the coast drive differences in
158 community structure among regions, though sites within each region have consistent community
159 structure (Menge *et al.* 2015). Our study focused on the association between *S. sessilis* and a
160 diverse understory that varied in species composition among regions but was always comprised
161 of a macroalgal turf and invertebrate mosaic. Given the species turnover across regions, we

162 followed a commonly-used functional group approach (Steneck & Dethier 1994) to balance our
163 interest in how species groups interact (group = similar functional morphology) with the
164 difficulty of factorial determination of interactions in a diverse system. The functional groups
165 included the abundance of non-calcified (“fleshy”) algal turf, coralline turf, algal crusts,
166 macrophyte blades, and sessile invertebrates (Appendix A Table A2).

167 ***Experimental Design***

168 We measured the reciprocal interaction between the kelp canopy and the understory
169 using two separate pulse removal experiments. In each, we established 15 x 15 cm plots around
170 the center of a single adult *S. sessilis*, marked with stainless steel lag screws at each corner.
171 Unlike massive subtidal kelps, *S. sessilis* is relatively small (mean *S. sessilis* length during wave-
172 exposure experiment = 20.73 cm \pm 0.87), thus a 15 x 15 plot captures the area directly around the
173 kelp holdfast and under the kelp blades to isolate the interaction between a single kelp and the
174 understory community. Three treatments were applied to the plots: kelp (*S. sessilis*) removal (-
175 K), understory removal (-U), and a no-removal control (C) (Fig. 2). In the removal plots, the
176 focal removal functional group (either *S. sessilis* or the understory) was carefully scraped away
177 down to bare rock at the start of the experiment. After the original removal, the plots were
178 allowed to recover for two years. Each treatment was replicated five times in a complete block
179 design, with each of the three treatment plots established in five blocks. Canopy intact and
180 removal plots within each block were close enough to encompass the same environmental
181 conditions (block size = ~1.5 m), but far enough apart that the canopy intact plots did not shade
182 the canopy removal plots (~0.5 m apart). Overall, due to the necessary functional-group
183 approach of these experiments, and the pulse (rather than press) nature of the species removals
184 (Bender, Case & Gilpin 1984), these experiments more closely reflect functional group responses

185 rather than species interaction estimates (Novak & Wootton 2010), though we continue to refer
186 to species interactions to facilitate interpretation.

187 *Experiment 1: Species Interactions across Regions.* To first test whether species interactions
188 varied among four regions in Oregon and California on the U.S. west coast, we conducted the
189 removal experiment described above in a spatially nested design, at multiple sites per region for
190 a total of 10 sites and 150 experimental plots (Appendix A Table A1, Fig. 1). This experiment
191 ran from April-May 2008 to August 2009, at which time all species were identified, recording
192 percent cover for the sessile organisms and number of *S. sessilis* recruits.

193 *Experiment 2: Species Interactions and Wave Exposure.* We tested for the effects of wave
194 exposure on the interaction between *S. sessilis* and the understory at Fogarty Creek (FC),
195 Oregon (Fig. 1). In May 2012, we established the same treatment plots as described above in
196 three locations at the site that differed in wave exposure (protected, intermediate, and exposed).
197 The wave-intermediate location was the same area of FC where we conducted the regional
198 interaction experiment. The wave-exposed area was chosen because of its known high wave
199 activity (Blanchette 1997), and it is the area before the wave-adapted kelp *Lessoniopsis littoralis*
200 begins to dominate, suggesting it is the wave-exposure distributional limit of *S. sessilis* (Dayton
201 1975; Menge *et al.* 2005). The wave-protected area was selected for its protection by rocky
202 outcrops that shelter the intertidal from breaking waves, with overall lower relative wave
203 acceleration than the wave-intermediate and exposed areas (Appendix B). The three areas have
204 similar slope ($\text{slope}_{\text{exposed}} = 4.08 \pm 2.12^\circ$, $\text{slope}_{\text{intermediate}} = 7.14 \pm 2.11^\circ$, $\text{slope}_{\text{protected}} = 7.20 \pm$
205 1.51°) and aspect ($\text{aspect}_{\text{exposed}} = 234 \pm 7.5^\circ$, $\text{aspect}_{\text{intermediate}} = 292 \pm 8.6^\circ$, $\text{aspect}_{\text{protected}} = 340 \pm$
206 6.3°), measured at the block level. We conducted a monthly survey in May-August of 2012 and
207 2013, collecting the same data as in the regional interaction experiment.

208 *Observational Recruitment Surveys*

209 We used targeted observational surveys of *S. sessilis* to assess the role of understorey
210 substrate type on kelp recruitment. In 2010 and 2012, we conducted surveys at 8 sites, a subset of
211 the experimental sites (from north to south: FC, BB, YB, SH, CB, RP, CMN; Fig. 1). At each
212 site, the intermediate-wave exposed *S. sessilis* zone was examined for presence of *S. sessilis*
213 recruits (defined as $< \sim 1$ cm holdfast diameter, Markel & DeWreede 1998). Ten 0.25-m²
214 quadrats were placed where recruits were found and we counted the number of recruits on five
215 functional understorey substrates: bare rock, coralline crust, coralline turf, non-coralline algal
216 turf, and *S. sessilis* holdfast.

217 *Statistical Analyses*

218 *Focal Response Variables in the Experiments.* To characterize the effect of the understorey on
219 kelp, we used total adult *S. sessilis* percent cover (blades + holdfast) to compare understorey
220 removal treatments (-U) with controls (C). We also evaluated the effect of both kelp and the
221 understorey community on the number of *S. sessilis* recruits, using the last time point (August
222 2008) in the regional interaction experiment, and the end-of-summer time points (August 2012,
223 2013) in the wave exposure experiment. To characterize the effect of kelp on the understorey
224 community, we first compared the response of overall understorey community structure in the
225 kelp canopy removal treatment (-K) with the control (C), then individually analyzed this
226 response by understorey functional group.

227 *Statistical Models.* We analyzed the reciprocal effects of the understorey on *S. sessilis* adults and
228 recruits, and *S. sessilis* on the understorey community, using a linear framework. For the regional
229 interaction experiment, we used general linear or generalized linear mixed effects models
230 (general, Gaussian response = GLMMs; generalized, Poisson response = GLIMMs) to account

231 for the nested structure of the data and to assess the fixed effects of treatment and region on the
232 response variables. A random intercept model accounted for the spatial nesting of sites within
233 regions. For the wave exposure experiment, we used general linear models (GLMs) on the last
234 time point only to facilitate comparison between the two experiments (see Appendix C for full
235 repeated measures methods and results for the wave exposure experiment). To construct the
236 fixed effects for both experiments, we used Akaike's Information Criterion corrected for small
237 sample sizes (AICc) to compare the fit of a treatment-only model to a model that included a
238 treatment by region interaction or a treatment by wave exposure interaction, depending on the
239 experiment. When analysis indicated that region should be included in a model, we used AICc to
240 test whether a model including site as a predictor was a better fit. For models with interaction
241 terms, we used Tukey post-hoc contrasts to compare the treatment of interest to the control
242 within region or wave exposure.

243 To examine the effect of kelp removal on overall understory community structure, we
244 conducted a blocked 2-way permutational multivariate analysis of variance (PerMANOVA)
245 based on Sørensen (i.e., Bray-Curtis coefficient) dissimilarities (n permutations = 999; Anderson
246 2001). PerMANOVA considers all species abundances as a response, rather than simplifying to a
247 single diversity metric. Thus, for this analysis, we analyzed the whole-community matrix instead
248 of functional groups. This matrix was relativized as percent of the maximum for either percent
249 cover or counts (column totals) in order to standardize the units of species abundance (McCune
250 & Grace 2002). We first tested if there was an interaction between canopy removal and either
251 region or wave exposure, depending on the experiment. Neither showed an interaction (regional
252 interaction experiment: $p = 0.239$, wave exposure experiment: $p = 0.856$), so we conducted a
253 second analysis without the interaction. We tested whether certain species were consistently

254 associated with kelp removals, as found by Dayton (1975), using a blocked indicator species
255 analysis with permutations randomized within blocks, using the indicator value metric of
256 Dufrière & Legendre (1997). Indicator species analysis measures the strength of association
257 between each species in the community and different habitats, or in this study, different
258 treatments, to determine the degree of habitat/treatment fidelity of each species (see De Cáceres
259 & Legendre 2009 for more information).

260 We conducted two more analyses to further examine the relationship between adult *S.*
261 *sessilis*, *S. sessilis* recruitment, and the understory. To examine the potential relationship
262 between adult *S. sessilis* and *S. sessilis* recruitment, we regressed the percent cover of adult
263 canopy on recruitment for the regional interaction experiment (the wave exposure experiment did
264 not have enough samples) using GLIMM to account for differences in *S. sessilis* abundance
265 among regions. We tested whether a linear model fit the data better than a nonlinear model using
266 AICc. Finally, the relationship between *S. sessilis* recruitment and various understory functional
267 groups in our observational surveys was examined using a Poisson GLIMM to assess the effects
268 of site and understory substrate (bare rock and five algal functional groups) on the number of *S.*
269 *sessilis* recruits. We accounted for differences in sampling years and amount of available
270 understory substrate among sites by allowing intercepts and slopes to vary randomly with year
271 and sites, respectively. For all response variables, percent cover was transformed *a priori* with an
272 arcsine square root transformation to meet the assumptions of normality. All counts (number of
273 kelp recruits) were analyzed using a Poisson distribution in a generalized linear model (GLIM or
274 GLIMM). All analyses were conducted in R 2.3.03 (R Core Team 2014), with main analyses
275 using the packages ‘lme4’ (Bates *et al.* 2013), ‘lmerTest’ (Kuznetsova *et al.* 2014), ‘vegan’
276 (Oksanen *et al.* 2013), and ‘indicspecies’ (De Cáceres & Legendre 2009).

277

278 **Results**

279 *Effects of the Understorey Community on Kelp Adults*

280 The understorey community had a strong, positive effect on the *S. sessilis* canopy (Figs 3
281 and 4, Appendix A Fig. A1). Understorey removal decreased the abundance of the kelp canopy
282 in all experiments (regional interaction experiment GLM, $\beta_U = -0.25 \pm 0.071$, $p = 0.00070$; wave
283 exposure experiment GLM, $\beta_U = -0.37 \pm 0.16$, $p = 0.028$; Appendix A Table A3) and had a
284 consistent effect across region and wave exposure regime. We observed that adult *S. sessilis* was
285 frequently removed from the rock in the absence of the understorey community (Fig. 2D).

286 *Effects of Kelp Adults on Understorey Community*

287 *S. sessilis* canopy removal had mixed effects on the structure of the understorey
288 community. In the regional interaction experiment, understorey community structure changed
289 with the removal of kelp (PerMANOVA, $p = 0.017$, Appendix A Table A4), though treatment
290 explained little of the variation relative to region ($R^2_{\text{treat}} = 0.022$, $R^2_{\text{region}} = 0.17$), and unexplained
291 variance in community structure was high. Across a broad spatial scale, three species were
292 associated with the removal of the kelp canopy (regional interaction experiment): two red algal
293 turf groups (the *Cryptopleura/Hymenena* complex and *Osmundea spectabilis*), and the surfgrass
294 *Phyllospadix* (indicator species analysis: $\text{indval}_{\text{crypto}} = 0.601$, $p = 0.001$; $\text{indval}_{\text{osmund}} = 0.345$, $p =$
295 0.008 ; $\text{indval}_{\text{phylo}} = 0.320$, $p = 0.042$). Across wave exposure, canopy removal had no effect on
296 overall understorey community structure (wave exposure experiment PerMANOVA, $p = 0.71$,
297 Appendix A Table A5). However, as in the regional experiment, *S. sessilis* removal plots were
298 associated with the *Cryptopleura/Hymenena* complex (indicator species analysis: $\text{indval} =$
299 0.663 , $p = 0.015$).

300 *S. sessilis* had some negative, but mostly neutral, effects on understory functional groups
301 (Fig. 3, Appendix A Fig. A1). Overall, the effect of *S. sessilis* was consistent across region and
302 wave exposure regime (no interaction). Similar to the indicator species analysis, in both
303 experiments *S. sessilis* had a negative effect on non-calcified algal turf abundance (regional
304 interaction experiment GLMM, $p = 0.014$; wave exposure experiment GLM, $p = 0.014$;
305 Appendix A Table A6). However, *S. sessilis* had no effect on coralline turfs (regional experiment
306 GLMM, $p = 0.16$; wave exposure experiment GLM, $p = 0.69$; Appendix A Table A7) or
307 macrophyte blades (regional experiment GLMM, $p = 0.76$; wave exposure experiment GLM, $p =$
308 0.11 ; Appendix A Table A8) relative to the controls. The effect of *S. sessilis* on understory algal
309 crusts was inconsistent across experiments (Fig. 3), with a positive effect in the regional
310 experiment (GLM, $p = 0.0051$; Appendix A Table A9) and no effect in the wave exposure
311 experiment (GLM, $p = 0.18$; Appendix A Table A9). The *S. sessilis* canopy did not affect sessile
312 invertebrate abundance in either experiment (regional experiment GLMM, $p = 0.72$; wave
313 exposure experiment RM-GLMM, $p = 0.45$; Expt. 2 GLM, $p = 0.46$; Fig. 3; Appendix A Table
314 A10).

315 ***Experimental Effect of Kelp Adults and Understorey Community on Kelp Recruitment***

316 Removals of both adult kelp and understory algae had context-dependent effects on the
317 number of *S. sessilis* recruits (Fig. 4). In the regional interaction experiment, the effect of
318 treatment on recruitment depended on region (GLIM treatment x region interaction, $p = 0.0014$;
319 Fig. 4A; Appendix A Tables A11, A12) with a negative effect of understory removal relative to
320 the control in the Cape Blanco region (contrasts, $p < 0.01$; Fig. 4A, Appendix A Table A12) and
321 no effect in other regions. Similarly, in the wave exposure experiment, the effect of treatment on
322 *S. sessilis* recruitment depended on wave exposure and year (GLIM treatment x exposure

323 interaction, $p < 0.0001$; year, $p < 0.0001$; Fig. 4B, Appendix A Tables A11, A13) with
324 recruitment higher after the first summer (2012) than the second ($\beta_{2013} = -1.27 \pm 0.15$, $p <$
325 0.0001 ; Appendix A Table A15). In 2012, recruitment was lower in understory removal plots
326 than the control (post-hoc, intermediate exposures $p < 0.01$, Appendix A Table A13) but in 2013
327 recruitment did not differ among treatments (all post-hoc contrasts $p > 0.05$, Appendix A Table
328 A15, Appendix A Fig A2). Kelp removal plots at wave protected exposures tended to have
329 higher recruitment than the control plots (2012 only, post-hoc $p = 0.067$, Fig. 4, Appendix A
330 Table A13). Moreover, in the regional experiment, *S. sessilis* recruitment was highest at
331 intermediate cover of *S. sessilis* adults (polynomial vs. linear model, $\Delta\text{AIC} = 10.13$), indicating
332 recruitment inhibition at low and high cover of kelp adults ($\beta = -2.23$, $p = 0.0015$, Appendix A
333 Table A14, Appendix A Fig. A3).

334 ***Observational Effect of Understorey Community on Kelp Recruitment***

335 *S. sessilis* recruitment differed among understory substrate types (GLIM substrate term,
336 $p < 0.0001$; Appendix A Table A15). After accounting for differences in understory substrate
337 abundance among sites, recruitment to coralline turf was orders of magnitude greater than
338 recruitment to bare rock or other algal functional groups (Fig. 5, Appendix A Table A16). Kelp
339 recruits rarely were observed on alternative recruitment surfaces including on the base of *S.*
340 *sessilis* holdfasts, coralline crust, non-coralline turfs, and bare rock (Fig. 5, Appendix A Table
341 A16).

342

343 **Discussion**

344 We used experimental and observational tests to disentangle species interactions in a
345 diverse rocky intertidal community and found a complex array of positive and negative

346 interactions (Fig. 6). Importantly, although the kelp canopy had a negative or neutral effect on
347 the understory community as a whole, kelp removal had no negative effects on the coralline
348 turfs that facilitate kelp recruitment (similar to Duggins & Dethier 1985). The canopy had a
349 negative effect on non-calcifying algal turfs, as has been found in other studies in intertidal
350 systems (Dayton 1975; Paine 1984; Schiel 1988) and subtidal kelp forests (Dayton *et al.* 1984).
351 Because articulated coralline algae and non-calcifying algae have been shown to compete in
352 northeast Pacific rocky intertidal systems (Dayton 1975; van Tamelen 1996), we infer that by
353 suppressing the abundance of competing non-calcifying algae, kelp canopy likely indirectly
354 promotes the persistence of the corallines (Fig. 6). In turn, coralline turfs facilitate the
355 recruitment of the kelp canopy, and the understory as a whole promotes the persistence of the
356 adult canopy (Fig. 6). Thus, coexistence of macroalgal species in this system may depend on the
357 positive feedback between the subdominant coralline understory and the dominant kelp, *S.*
358 *sessilis*.

359 Despite previous research suggesting that strong negative canopy-understorey
360 interactions are ubiquitous, our study reinforces empirical and theoretical work that suggests that
361 facilitation is both common and important for coexistence in plant canopy-understorey
362 communities (Holmgren *et al.* 1997; McIntire & Fajardo 2014). Countering the general finding
363 that kelp canopies have a negative effect on all understory recruitment, recent studies have
364 found that subtidal kelp canopies can facilitate the recruitment of some understory algal species
365 (Connell 2003; Bennett & Wernberg 2014; Benes & Carpenter 2015). In this study, we found
366 that certain understory species directly facilitate the recruitment and persistence of the kelp
367 canopy. The strong facilitation of the dominant kelp canopy by coralline turf was unanticipated,
368 given that in subtidal and some intertidal systems, algal turfs have been widely found to inhibit

369 kelp recruitment even in the absence of canopy shade (Dayton *et al.* 1984; Graham 1997), with
370 strong negative effects of both crustose coralline algae (Okamoto *et al.* 2013) and articulated
371 coralline algae (Reed & Foster 1984; Schiel & Lilley 2011) on canopy recruitment. Recruitment
372 facilitation, in theory, has the potential to promote coexistence when a subdominant competitor
373 facilitates either a competitive dominant in a meta-community (Gouhier *et al.* 2011) or the
374 consumer of a competitive dominant, through indirect effects (Baskett & Salomon 2010).
375 Indirect facilitation by the canopy has also been found to be key for species coexistence. For
376 example, a dominant competitor for light in the northeast Pacific subtidal, the kelp *Macrocystis*
377 *pyrifera*, indirectly facilitates sessile invertebrates through suppression of their competitors,
378 understory macroalgae (Arkema *et al.* 2009). Similarly, in this study, if the canopy kelp
379 suppresses competition from non-calcifying algae, a positive indirect effect of the canopy on
380 coralline algae results, which could counter any direct negative effect of the canopy, for a neutral
381 net effect, as observed here. More nuanced experiments are needed to tease apart the generally
382 strong net effects observed in this study to fully understand the bidirectional nature of canopy-
383 understory interactions in this system.

384 Unlike the widespread evidence that many species interactions are highly context-
385 dependent (Chamberlain *et al.* 2014), and contrary to our expectation, we found a general lack of
386 environmental contingency in this system through repeated local interaction experiments. In fact,
387 there was only one context-dependent interaction: the interactions among *S. sessilis* recruits,
388 adults, and the understory. However, some context-dependency in the interactions might be
389 masked either by context-dependency in the recruitment process (Wernberg *et al.* 2010) or by the
390 use of functional group abundance as a response, especially in the regional interaction
391 experiment, given species turnover among regions (both discussed below). Nevertheless, the

392 effect of canopy removal was not context-dependent in either experiment when we analyzed
393 whole-community structure despite known regional differences in community composition
394 (Menge *et al.* 2015). Overall, though, unlike other studies of kelp canopy-understorey systems
395 (Wernberg & Connell 2008; Smale, Wernberg & Vance 2011) and what we expected,
396 interactions varied little in space, along either a wave exposure gradient or among regions
397 exhibiting variation in light and nutrient availability. Instead, a few strong interactions were
398 spatially consistent, suggesting that the mechanism of these interactions is not strongly affected
399 by the environment.

400 The positive effect of coralline turf on *S. sessilis* recruitment has been previously
401 hypothesized (Milligan & DeWreede 2000), and here we experimentally demonstrated a positive
402 interaction among kelp recruits and coralline turf. Recruitment to coralline turfs was much
403 greater than any other understorey substrate, suggesting that coralline turfs are unique in
404 facilitating recruitment in the northeast Pacific rocky intertidal region. However, kelp
405 recruitment showed some context-dependency, with temporal and spatial variation in abundance
406 of recruits between oceanographic regions. Such context-dependency may be due to dependence
407 of early life-history stages on environmental conditions. For example, in warm climates, subtidal
408 kelp recruitment can be sensitive to climate after disturbance events, such that kelp recruitment
409 and subsequent canopy recovery is suppressed (Wernberg *et al.* 2010). Further, context-
410 dependency in the recruitment process across our sites may not reflect variation in environmental
411 conditions *per se*, but may be a function of spatial variation in biotic factors, e.g., reproductive
412 phenology, variation in density of adult kelps (discussed below), or the presence of other algal
413 recruits (Reed 1990). Given the importance of recruitment for the maintenance of the canopy and
414 its understorey community, attention should be paid to understanding the mechanistic basis for

415 variation in kelp recruitment, and its link to environmental conditions. Alternatively, the
416 observed variation in *S. sessilis* recruitment could be an artifact of our functional group
417 approach. In particular, the articulated coralline algae of Oregon and California are comprised of
418 ~5 common species, and if species turnover among sites in this region is high and if *S. sessilis*
419 recruits differentially to these different coralline species, then shifts in the abundance of the
420 coralline species across latitude may explain variation in *S. sessilis* recruitment.

421 The overall mechanism of this recruitment facilitation is unclear, but we suggest four
422 hypotheses: (1) kelp recruits may be less susceptible to wave dislodgement when attached to
423 articulated algae (Milligan & DeWreede 2000), (2) recruits may be less vulnerable to herbivory
424 when embedded among unpalatable coralline turfs (Markel & DeWreede 1998), (3) recruits
425 might be buffered from desiccation stress by water-retaining algal turf (Johnson & Brawley
426 1998), or (4) coralline algae may support higher recruit densities due to high structural
427 complexity relative to other turf algae (Coull & Wells 1983). In this study we examined only
428 emergent recruitment patterns, and may have missed important interactions occurring at the
429 spore, gametophyte, or microscopic sporophyte stages. Further work is needed to test these
430 hypotheses to mechanistically understand why *S. sessilis* recruits occur almost exclusively in
431 coralline turf. A first step may be to identify whether *S. sessilis* preferentially recruits to a single
432 coralline species, or is indiscriminate in its choice of coralline turf species.

433 Kelp recruitment, though generally unaffected by the presence of the adult *S. sessilis*,
434 experienced context-dependent intraspecific competition with the adult canopy, which may
435 provide a negative control on the positive feedbacks in this system. Density-dependent mortality,
436 or “self-thinning”, is common in terrestrial plant communities (Antonovics & Levin 1980) and
437 subtidal kelp forests (Schiel & Foster 2006), and two lines of evidence in this study support our

438 hypothesis of intraspecific competition among life-history stages. First, the number of *S. sessilis*
439 recruits increased when the canopy was removed in wave-protected plots in the wave exposure
440 experiment. Conditions in this wave-sheltered location may be optimal for *S. sessilis*, as
441 measurements of *S. sessilis* growth show that adult growth was higher there than in more wave-
442 exposed locations (A. K. Barner *unpubl. data*; measured as meristematic growth every two
443 weeks). If *S. sessilis* performance is enhanced and abiotic conditions are benign, intraspecific
444 competition is likely to be strong, and the reduced number of *S. sessilis* recruits in this area may
445 be due to increased competition for resources, such as light. Recruitment inhibition by kelp
446 canopy shading is common in subtidal kelp communities (Reed & Foster 1984). Second, we
447 found that recruitment is inhibited under higher cover of *S. sessilis* adults across all treatments in
448 the regional interaction experiment. Future work should explicitly incorporate density estimates
449 of both adults and juveniles. Overall, a positive effect of coralline algae on *S. sessilis* may result
450 in large, dense canopies that shade recruits, thus creating a density-dependent indirect control to
451 May's (1982) "orgy of reciprocal benefaction" in networks dominated by positive interactions.

452 The understory had a positive effect on adult *S. sessilis*, though as with recruitment
453 facilitation, the mechanism was unclear. If the understory retains enough water at low tide,
454 water retention may benefit *S. sessilis* adults as the blades lie atop the turf mosaic. Understories
455 have also been hypothesized to cushion the canopy against tattering due to strong waves
456 (Milligan & DeWreede 2000). However, since we did not see a differential effect of the
457 understory on the canopy across wave exposures, vulnerability to waves alone is unlikely to
458 drive the positive effect of the understory. Another alternative is that understory removal may
459 provide access for herbivores whose movement is inhibited by turf. Trophic interactions were not
460 considered in this experiment, given the weak effect in earlier studies of grazing on algal

461 succession and adult kelp in the *S. sessilis* zone (Dayton 1975; Burnaford 2004; Menge *et al.*
462 2005). However, in regions north of our study, the herbivore chiton *Katharina tunicata* has been
463 found to weaken the holdfasts of young *S. sessilis*, increasing mortality (Markel & DeWreede
464 1998). The positive effect of the understory on the canopy is likely to be complex, with possible
465 synergisms that deserve more detailed treatment.

466 That the canopy kelp affected understory community structure in a multitude of ways
467 was an anticipated result, given previous rocky intertidal removal experiments (Dayton 1975;
468 Paine 1984). Dayton (1975) hypothesized that the canopy has both positive and negative effects
469 on the understory, and showed that when the canopy was removed, obligate understory algae
470 disappeared and weedy “fugitive” species increased in abundance. We found that overall, fleshy
471 turfs as a whole benefited by *S. sessilis* removal (mostly “fugitives”), with few obligate
472 understory species. Interesting exceptions include a positive effect of the canopy on crustose
473 algae (dominated by encrusting corallines: mean proportion of total crusts that are coralline =
474 0.830 ± 0.128 [standard error] in the regional experiment, 0.877 ± 0.0452 in the wave exposure
475 experiment), and no direct effect of the canopy on articulated coralline algae. Previous research
476 has found that percent cover of encrusting corallines can be higher under subtidal kelp than
477 under less dense canopies or no kelp (Melville & Connell 2001), and experimental subtidal kelp
478 removal decreased encrusting corallines (Kennelly & Underwood 1993). Kelp canopies have
479 been hypothesized to promote coralline crust persistence by inhibiting the growth of epiphytes,
480 either by reducing light or attracting mobile invertebrates that graze on epiphytes (Duggins &
481 Dethier 1985; Melville & Connell 2001). Few studies have examined the effect of kelp canopies
482 on articulated coralline algae, but the absence of an effect of the *S. sessilis* canopy on these
483 coralline turfs is tantalizing and more explicit work is needed to understand the specific

484 mechanism of a potential positive feedback. Ultimately, examination of species coexistence in
485 this community will require further characterization of the mechanisms driving both fitness and
486 stabilizing niche differences, likely involving significant empirical and theoretical work
487 (Siepielski & McPeck 2010).

488 *Conclusions.* Here we examined a web of interactions in a rocky intertidal community
489 and found that positive and negative species interactions contributed to the interaction network.
490 Critical to understanding coexistence mechanisms is examining interactions in such a way as to
491 move beyond examining unidirectional, pairwise interactions (Wootton 1994; Hacker & Gaines
492 1997; Brooker *et al.* 2007). Additionally, the contribution of species interactions to coexistence
493 should be examined across multiple life history stages, given different positive effects of the
494 understory on the canopy at early and adult stages. Furthermore, this study provides empirical
495 support for recruitment facilitation as a possible mechanism of coexistence, where a
496 subdominant species can persist in a metacommunity if they facilitate the recruitment of a
497 dominant species (Gouhier *et al.* 2011). Finally, our study underlines the importance of testing
498 reciprocal species interactions (Schöb *et al.* 2014), as there may be important hidden interactions
499 that feedback to the dominant. In summary, our experiments revealed a positive feedback that
500 may be important to the coexistence of a dominant canopy-forming kelp and its understory
501 species. The interaction among these species was generally stable and consistent across multiple
502 spatial scales and environmental contexts. In addition, we have demonstrated the importance of a
503 guild of subdominant algae for promoting the persistence of a dominant foundation species.
504 Future empirical and theoretical work should explicitly consider the potential consequence of
505 positive feedbacks, through direct paths or facilitation cascades (Thomsen *et al.* 2010), for
506 species coexistence.

507

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520

521 **Data Accessibility**

522 Data associated with this paper are deposited in the Dryad repository (doi: 10.5061/dryad.7950f).

523

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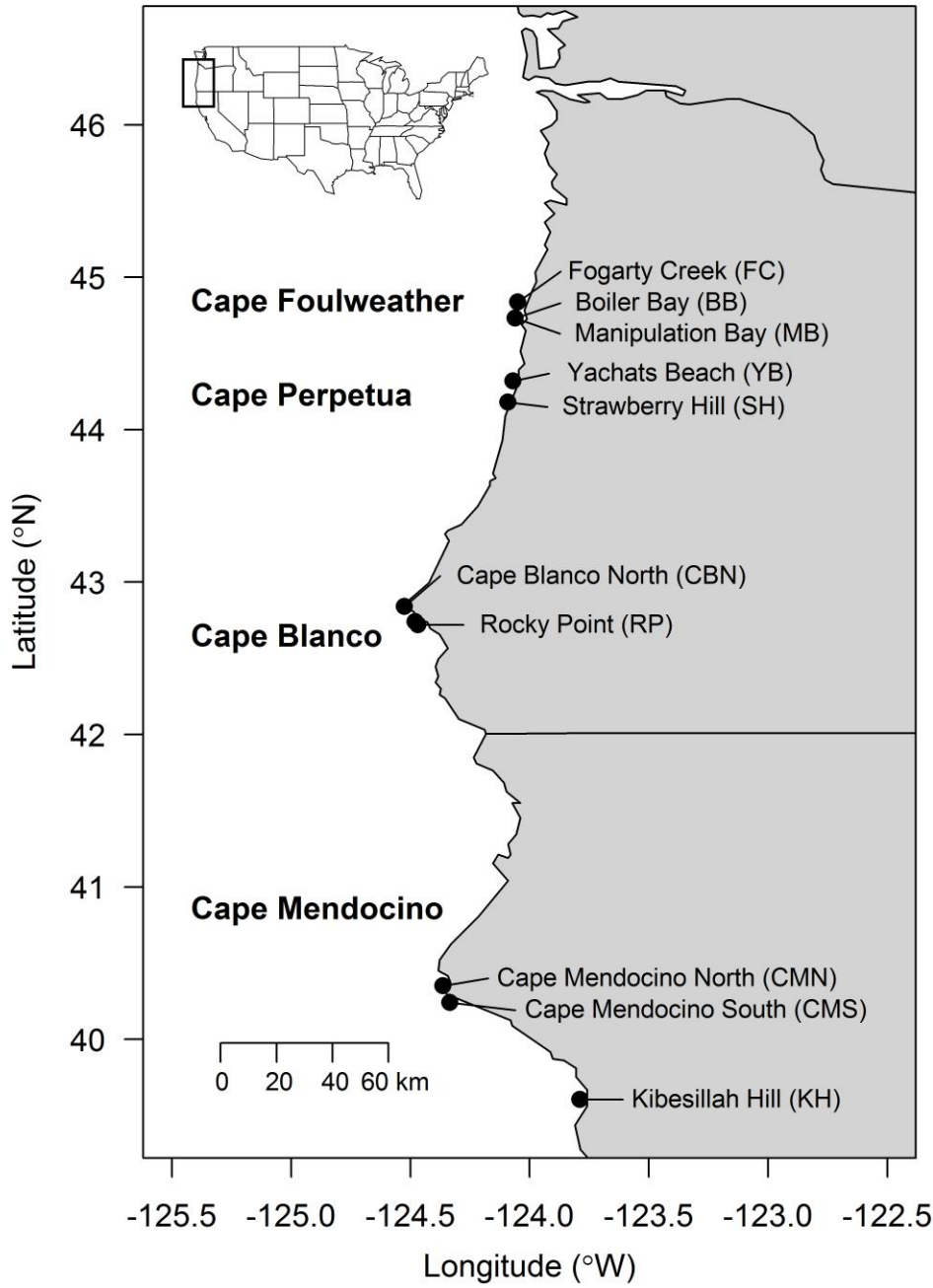
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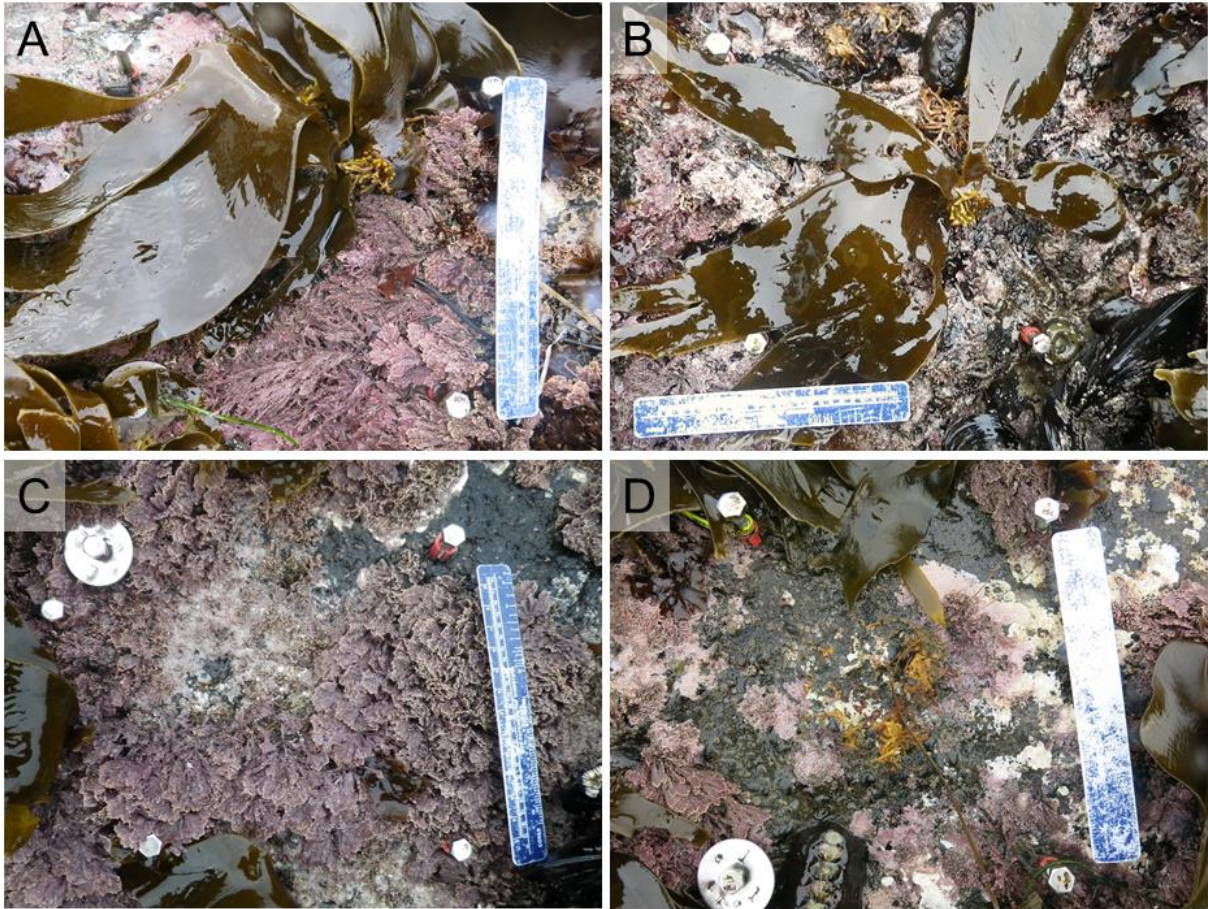
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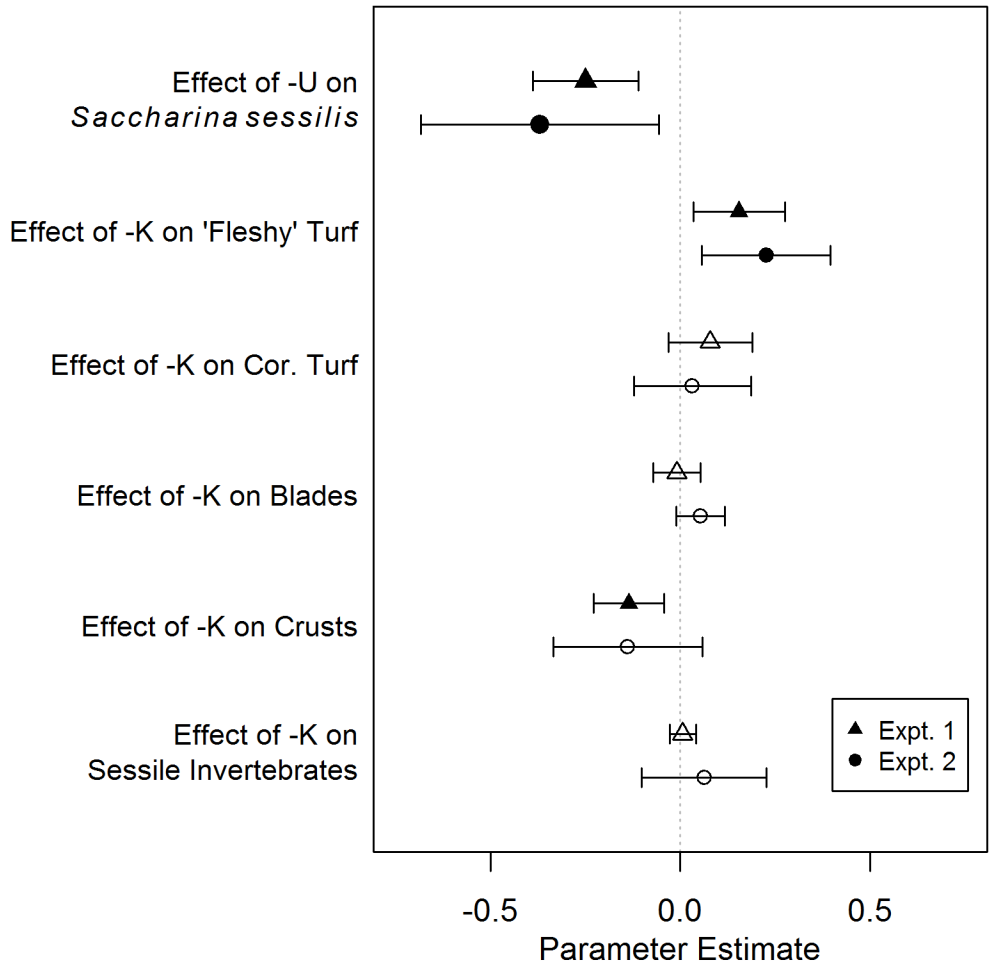
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721 **Fig. 1.** Map of study sites within the four regions (capes). The regional interaction experiment
722 occurred at all 10 sites, while the wave exposure experiment took place at Fogarty Creek (FC)
723 only.



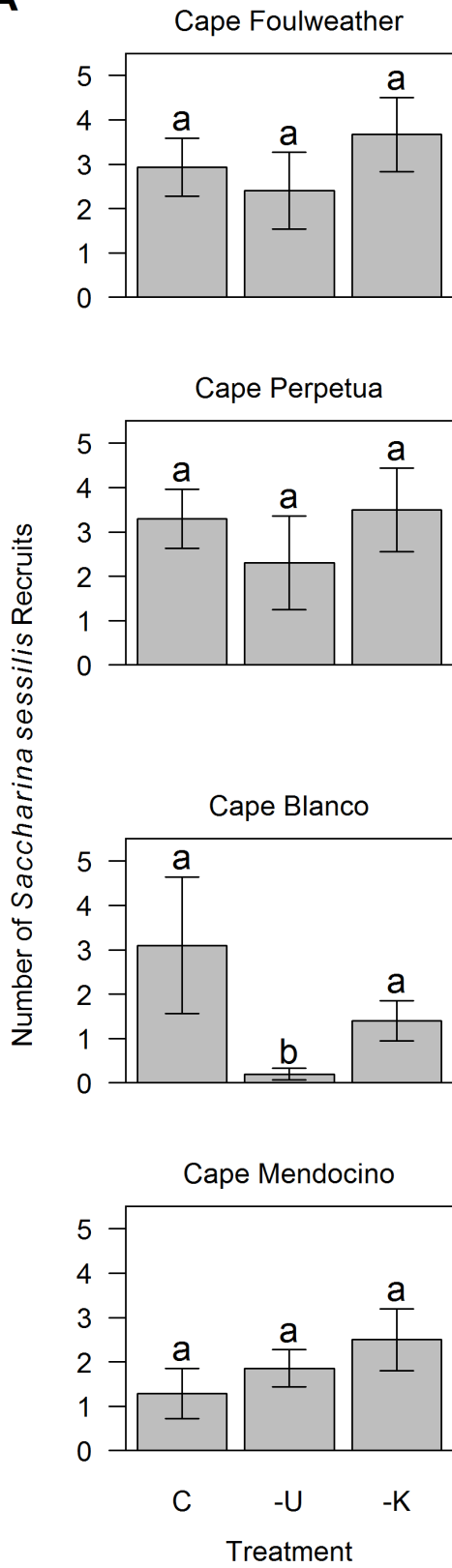
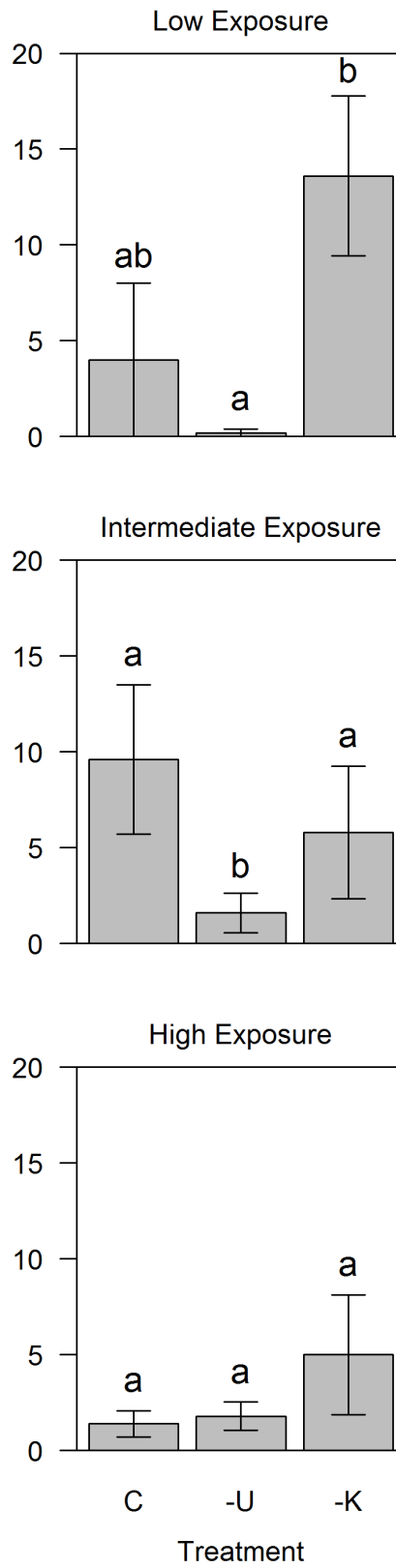
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725 **Fig. 2.** (A-C) The three experimental manipulations used for both experiments: (A) control, (B)
726 understorey removal, and (C) canopy removal. (D) An example of an understorey removal plot
727 where the *Saccharina sessilis* canopy has fallen off the substrate. In each photograph, the square
728 plot is marked by lag screws in each corner, with a 15 cm ruler for scale.

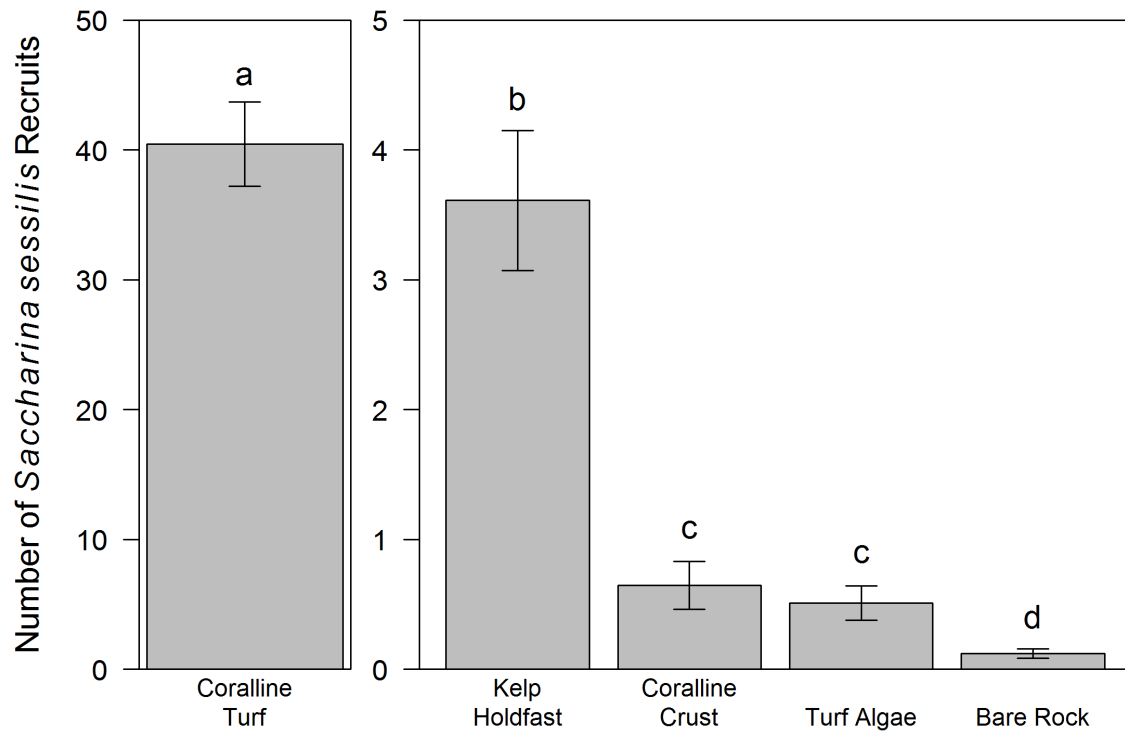


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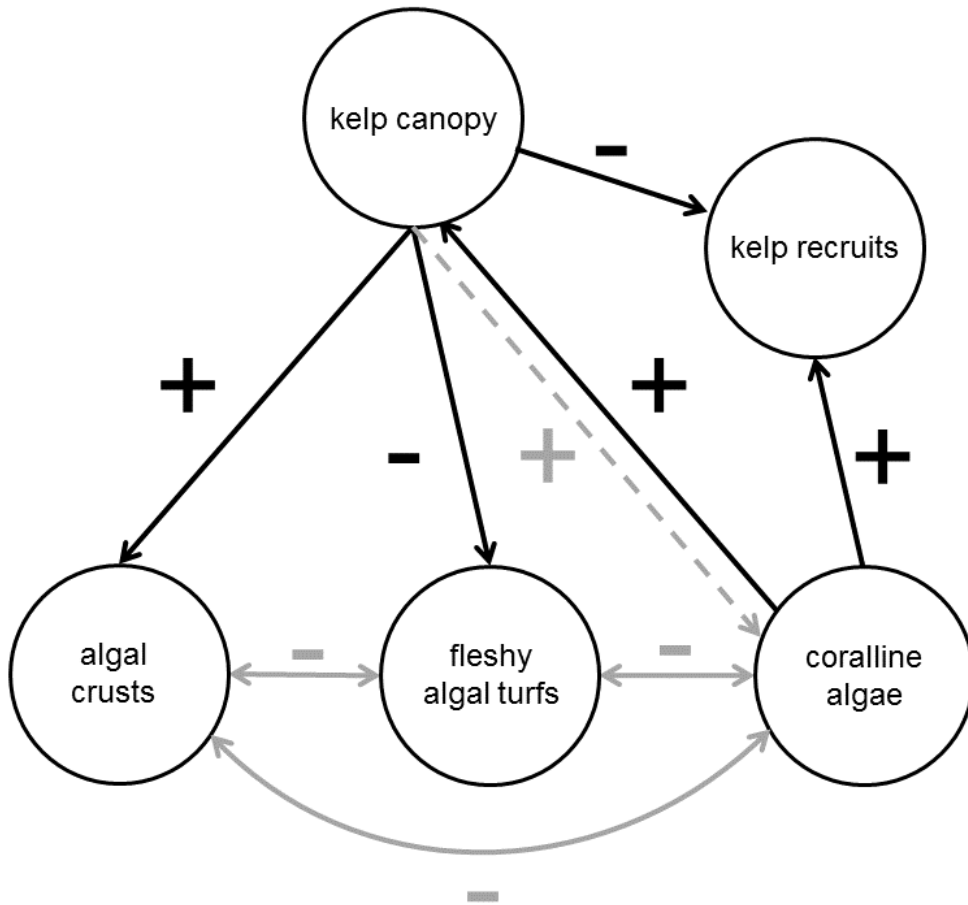
730 **Fig. 3.** Regression coefficients for the effect of a removal treatment (-K, kelp removal, or -U,
 731 understory removal) compared with the control reference group, with 95% confidence intervals,
 732 for the main functional groups in Experiment 1 (regional interaction experiment) and Experiment
 733 2 (wave exposure experiment). Closed symbols indicate significance for $\alpha = 0.05$. Symbols are
 734 coded by experiment. A negative response of species 2 to removal of species 1 can be interpreted
 735 as a positive effect of species 1 on species 2, and vice-versa. Responses with significant
 736 interaction terms are plotted in Fig. 4 (kelp recruits).

A**B**

738 **Fig. 4.** Effect of canopy (-K) and understorey (-U) removal on the number of *Saccharina sessilis*
739 recruits at (A) different regions and (B) different wave exposures (2012 only, see Appendix A
740 Fig. A2 for 2013 results). Lowercase letters represent post-hoc contrasts (differences for $p <$
741 0.05) among treatments within a level (region or exposure).



742
743 **Fig. 5.** Number of *Saccharina sessilis* recruits observed living on various understorey substrates
744 (coralline turf, *Saccharina sessilis* holdfast, coralline crust, turf algae, bare rock), all sites
745 combined. Lowercase letters represent post-hoc pairwise contrasts (differences for $p <$ 0.05).
746 Note the different y-axis scale between coralline turf and other understorey substrates.



747

748 **Fig. 6.** Emergent species interaction network for the *Saccharina sessilis* canopy-understorey
 749 community. Black, solid arrows represent direct effects found in our experimental and
 750 observational study. Grey, solid arrows represent hypothesized direct effects with empirical
 751 support in the literature, though untested in this study. The single grey, dashed arrow is the
 752 emergent positive indirect effect of the *Saccharina sessilis* canopy on corallines if the other
 753 hypothesized (grey) interactions hold. Further work is needed to verify the existence of these
 754 competitive and indirect effects.

755

756 **Supporting Information**

757 Additional supporting information may be found in the online version of this article:

758

759 **Appendix A.** *Supplementary tables (Tables A1 – A16) and figures (Figures A1 – A3)*

760 **Appendix B.** *Supplementary methods & results for wave exposure measurement*

761 **Appendix C.** *Supplementary material for wave exposure experiment (repeated measures)*

762

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